

A STUDY OF
EMOTIONAL BEHAVIOUR
IN FOUR COAT COLOUR GENOTYPES OF
THE GOLDEN HAMSTER (MESOCRICETUS AURATUS)

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ABSTRACT

The study investigated aspects of emotional behaviour in two piebald and two non-piebald genotypes of hamster, to confirm anecdotal reports that piebald hamsters were more fearful than other types. Behavioural differences were hypothesized to relate to psychological functions and to be associated with the recessive piebald gene, thereby representing a major gene effect which could merit further investigation by a behavioural geneticist.

Limitations on uses of the terms 'fear' and 'emotionality' were acknowledged, and evidence that they were unlikely to refer to unitary states was discussed.

Genetic, maternal and sibling effects were controlled for, so that a single cross could produce the four genotypes in any litter. The hamsters were bred by a geneticist, Roy Robinson. On arrival at four weeks of age they were housed solitarily or in small groups for about three weeks when they were all isolated; experiments began at eight weeks of age.

Behavioural and nonbehavioural tests, designed to measure emotionality, were based on previous work and a priori reasoning. They included reaction to handling, the open field, novel situation, activity, aggressive encounter, passive avoidance learning, and measures of body weight, food intake, adrenal gland weight, gastric ulceration and mortality.

The results from the experiments were subjected to analyses of variance tests; significant genotype, sex and housing differences were discussed. It was concluded that hamsters carrying the piebald gene could be described as more emotional than golden or brown hamsters.

although there was no consistent pattern shown by either sex or differentially housed hamster in terms of emotionality. The piebald hamster may thus provide a starting point for investigations into a gene-behaviour pathway.

The data were compared with other rodent studies on emotionality and how findings contributed information as to whether fear was a unitary condition assessed.

One type of organization responsible for emotionality could be studied in the piebald hamster and this may contribute more generally to literature on physiological and behavioural expressions of fear.

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CHAPTER ONE

INTRODUCTION

Genesis

At the start of this project I was interested in the fields of stress, fear and emotion from a genetic, physiological and behavioural viewpoint and wished to study aspects of them. In particular, my interest in the piebald hamster was evoked by certain comments in the literature concerning them.

Foote (1949) said "in general piebald animals appear to be of smaller body size than normal and piebald young are consistently smaller and less resistant to changes in environmental conditions than are litter mates." Foote's impression remains unclear until further investigation determines the nature of the environmental changes and apparent lack of resistance. Again, Foote and Foote (1950) talked of reduced piebald body weight compared to normal. In an extensive weight study they found normal males to be heaviest followed by normal females, piebald females, then piebald males. Robinson (1958) found piebalds weighed 76 percent of normals, on average.

Urinogenital abnormalities were found by Foote and Foote (1950) to be "more marked in females than males" and "cases of nonfertile matings are more common among piebald animals than in normals". Of 46 piebald males they studied, only two had anomalies, whereas 10 of 48 piebald females showed them.

On the question of litter size and mortality Foote and Foote (1950) stated that "in the hamster, fewer young are born to piebald mothers than to normal mothers and the mortality of the young is higher. The young from piebald parents are smaller and weaker than normal young and as a result the mother animals, whether normal or

piebald, are more prone to destroy them piebald mothers are more nervous and do not care for their young" Quite an observation!

Robinson (1958, 1968) noticed that "piebald hamsters appear to require more considerate handling than the normal animal." In comparing four hamster genotypes, agouti (normal), cream, ruby-eye and piebald, Robinson (1962a) described cream as more placid than normal, while ruby-eye and piebald were "more nervous and excitable." "Piebald is noticeably more irascible than ruby-eye". He ranked a scale of 'nervousness' with piebalds at the nervous extreme. Searle (1968) also described piebalds as "small and nervous" (p. 109).

Finally, the piebald viability was estimated by Robinson (1968) as 40-60 percent of normal, with most estimates tending toward the lower figure.

Here then, is a hamster known to have a smaller body size, lower viability, higher infant mortality, physiological, behavioural, sexual, and maternal abnormalities, and which is observed as needing more careful handling and as being 'nervous'. No psychologist has clarified, validated, or considered these descriptions which could be largely behaviour orientated.

The piebald coat colour mutation in hamsters was first described in 1949 by Foote and the gene thought to be recessive and inherited in a Mendelian fashion, (Orsini 1952). It causes a variable amount of white spotting on the body and face. Unlike most mutant forms, the piebald hamster does not possess a gross physiological defect which could account for its behaviour. For example, Searle(1968) described an extreme microphthalmic white mutant hamster, whose eyes are very small or absent, as having "extreme nervousness". Blindness may not be the cause of 'nervousness' but it would be surprising if it did not play a contributory role.

Wilcock (1969) gave a concise review of the work on single gene effects. The future of psychogenetics would seem to be a search for gene pathways, but Wilcock claimed that most demonstrated behavioural differences based on single gene effects did not merit further investigation. He argued that most pleiotropic effects of genes were predictable from the nature of the mutation. For example, if a gene action reduced the number of retinal receptors, the reduced visual acuity was an expected peripheral effect of the gene change, which in turn resulted in certain kinds of behaviour. This does not seem to clarify any ideas about how genes affect behaviour, and in relation to behaviour, most major gene effects are of this nature. If on the other hand, a gene mutation resulted in some disturbance of the central nervous system, as well as, for example, affecting coat colour, and the altered central nervous system changed behaviour, this would link coat colour and behaviour. The link would probably be unpredictable and involvement of the central nervous system would at least suggest "psychological" changes (Wilcock 1969).

There are two considerations relevant to the action of single genes:

1. A single gene must affect behaviour by influencing the structure and physiology of an organ, neural pathway or hormonal system and it acts in this way on a continuum ranging from crude structural changes, for example, in the microphthalmic white hamster, which will consequently show a variety of abnormal behaviour patterns, to complex structural and physiological effects, for example, changes in the efficiency of a neural transmitter in the central nervous system. Animals affected in the latter way would show a variety of abnormal behaviours also, but the cause of these would be a comparatively subtle result of the one gene effect and could lead to general research on how neural transmitter efficiency affects behaviour.

2. For any kind of behaviour, ideas have evolved about which areas of the peripheral and central nervous system are its mediators. For example, the limbic-midbrain and neuroendocrine systems have been linked with emotional behaviour. As regards the subject of study in this project, that is, emotional behaviour, a single gene can affect a relevant area of the brain such as the limbic system, or produce an abnormality in an area which is not relevant, for example, in the visual system, which may affect emotional behaviour indirectly.

If a single gene causes a subtle effect on a relevant structure, Wilcock's requirements that the behaviour studied is psychologically important and that it is affected in a subtle rather than a trivial way, would seem to be fulfilled. It is hoped that the piebald hamster will be shown to meet these demands. The gene responsible for the piebald coat colour is recessive and inherited in a simple Mendelian fashion. Its known pleiotropic effects are not universal and none can explain the occurrence of the hypothesized correlated behaviour. Therefore the first step in the study of the piebald hamster would seem to be investigation of its behavioural differences (compared to the wild type) and their nature, before consideration to physiological and biochemical mediators is given, as these would probably not be worth studying if the behavioural effects appeared to be psychologically unexciting.

Hamsters were thought to be useful as laboratory animals, because, agreeing with Billingham and Silvers (1963) they are "about mid-way between the mouse and rat in size, reasonably placid, clean and prolific and easy to maintain and handle." Also they are all derived from a single litter captured in 1930. Their genetic background must be minimally varied compared to other laboratory species and therefore especially useful genetically.

Aims of the Research

The aims of the research were as follows:

1. To substantiate the largely incidental observations of the piebald hamster mentioned earlier, notably that they are more 'nervous', by means of several behavioural and a few nonbehavioural tests, consequently arriving at an objective measurement of this aspect of their behaviour. Emotionality has not been studied in hamsters so information gained may add to the rodent literature. In addition, by strict genetic control, it was aimed to show that the piebald gene (or a gene closely linked to it) is responsible for behavioural differences between piebald and non-piebald hamsters, with the likelihood that the structural change causing piebalds to behave in a particular way represents a subtle effect on a relevant structure. Incidental observations were carried out to check whether peripheral flaws could account for the behavioural changes.
2. To clarify the usage and application of the terms 'stress', 'fear' and 'emotionality'; and to assess the validity of some of the measures used to determine the degree of emotionality or fear experienced by an animal; then to use the mutant piebald gene as a treatment affecting the central organization of fear and emotionality in the hamster, thereby discovering more about the nature of these psychological concepts.
3. To discover, by consideration of the literature and the findings of this study, whether Gray's proposition (1971a, b) that rodents display consistent sex differences in fear behaviour is tenable.
4. To determine whether the piebald hamster is a suitable model of a rodent high in emotionality, which could serve for research to give information on genetic, physiological and behavioural aspects of emotionality, which may be pertinent to other species.

Outline of the Thesis

The next six chapters discuss the work on major gene effects, conceptual problems involved in the topic of this thesis, variables that should be controlled and previous experiments associated with the project undertaken.

Chapter Two examines the contribution that studies of major genes can make to psychology. Chapter Three considers the concepts of 'stress', 'fear' and 'emotionality' and their application. Chapter Four looks at the contribution of animal work to the study of emotional behaviour. Chapter Five considers how prenatal and postnatal influences can add to genetic variability and how housing conditions interact with all three factors. The conclusions drawn point to the need to control not only for genetic, but maternal, sibling and maintenance factors in all rodent studies, if meaningful behavioural data are to be obtained.

Chapter Six reviews some of the literature on ulcer formation in animals and its relationship to behaviour in other situations, such as the open field, and briefly regards the concept of stress-linked parasitism.

Chapter Seven examines some of the work on tests thought to differentiate animals on emotionality and considers whether the sex differences found among rodents in a variety of experiments form an interpretable pattern with regard to emotionality.

Chapter Eight reports the pilot study, aimed at determining whether piebald hamsters differed from the wild type in some of the predicted ways (based on the observations of Foote, Robinson etc. referred to earlier), and initial findings, which led to the main study, compiling a more thorough investigation of emotional behaviour in four genotypes of hamster. The methods for each experiment are presented

and the results discussed in Chapters Nine to Twelve. A general discussion, Chapter Thirteen, follows.

This thesis could be said to follow a circular pattern, in so far as the final chapter indicates how the findings from the experiments correspond with principles adumbrated in the early chapters.

CHAPTER TWO

THE CONTRIBUTION OF MAJOR GENE STUDIES TO PSYCHOLOGY

A. INTRODUCTION

Psychology and genetics have come together to form the field of behavioural genetics. Hall's paper (1951) was probably one of the first to indicate possibilities for this new area of research.

Workers have experimentally manipulated animals by injecting drugs, handling them, altering their diet and exposing them to different environments, and have observed the consequent behaviour, but, in the past, the possibility that genetic factors may have contributed to the behaviour has been largely neglected. Such neglect could lead to an incorrect interpretation of the results, but is more likely to lead to an inflation of error variance and imprecise experimental findings - a serious fault in a scientific subject (Broadhurst 1972). However, Broadhurst (1971) considered that there was an increasing acknowledgement of genetic variables in psychology, increasing the realization that behaviour, a phenotypic property, was generated through an interaction between genotype and environment. The genotype is the organism's combination of chromosomal genes and the more recently discovered cytoplasmic 'genes', inherited and determined at fertilization.

The equation emphasizes that phenotype equals genotype plus environment. The importance of environment has continually been found and stressed. Watson, for example, was an extreme environmentalist and even today, some researchers will not accept genetic factors. Kurtzin (1968b) stated that there was no convincing evidence of any predisposition to psychosomatic diseases, other than the fact that there was a statistically higher frequency of gastric and duodenal ulcers in certain families. But is not the latter statement enough to cause doubt about a complete

lack of hereditary factors in the onset and prognosis of psychosomatic ulcers?

There have been psychologists who have ignored genetics, but geneticists, on the other hand, have not totally ignored environmental factors. They may not have carefully differentiated them, but at least have accepted their importance.

Now geneticists and psychologists are coming together to try to determine the nature of the genotype-environment interaction. There are two approaches to the study of behavioural genetics. The unifactorial method involves the study of the effect of major genes on behaviour, whilst the multifactorial or biometrical method investigates the effects of the interaction of many genes on behaviour.

If an experimenter wishes to study the genetic basis of a particular behavioural phenotype, he will find individual variations and can investigate them by crossing experiments and will probably find that the behaviour shows polygenic inheritance (Caspari 1967). Caspari suggested that one reason for the finding of a predominance of polygenic differences is because the experiments are based on the selection method which was designed for the analysis of polygenes, or on the study of inbred lines. There are various discussions of the principles and methods for the study of polygenic inheritance (e.g. Broadhurst 1967, 1971, 1972, Bruell 1967, Roberts 1967).

The main advantage of polygenic studies lies in the fact that most behaviour is controlled by a large number of genes and not by a single one. Such genes are called polygenes, and the variation, polygenic. The biometrical approach shows the existence of genes which mediate normal behavioural variability and gives a rough estimate of their number and their average dominance levels, but cannot specify the loci at which the

genes act. Major genes, however, can be located on chromosomes and thus manipulated, and it is only with this situation that insight into gene action on behaviour can be gained (Wilcock 1969). Therefore, this is a principle advantage of the unifactorial method. Single gene studies and the biometrical method have different advantages and the future of behaviour genetics may lie in a combination of the two techniques, as for example, is illustrated by Thoday's work (1961, 1967).

There are a number of reviews covering different aspects of the field of behavioural genetics (e.g. Fuller 1960, Broadhurst 1960a, McClearn and Meredith 1966, McClearn 1960, 1971, Lindzey, Loehlin, Manosevitz and Thiessen 1971, Broadhurst, Fulker and Wilcock 1974) which cite a number of reference sources, but an aspect of this thesis relates to a particular area of behavioural genetics and relevant work only will be discussed in greater detail in this chapter. Therefore, I shall try to assess the contribution of work on major gene effects to the study of behavioural genetics and to psychology.

B. STUDIES OF MAJOR GENE EFFECTS

Studies of major gene effects in insects, birds, rats, mice and men have been carried out since Yerkes's work (1907) on the Japanese waltzing mouse. A number of references to such work can be obtained from Wilcock's paper (1969).

Pleiotropism

Sometimes a number of effects can be related to a major gene defect. For example, Gruneberg (1947) showed that a defect in cartilage formation in mice resulted in skeletal, respiratory and circulatory anomalies. Falconer, Fraser and King (1951) related abnormal pinnae, crinkled tails, corneal ulceration, respiratory disorders and abnormal coat texture to the effect of a recessive gene on hair follicle

development. The phenomenon whereby a single gene has multiple effects is termed 'pleiotropy' and it is to the pleiotropic action of major genes that behavioural changes are usually ascribed.

The main argument of Wilcock's paper (1969) would seem to be that behavioural pleiotropism will be expressed in a variety of ways, some of which would be "important" and others that would be "trivial" and explicable by the nature of the mutation. An example of trivial pleiotropy would be when a gene which reduced the number of retinal receptors also reduced visual acuity so that these animals would be deficient in a visual discrimination task. This deficiency would be predictable from the nature of the gene change and does not lead to hypotheses regarding the role of gene-action in behaviour.

Fuller (1967) found that albino mice escaped more slowly from water, were less active in an open field and made more errors on a black-white discrimination task when compared to their pigmented congeners. No differences were found in activity in a revolving cage or on measures in relation to reproduction. Fuller does not mention the role of illumination in the open field or discrimination test but if used, it could well partially account for the albino results. Wilcock also proposed that difference in buoyancy between the two mice lines could explain the behavioural differences in water escape, as he suggested was also the case in an experiment by Werboff, Anderson and Ross (1967). It was hypothesized that qualities of the coat in relation to coarseness, dryness and density may differentiate albino from non-albino mice and affect buoyancy.

Fuller (1967) proposed that the poor albino performance in the tests he used relates to the reduction of tyrosinase and dopa metabolites in the central nervous system. They have been shown to be reduced in the skin of albino animals (Silvers 1961). Wilcock acknowledged this

hypothesis as reasonable and interesting as it involves the central nervous system and psychological functioning. However, he pointed out, rightly, that peripheral effects directly related to the albino gene should be examined and excluded before complex hypotheses suggesting central nervous system involvement are made.

Keeler-King Hypothesis

In the field of emotional behaviour, early work by Keeler (1942, 1945, 1947a, b, 1948) and Keeler and King (1942) related tameness to coat colour in rats. Specifically, a mutation from the dominant wild type coat colour to a recessive black coat colour was hypothesized as having a pleiotropic effect on docility which allowed domestication to occur. Keeler (1947a) represented diagrammatically the effects that a single gene may have on various developmental reactions by means of a branching tree of consecutive chains of reaction - the root of which is the mutant gene. However, Keeler argued, the development from gene to resulting structure and function is more complicated than this because all characteristics are affected by many genes which interact. Therefore, a mutant gene initiates a complex series of altered biochemical reactions; these reactions set off other altered reactions and so on. Certain structural changes will modify physiology which in turn may produce different behaviour.

Although this description of the process of how a coat colour gene could affect behaviour seems valid, there is little evidence to support Keeler's (1942) and Keeler's and King's (1942) specific suggestion that black rats were more tame than grey ones. For example, Broadhurst (1960a) tested the effects of the black gene in contrast to the brown gene against a homogeneous background of other genetical characteristics. There were no differences between the rats on open field defecation and ambulation, so that they do not differ on emotionality measured this way.

In addition, Broadhurst (1960a) gave evidence from an albino strain selectively bred for low defecation which was not homozygous for coat colour. Crosses to black-hooded rats gave rise to brown-hooded and black-hooded offspring. His records could indicate which descendants of the albino parents carried either the brown or black genes and the results revealed that rats carrying the black characteristics tended to defecate more and ambulate less than rats carrying the brown gene. These results confirmed the trend shown in his previous experiment and suggested that if there was an effect of coat colour on behaviour, it was in the opposite direction to that predicted by Keeler and King. That is, black rats appeared to be more emotional in the open field test (and therefore less tame?) than brown rats.

Wilcock (1969) has criticized Keeler's methodology in testing rat behaviour in that Keeler tended not to mention standardization procedures or control for order effects in a handling experiment. Wilcock (1969) also suggested that interpretation of the results is difficult in the Keeler and King study (1942) because they have no objective measures of 'wildness' or 'savageness' in which animals are claimed to differ. Keeler (1947a) prefaces a description of behaviour in various mammals, identified according to coat colour, with the statement that "much of the following list of cases must of necessity be anecdotal". Wilcock's criticisms would therefore seem to apply to much of Keeler's work.

In addition, Thompson (1953) tested fifteen mouse strains for differences in food drive, emotionality and exploratory activity and could find no definite relationship between the behavioural traits studied and coat colour or other morphological characteristic.

Although there seems to be little evidence to support the Keeler-King hypothesis (Broadhurst 1960a) or that among certain lines of mice

there is a relationship between coat colour and behaviour (Thompson 1953), nevertheless a large number of studies throughout the animal kingdom have related coat colour and morphological characteristics to behaviour (Wilcock 1969). The critical point is that to a large extent the behaviour concerned results from single gene pleiotropism in its "trivial, psychologically unimportant sense" (Wilcock 1969) so that many behavioural differences so far attributable to major gene effects do not merit further attention, because the explanation can be sought from the peripheral effects of the gene (Wilcock 1969). In turn, these predictable results would not seem to lead to worthwhile hypotheses which could aim to clarify the nature of gene-behaviour pathways. It does not necessarily follow that there are therefore no incidences where a morphological characteristic relates to central nervous system activity and behaviour through pleiotropy of a single (major) gene, and Wilcock concedes that if a major gene mutation altered, for example, central nervous system conduction and hence behaviour, in addition to a peripheral factor, such as coat colour, this would link coat colour and behaviour. The link would be unpredictable and involvement of the central nervous system would suggest 'psychological' changes.

In the future, psychologists should take more care when choosing to study a major gene change and examine all available information about it before prematurely invoking psychological concepts to explain behavioural results.

Caspari made a similar point in 1964 "... pleiotropic effects on sensory and motor organs certainly exist; but they may be regarded as trivial, since the main interest centres on the effects of genes on the activity of the nervous system". Essential questions would seem to be how far and in what way can genetics be expected to make a contribution to our understanding of behaviour? (Caspari 1963). Specifically, I have

mentioned areas and cited references that show which type of major gene studies add little either to the understanding of behaviour or to the knowledge of behaviour genetics, but in what way can they contribute?

There seem to have been two approaches to the study of major gene action (Wilcock 1969). Both involve developmental and physiological factors and the second method, called cross-sectional, would seem to involve a specific instance of the first, called developmental.

Developmental Approach

In a paper entitled the "Genic Control of Development", Caspari (1960) described this method. From the adult phenotype, the mutant characters are traced back in development step by step. If several mutant characters are dependent on one gene, each of them is traced back and finally linked up with an earlier appearing deviation from the normal development. Therefore, a number of phenotypic effects of one gene may be obtained, the earliest observed deviation from normal development being supposed the cause of later appearing ones. The primary action of a gene is thought to be unitary in that it appears at a particular time of development and in a particular type of cell. Later effects of the same gene are interpreted as developmental consequences of this primary effect.

Gruneberg (1963) has used this type of approach in a study of skeletal development, and it can also be used to study the genetic basis of behaviour.

For example, Fox (1965) examined the neuro-ontogeny of reflex responses in 56 neuromuscular mutant mice and 126 normal littermates. Neurologic tests were applied because drug studies designed to intensify, subdue or arrest the development of neuromuscular symptoms in mutant mice could be facilitated if affected mice could be identified at an early age.

Neuromuscular mutants are also of great value for the study of development and the structural and functional activities of the brain in relation to myelinogenesis and disease processes of the central nervous system.

Fox concluded from his study that reflexes may be used to investigate the neuro-ontogeny of the mouse and give reliable information regarding the normal and abnormal development of the nervous system. Such findings could be correlated with physiological and behavioural tests to give information of the structure and function of the developing nervous system and how behaviour may be modified genetically or pharmacologically.

Along similar lines, van Abeelen (1968) compared the behavioural development of looptail mice and normal mice in relation to wobbly head movements, frequency of twitching, pivoting, grooming activities, learning postures, rearing, climbing and vibrating with the forelegs.

The results showed that the looptail locus affects several segments of mouse behaviour that occur during various developmental periods. These are likely to be traced back to the abnormal ontogenesis of extrapyramidal motor systems in the forebrain, although the behavioural effect may be exerted through other developmental pathways.

Thiessen (1965) studied the wabblers-lethal mouse in which a major gene is responsible for myelin degeneration of the central nervous system. Thiessen examined behavioural and morphological development of the wabblers-lethal mouse from day five postpartum to day 25, and in addition considered the effect of environmental stimulation. The author hopes that eventually the wabblers-lethal will lend itself to the system of analysis used by Fox. The behavioural defect is obvious, is closely related to demyelination and is regulated by a single gene change. However, even this simple model will give rise to difficulties when

studied because the behavioural modification is not an all-or-none phenomenon as shown by Thiessen's study. It develops in time, is expressed in various ways depending on the stage of development or environmental circumstances and is affected by pleiotropic actions such as hypoglycaemia.

Thiessen (1965) suggested that in view of these factors, behaviour analyses can serve different purposes at different times. For example, during the early stages of development before the onset of evident myelination, behaviour may reflect biochemical activities that are involved in the demyelination of central structures; during the later stages of development new insights into the relation between pleiotropic effects of modification of behaviour and physiology may be gained.

In 1966, Thiessen suggested that beginning with a genetic deviation and working back to trace the major gene pathway may lead to "construction of a genetic ethogram as important to the behaviourist as gene markers have become to the classical geneticists".

Gutherz and Thiessen (1966) tested the onset of audiogenic seizure susceptibility in a number of mouse strains, including albinos. Testing began on different days after birth, the first starting on day 14 and the last on day 21. Latency to first seizure, recovery and death were recorded. Albino mice showed retarded onset of seizure susceptibility compared to pigmented animals, although they died on approximately the same day. The authors offered no explanation of this but suggested that as more than one noise exposure was needed to provoke a seizure in any genotype, the origin related to development and the study pointed to the importance of studying developmental factors and "research gain derived from isolating major gene effects".

These experiments represent one way in which the study of major genes may advance knowledge of how genes affect behaviour. Thiessen (1965)

outlined this advantage when he wrote "... the choice of a relatively discreet behaviour, regulated by a simple genetic mechanism and thus highly reproducible will lend itself to the type of developmental inquiries necessary for the understanding of gene-behaviour pathways".

Cross-sectional Approach

A second approach to the analysis of major gene action is more cross-sectional, so that the mutant and normal animal are studied at a particular point in time, and could be regarded as a special case of the first approach.

Most studies involving a mutant gene have merely correlated behavioural differences with a major gene locus. This does not lead to either greater understanding of behaviour or give information on how genes act on the nervous system. However, it should be possible for major gene studies to contribute to both these areas and a few workers are designing their experiments accordingly.

Even though many behaviours of psychological interest are polygenically inherited, Thiessen, Owen and Whitsett (1970) suggested that a single gene responding in a critical pathway of development could dramatically alter an organism. For example, recessive genes reduced activity of the enzyme phenylalanine hydroxylase in the liver which prevents phenylalanine from being converted to tyrosine; this results in severe metabolic and behavioural consequences, including mental retardation, known as phenylketonuria in human beings. Other genetic units affect behaviour, such as neurologic lesions, of which many are known in the mouse, and some coat colour variants which are found in this species.

Behaviour is the response of an organism to stimulation through external or internal pathways. Genes operate at the molecular level of organization, that is, on DNA, whose effects are describable in

psychophysiological and chemical terms (Fuller and Thompson 1960).

Enzymes, hormones and neurons may be regarded as successively complex intermediaries between genes and psychological characteristics (Fuller and Thompson 1960).

A gene operates through an intricate network of developmental channels. Initially a protein, usually an enzyme, is produced; this results in histogenesis, later morphogenesis and organization of organ systems. At every step there is interaction with environmental pressures and other genetic effects. Therefore, behaviour should be considered as a pleiotropic reflection of physiological processes, that is, genes affect enzyme activity, hormone level, tissue sensitivity, membrane permeability and a variety of other structures and functions, but their influence on behaviour is indirect. By studying many individual gene variations it should be possible to specify the relative importance of various pathways intervening between gene action and behaviour. In this way behavioural phenotypes may be mapped on chromosomes and these can then be used to trace the genetic developmental pathway. A start on this type of procedure has been made by Thiessen, Owen and Whitsett (1970) using 15 coat colour alleles and attempts to provide a basis for research into the mechanisms through which gene differences become expressed as behavioural differences, indicating the potential usefulness of the single locus approach (McClearn 1970).

There have been a number of studies on the genetics of audiogenic seizure susceptibility. For example, Witt and Hall (1949) proposed a monogenic hypothesis to explain data obtained from several strains of laboratory mice, which was followed by a polygenic model based on more extensive data (Fuller, Easler and Smith 1950). Schlesinger, Elston and Boggan (1966) used a number of indices and found that some (e.g. lethal seizures at 21 days of age) were consistent with single locus

models whereas others required polygenic assumptions. Collins and Fuller (1968) have also suggested different subprocesses, with susceptibility on first exposure being determined by a single allelic pair in linkage group VIII and with risk on subsequent exposures being influenced by other genetic factors.

However, it is Ginsburg's work on audiogenic seizure susceptibility involving a two-gene model (Ginsburg and Miller 1963) that represents an example of a type of approach using major genes that is important to behavioural genetics.

Ginsburg and Miller (1963) have demonstrated that two major autosomal loci interact to produce various levels of seizure susceptibility as a result of crosses between DBA (seizure susceptible) and C57 (seizure resistant) mice. One of the genes (A) is associated with an enzymatic effect on nucleoside triphosphatase in the hippocampus and the other (B) with the responses of these strains to glutamic acid decarboxylase activity. Sze (1970) has demonstrated that manipulating the level of the product of this reaction (gamma-aminobutyric acid or GABA) at the appropriate time in development can convert a genotypically seizure resistant animal into one that is phenotypically seizure prone and vice-versa. Since an elevation of GABA at about 18-19 days postpartum will prevent the later development of seizures in an otherwise seizure prone mutant, Sze has postulated that GABA is acting to repress the activity of the gene that will otherwise be expressed at this time, thereby altering the developmental course in such a way that the phenotype to be expected under normal developmental conditions does not arise.

Another line of high seizure mice (HS) are not affected by glutamic acid (Ginsburg 1954) and it was unclear on the basis of hippocampal histochemistry whether the A gene was involved (Ginsburg 1967). A fourth high seizure line showed brain histochemistry which implied that the A locus is not involved and experiments were ongoing to determine

whether their response to glutamic acid is in the direction expected if the B locus is involved. It may be shown that the mutation has occurred at an altogether different locus (Ginsburg 1967).

These results indicate that seizure susceptibility occurs in laboratory mice on several rather simple genetic bases, each of which produces distinct morphological and/or biochemical effects in the brain (Ginsburg 1958, 1967). It is emphasized (Ginsburg 1967) that genotype and phenotype do not have a one-to-one relationship. The genotype is a potential for development that may vary with varying environmental circumstances. A single phenotype may rest on a multiplicity of genetic bases, each involving a different developmental pathway.

Appropriate genetic controls are necessary if the components of a behaviour pattern are to be separated and identified. Once this has been accomplished, the problem becomes one of analysing gene action in behaviour, that is, in tracing the pathway of gene expression by physiological experimentation (Ginsburg 1963).

Ginsburg's gene action experiments on audiogenic seizure susceptibility should be regarded as an approach to the study of underlying causes of behaviour. It is questioned how a single gene contributes to a particular 'unit of behaviour' and as the genetic differences can be reassorted by means of appropriate crosses, it becomes possible to determine whether correlated events can be dissociated from the particular gene producing a behavioural effect (Ginsburg 1966).

This approach also indicated that the same behavioural end result can be brought about in a variety of genetic ways, and that the underlying mechanism may be different in each case, so that what works as a palliative measure in one instance may not be expected to work in another. If the physiological reactions associated with any one gene are determined, a greater understanding of the phenotype, that is, the

behaviour pattern, will be achieved (Ginsburg 1966).

Therefore, Ginsburg's type of approach would seem to fulfill two realistic aims of major gene studies. One of these gives information on how genes can affect the nervous system, that is, on pathways of gene expression, and the other tells more about the nature of the behaviour investigated.

Rodgers (1970) underlined one of these when he argued that the goal of behaviour genetics should not be in relating phenotype to genotype, but in using genotype to understand the essential mechanism underlying any given phenotype of interest.

C. ADVANTAGES OF MAJOR GENE STUDIES

Most of the foregoing points to the main impact of major gene studies being on physiological and developmental genetics.

Merrell (1965) considered that study of gene substitutions, one or a few at a time, while the others were held more or less constant, offered opportunity to learn about the genetics of a behavioural trait and about the trait itself. It will probably be discovered that a number of mutant genes affect any one type of behaviour (Ginsburg has found this with respect to audiogenic seizure susceptibility) and as these mutants are unlikely to have identical effects on the behaviour, an analysis of the complexity of the behavioural trait becomes possible (Merrell 1965).

Fuller (1967), who also discusses some advantages of major gene studies, suggested that behavioural observations of mutants may clarify mechanisms underlying the rather abstract concept of fitness of the trait. Other workers have considered that single gene experiments may have evolutionary implications and this is discussed by Hawkins (1970).

In addition, Fuller advised that major gene substitutions should

be used as treatments in behavioural experiments when they produced a physiological change which could be accomplished by other means only with difficulty or not at all. It follows as an ideal that mutant genes in behavioural research should actually be methods of producing biochemical and anatomical effects which are related to important behavioural systems.

Developmental and physiological genetics can combine the above principle advantages of major gene studies. It was pointed out by Ginsburg (1971) that a study of genetic vulnerability with respect to the development of the nervous system and behaviour could provide a biological model of which reactions can be altered at what particular times in order to bring about changes in behavioural capacities. It is possible, as shown in audiogenic seizure susceptible and resistant mice, to interfere at particular times in development thus activating or suppressing different aspects of the genetic potential, and in some cases (e.g. Ginsburg 1967) inducing a permanent change that is indistinguishable from one that would have resulted from the mutation. The analysis and discovery of such mechanisms depend on our ability to create single gene mutations on otherwise isogenic backgrounds to produce biologically simple systems. The important point that Ginsburg makes (1971) is that once these systems are available, they can be investigated in biologically more complex models, where presumably similar relationships hold but which would have been much more difficult to demonstrate in the first instance.

D. CONCLUSION

Returning to Wilcock's critique (1969) of major gene studies, he concluded that they should aim to discover one pathway of gene expression and that the nature of this would determine the "psychological importance of the observed effect". In a number of studies, the behaviour

concerned is mediated by a peripheral effect of the mutant gene and there is no need to invoke psychological concepts such as 'fearfulness' to explain the behaviour. In view of the evidence he cites, Wilcock's claim that "many of the demonstrated behavioural changes do indeed turn out to be trivial or at best psychologically unexciting" is justified, as is the following statement that "investigations of behavioural pleiotropisms in known mutants so far have contributed little of interest to psychology".

Even so, studies of major genes and their pleiotropic effects would seem to have potential offerings for psychology in two ways, seldom exploited in the past. One of these relates to developmental and physiological genetics, so that pathways between gene and behaviour can be sought and should provide models of how genes operate on the developing nervous system, thus increasing knowledge of behaviour genetics.

The other involves the use of single genes as physiological treatments when studying behaviour complexes such as emotionality or aggression. Genotypes differing in a single gene and also in behaviour may provide insights into that behaviour, thus allowing greater understanding of the concepts invoked, which could be important, especially when studying that aspect of behaviour in different species and circumstances.

In the study to be reported, the piebald hamster was chosen, because it was hypothesized that the piebald gene would act as a treatment to produce a natural lesion of the brain and/or nervous system. Although the position of the lesion is unknown, this does not matter at this stage as the project is not concerned with the biochemical analysis of the gene-behaviour route. However, it is relevant that behavioural changes

observed should not be related to a peripheral effect of the piebald gene. There was no evidence for this at the outset and concentration therefore was devoted to studying the nature of the behavioural changes.

In this way, one of the primary aims of this thesis, that is, the seeking of a greater understanding of the concepts of fear and emotionality, could be enhanced. In addition, the project explored the usefulness of one rodent strain/genotype for a specific research area, so it was essential that genetic effects were controlled and the main study of this thesis has abided by this constraint.

CHAPTER THREE

USE OF THE TERMS 'STRESS', 'FEAR' AND 'EMOTIONALITY'

The concepts of 'stress', 'fear' and 'emotionality' are very wide and are considered variables in such fields as conflict, frustration, learning and anxiety in animals and man. (In this thesis whenever the word 'animals' is used, it excludes man.) Neurotic and more severe disorders are sometimes considered to be stress reactions to a particular situation, thus widening the field. It seems desirable therefore, that studies of this kind of behaviour should be interdisciplinary, involving psychology, psychiatry, medicine, physiology, biochemistry, zoology, genetics, sociology and anthropology.

Selye introduced the concept of stress as a result of findings reported in 1936, 1937 and 1946 and it has since been used in psychology. Selye (1946, 1956) held that stressful stimuli were responsible for the general adaptation syndrome (GAS), which is predominantly an endocrine response consisting of three phases:- the alarm reaction, a stage of resistance and a stage of exhaustion - characterized by enlargement of the adrenal cortex; by atrophy of the thymus, spleen and lymph nodes and almost complete disappearance of the white blood cells; and by duodenal and gastric ulcers. In addition there are depression of both thyroid activity and secretion of the growth hormone, and lowered sexual and reproductive behaviours. Any agent which resulted in an alarm reaction was an "alarming stimulus" (Selye 1946) and there were a wide range of such stimuli, for example, traumatic shock, obstetric shock, muscular exercise, infectious disease, haemorrhage, nervous shock, exposure to cold, burns and drugs. Selye added that purely "functional nervous commotions" such as rage and fear may act as strong alarming stimuli. He insisted on the nonspecific nature of the reaction

and was thus defining stress reaction as a physiological response to a variety of stimuli.

Gray, a modern protagonist of the concept of fear, clearly linked the GAS response to psychologically alarming stimuli and wrote that the same physiological pattern (GAS) arose whatever the nature of the stimulation (1971a).

He divided alarming stimuli arbitrarily into three types - physiological, for example toxic injection, environmental, for example extreme cold, and psychological, such as a threatening predator or learning to avoid electric shock. The main evidence in support of a GAS response to psychological stimulation is provided by the nature of the reaction to population density displayed by rats and mice.

Certain environmental conditions, such as lack of oxygen, are expected to lead to the general stress responses in all aerobic organisms, with little variation in their rate of development. However, less severe stimulation whose effectiveness at least partially depends on previous conditioning and learning, for example, social stimuli, will produce physiological reactions that will vary greatly in intensity and rate of development from animal to animal, person to person (Appley and Trumbull, 1967).

Therefore, Selye's original definition of stress referred to a general physiological response to a variety of stimuli, including psychological ones. Stimuli causing the GAS may be termed 'stressful'. However the word has since been used to describe situations characterized as new, intense, rapidly changing, sudden or unexpected; to describe responses in terms of emotional behaviour; and to define the physiological state within an organism. Stress is thus a concept which has been used as a label in all kinds of circumstances, from stimulus to response, from the cellular to the cultural level (Appley and Trumbull, 1967).

Appley and Trumbull (1967) suggested that the very general concept, stress, would be useful if stimulus, response and organismic elements could be adequately differentiated and if psychologists did not treat this subject as a "unitary, all-or-none phenomenon" (p. 2).

With reference to the experimental data of this thesis, 'stress' will be used in Selye's manner so that it relates to a physiological reaction, the general adaptation syndrome.

The term 'fear', like stress, is used commonly in everyday language, but has been brought into psychology predominantly by Gray (1971a, b). He defined fear generally as a "hypothetical state of the brain or neuroendocrine system, arising under certain conditions and eventuating in certain forms of behaviour" (1971a, p. 9). This suggested there were physiological and behavioural accompaniments to the emotion of fear. Gray (1971a) described fear more specifically as one form of emotional reaction to a punishment, where punishment was any stressful stimulus animals would try to terminate, escape from or avoid. The fear stimuli could be subsumed under one of four general principles: intensity, novelty, special evolutionary dangers and stimuli arising from social interaction. The resulting fear behaviour would be one of freezing, fight or flight, accompanied by autonomic activity.

Prolonged fear stimuli could lead to the second and third stages of the GAS, but occurrence of the GAS due to, for example, toxic injection, need not necessarily be accompanied by the emotion of fear and fearful behaviour.

Hall (1934) introduced the concept of emotionality to psychology and originally related it to behavioural and peripheral changes associated with high sympathetic activity, hence choosing responses of defecation and urination as primary measures of it. It has since become synonymous with fear.

As the result of the influence of Broadhurst's and his colleagues' more recent work, emotionality is now widely accepted as referring to a constitutional trait with drive properties, which could be measured by many behavioural reactions forming a continuum and all being related to autonomic activation.

For the study of emotionality, two rat lines have been selected for defecation responsiveness in the open field test (briefly described in Chapter Seven). The Maudsley reactive (emotional) rats defecate much and ambulate little in the open field, whereas the Maudsley non-reactive (nonemotional) rats defecate little and ambulate much more in this situation. These lines have since been tested in a variety of experimental situations. The reactive strain escape more quickly from electric shock and swim faster underwater to an exit than non-reactive rats. They also show slower emergence into a novel environment and less exploration of it. The reactive line learns the conditioned emotional response (CER) more easily.

It has therefore been claimed that selection has succeeded in affecting a general attribute of behaviour, namely, emotionality.

Emotionality was considered to be an inherited general characteristic with drive properties, which affected an animal's behaviour in a variety of situations (Broadhurst 1957b, Broadhurst and Eysenck 1964, Savage and Eysenck 1964, Denenberg 1964, Gray 1971a) and was thus conceived as a unitary drive concept.

Bindra (1969), extending this line of thought, unified motivation and emotion further (fear, anger, joy, depression etc.) to refer to a "central motive state" which arose from an interaction between a physiological state, such as hunger, and an appropriate class of stimuli, such as the sight and smell of food.

Examination of experimental studies that have been carried out during the last three or four decades, discloses that emotionality has been used to describe and explain behavioural differences between species, strains, sexes and animals experiencing different early environments, in a simple, unitary fashion.

However, over the years there has also been apprehension regarding the use of emotionality in this way.

For example, Broadhurst (1957a) found interactions between open field properties, sex, defecation and ambulation scores. Males and females increased their defecation score under loud noise conditions, compared to soft noise, although the males scored higher than females in both conditions. However, only the female increase was significant. Regarding ambulation in small and large arenas, both sexes showed a significant increase in the large arena, although females ambulated more than males on both occasions. Broadhurst therefore suggested that when considering differences in emotionality, different criteria may be needed for each sex. This type of approach agrees with some contemporary ideas regarding the study of sex differences, discussed towards the end of Chapter Seven.

Tobach and Schneirla (1962) examined the defecation response in the open field and conditioning apparatus in conjunction with manipulated early environments in mice. They did not find uniform trends in defecation score at different stages of development or in different experimental situations and suggested that emotionality was not a "constitutional unity" with a "common innate basis" (p.229). Defecation was thus viewed as a temporal- and situational-specific response in reference to emotionality, rather than a diverse, general indicator.

As organizer of a conference entitled "Experimental Approaches to the Study of Emotional Behaviour" in 1969, Tobach wrote that unfortunately many traditional formulations on the subject remained. Emotion was thought to be an innately organized drive with anatomical relationships in the adult being equivalent to those at earlier stages in the development of emotional behaviour. Emotional behaviour was still defined in operational terms rather than in terms of process and considered to be a disorganized response. Phyletic and ontogenetic properties were ignored (Tobach 1969). Clearly, Tobach felt the concept of emotionality should be reviewed.

King, J. A. (1969) was the chief critic of broad concepts at the conference. His own research on the development of motor patterns in deer mice led him to believe in the analysis of specific motor responses to specific stimuli, rather than the categorization of them under concepts such as stress, arousal, habituation and motivation. King added that, despite the subtleties of development, experimentalists regarded behavioural differences between animals as gross changes, so tried to measure them with crude tests (such as open fields, inverted screen discs, water tubs, shock grids) and explain them by use of global concepts.

Whitney's own paradoxical results (1970) whereby two measures of fear were negatively related in two strains of mice, illustrated, in his opinion, a major conceptual problem in the study of emotional behaviour in infra-human species.

A leap from a priori analogic reasoning, founded on human theory, to rigorous animal experimentation forms the core of much emotionality research. The lack of regard for the meaning of the concepts involved in relation to the behavioural organization of the species studied resulted too often in an experiment demanding post-hoc explanation and

which has an unknown relevance to the characteristic of original interest, that is fear (Whitney 1970). This author suggested that general information on the behaviour of the species studied may lead to greater precision of the conceptualization of fearfulness, thus acknowledging the disadvantages in the use of such terms as 'emotionality'.

The inconsistent trends in the results of an experiment involving different kinds of stimulation given to rats preweaning, in terms of emotionality, led Henderson (1968) to conclude that the term 'emotional reactivity' was inappropriate for describing early experience/late emotionality effects and to doubt the validity of this unitary construct.

Archer is a major proponent of the view that the term 'emotionality' cannot adequately describe strain, sex and early experience differences between animals in a unitary way (1971, 1973, 1975). Archer's work will be discussed in greater detail in Chapter Seven, but his general principles will be put forward here.

Archer (1973) presented strong evidence that there were a variety of behavioural and physiological outcomes shown by rats, mice and other species when used, in similar types of test situations, designed to measure emotionality. It is therefore doubtful whether this unidimensional concept is suitably sophisticated, incorporating appreciation of the complexities of the phenomena it is describing.

It would seem that standard measures of emotionality developed by Broadhurst (1957a, 1960a) and other measures commonly used, such as avoidance learning, are influenced by many variables. For example, open field defecation may be influenced by factors unrelated to sympathetic activity in the colon such as deposited odor stimulants or time since last eating. Therefore causation of behaviour cannot be attributed to a single emotionality state.

Archer (1973) suggested that the adaptation rate of any behavioural response to novelty and the measurement of a variety of emotional responses in a short time span should be used to give a general pattern of emotional responsiveness and/or the specificity of any emotional responses.

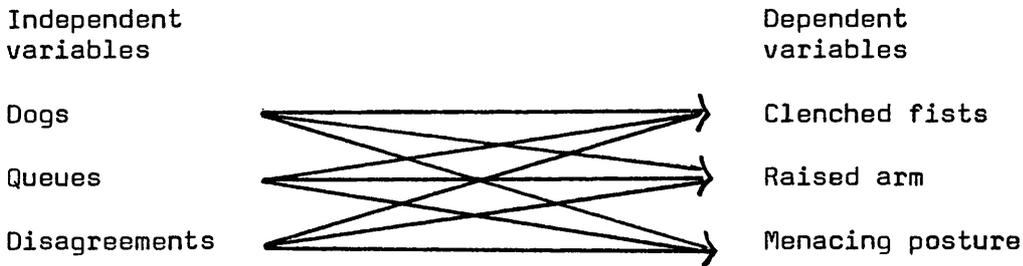
However, the conceptual problem centred on emotionality has been most clearly and consistently stated by Hinde (1966, 1970, 1974). It was stated earlier that emotionality was often considered to be a unitary drive concept, and Hinde, in 1966, acknowledged the tendency to use drive as a blanket variable to provide unitary explanations for a selection of behaviour that may depend on diverse mechanisms. A unitary drive indicates that these various aspects of behaviour are a result of the same underlying mechanism, although this may not be so, as suggested by Archer (1973, 1975). This is also borne out by Ginsburg's findings (1958, 1963, 1967) which suggested that a single behavioural pattern may relate to diverse genetic bases, involving different physiological pathways. Another model involving the genetic basis of a behavioural pattern, such as emotionality, could well hypothesize that in some cases behavioural expression is dependent on a number of major genes - one gene may affect one aspect of behaviour and another gene may affect a different mechanism and aspect. The behaviour must therefore be complex because the exact pattern expressed depends on which gene changes are involved.

Hinde also mentioned that drive concepts tended to oversimplify (1966, 1970). It was often implied that independent variables such as hormone dosage, hours of food deprivation or external stimuli affected behaviour by influencing drive and by their role as stimuli in influencing the kind of behaviour shown. But, Hinde stated, such variables could affect an animal in many ways, with resulting behaviour not necessarily being simply related to them.

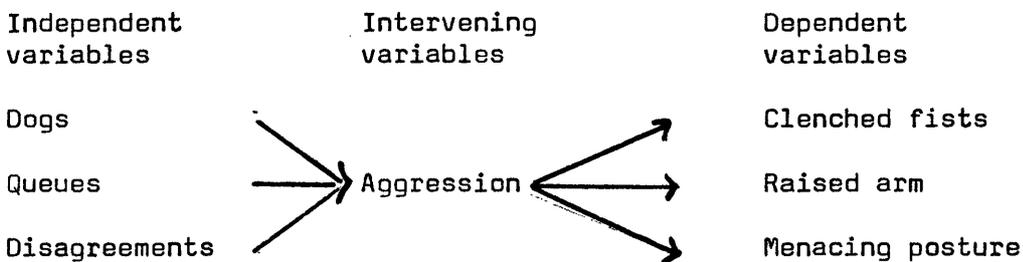
However, drive concepts, such as aggression and emotionality, are useful in certain conditions (Hinde 1974). For example, if waiting in a queue, having an argument and seeing a dog all cause a man to clench his fists, raise an arm and give a menacing posture, he is called aggressive. If the three situations (queues, disagreements and dogs) can produce any of the three reactions (clenched fists, raised arm or menacing posture), nine stimulus-response relationships can be predicted. However use of the intervening variable, aggression, between situation and response results in conceiving only six relationships and is therefore an economical device (Figure 1).

Figure 1 (from Hinde 1974 pg. 27)

(a) The relations between three independent variables and three dependent variables.



(b) The relations between three independent variables, one intervening variable and three dependent variables.



To postulate an intervening variable is only useful if the dependent variables are correlated with each other and with each independent variable. If a man hits a dog, but is considerate to people in

queues and can amiably disagree, then it is not correct to label him as aggressive. When there is a lack of correlation, the concept forming the intervening variable is misleading and "can be a positive hindrance" (Hinde 1974, p.27).

Classification forms the basis of all science because in order to study natural phenomena, they must be described and classified (Hinde 1974). Experimentalists search for global concepts that will unify observations into predictable hypotheses (King, J. A. 1969). Therefore, so that unifying principles which cover a wide range of observations and experiments may be formulated, concepts such as emotionality and fear must be retained, but their limitations acknowledged.

Therefore, in reference to my research, fear and emotionality will be used, as Hinde suggested, as intervening variables, descriptive of the relationship between stimulus and response.

Both Hinde (1974) and Archer (1973) emphasized that if the measures from the different experimental tests co-varied, so that an individual or a group scored, a priori, more emotionally on all tests, or so that two measures correlated on one test and in the same direction in a variety of tests, then concepts of fear and emotionality were descriptively useful. But when different animals scored more emotionally on different tests, which produced low correlations, these concepts were no longer meaningful.

For these reasons, emotionality/fear, in this thesis, will be attributed to the hamsters that can be shown to be consistently more fearful in a variety of circumstances. Dissociation will prevent the use of the terms.

Summary

In this chapter, use of the terms 'stress', 'fear' and 'emotionality' was discussed.

'Stress' has been used very generally to refer to a stimulus, a response or an internal state. The author prefers Selye's description of stress as a term associated with a systemic physiological response to a variety of environmental conditions.

'Fear' and 'emotionality' have been used as explanatory, unitary drive constructs, although this has led to uneasiness in some researchers, notably Hinde (1966, 1970, 1974) and Archer (1971, 1973, 1975). Their opinions on the validity and use of the concepts were discussed and accepted.

CHAPTER FOUR

THE USE OF ANIMALS IN THE STUDY OF EMOTIONAL BEHAVIOUR

Eysenck and Broadhurst (1964) considered the neuroticism dimension of human personality to be closely related to autonomic reactivity. Animals, as well as human beings, have autonomic nervous systems and although their systems differ with regard to lability, Eysenck and Broadhurst felt that it was logical to regard emotionality in animals as analogous to neuroticism in human beings.

This assumed that in animals and man the same parts of the brain and nervous system were responsible for these reactions. Although there may be similar underlying causal mechanisms, it now seems likely (cf., Chapters Two and Seven) that a variety of species-specific hormonal, perceptual and peripheral factors would tend to limit the extent of analogy.

Furthermore, neuroticism implicates such issues as the appraisal of threat, attack on the self-image and behaviour resulting from ideological or philosophical matters, which animal studies could not clarify.

However, in so far as animal emotionality and human neuroticism can be considered to be learned responses they must possess certain characteristics common to all learned responses (Wolpe 1967), namely, the behaviour should be like that evoked in the precipitating situation; the responses should be under the control of the stimuli that were present in the precipitating situation; and the responses should be of greatest intensity when the organism experiences stimuli most like the precipitating ones. Wolpe felt that animal emotionality and human neurosis could both be defined as persistent unadaptive habits, resulting from repeated exposure to anxiety provoking situations. Autonomic responses of an anxiety pattern were usually their pre-eminent constituent.

Certainly, studies of learning theory in animals have contributed to the now widely used behaviour therapy in human beings.

If the specific emotion of fear is considered, animals may freeze or flee when faced with a punishing or threatening agent. Man, in fear provoking situations, behaves similarly (Gray 1971a). If the organization of fear in the brain and neuroendocrine system is to be investigated, animals must be used, as human beings cannot be subjected to experiments which attempt to break these systems down. In addition, certain factors influencing susceptibility to fear could be controlled and analysed in animal studies. Genetic, maternal, sibling and other environmental control in experiments would be demanded to help elucidate important developmental effects in the ontogeny of fear, which may be similar in man. Study of the origins and organization of fear is necessary if the phenomenon is to be brought under control. Rachman, in a recent publication (1974), claims that his conception of human fears has been considerably influenced by research into fear in animals.

The ACTH network seems to play a key role in various behavioural situations, such as perception, habituation and learning (Henkin 1970) and must therefore have high adaptive significance in all mammals, including man (Levine 1971).

Pavlov pioneered the work on experimental neurosis in animals and this has led to corticovisceral theories of abnormal behaviour which Kurtsin (1968a) considered relevant to animals and man. The most complete study is reported by K. H. Bykov (Kurtsin 1968a). It was shown that through stimulation of the cortex, cardiovascular, respiratory, gastric, pancreatic, hepatic and gall bladder activity could be affected as also could the circulatory system, urination, thermo-regulation and sleep and wakening cycles. Integration between the corticovisceral

processes and endocrine glands was proposed. In considering psychosomatic disorders, Kurtsin (1968b) reported that in more than 300 dogs he found a correlation between interoceptive processes and susceptibility of certain organs to develop functional disturbances. He suggested that disturbance first occurred in organs that had a well established neural connection with the cortex. He cited evidence for this, for example, in dogs which have twice suffered acute gastritis, collision caused severe and chronic disturbance of the stomach, in terms of ulcers, compared to normal dogs, namely those that had not suffered gastritis. (Collision is the presentation of a negatively conditioned stimulus after conditioned positive stimulation). Perhaps gastritis gives a predisposition to stomach disorders but it is hard to understand what is meant by a "well established neural connection". (p. 114).

Despite hesitation about the terminology Kurtsin (1968a, b) uses, which may only be an outcome of translation, he interestingly relates neurosis and disease. He observed that burns on the skin healed more slowly in dogs suffering experimental neurosis, than in controls and that neurosis enhanced susceptibility to streptococci, staphylococci and diphtheria infection, and diseases such as tuberculosis and dysentery. Kurtsin claimed that corticovisceral theory could aid understanding of the aetiology and pathogenesis of cancer and added that immunological resistance was determined by the nervous system, especially the cortex.

A related area where the use of animals has been relatively neglected is psychosomatic disease (Saul 1962, Chertok and Fontaine 1963), and it was argued by Broadhurst (1960b) that animal studies had a place in the development of psychosomatic research.

Physiological disorders, for example, stomach ulcers, occur in animals and man. In man, this type of illness is thought to be related

to the emotion of fear. If this can also be shown to be the case in animals, then animal studies may provide valuable information on the onset, duration and recovery from such disorders.

A number of papers have demonstrated veterinary and agricultural examples of abnormal behaviour in animals (for example, Chertok and Fontaine 1963, Ewbank 1968, Fraser 1968a, b, Ferguson 1968, Rossdale 1968, Worden 1968, Fox 1968a, b, Schmidt 1968, Brunner 1968 and Joshua 1968) which may be considered to have a sociological and/or psychological basis. However, there seemed to be some confusion in the use of the term 'psychosomatic'. It appeared that it could be used in two ways (Lader 1970). It could refer to all illnesses, in that every type of illness has a psychological concomitant. This is thought to be regulated by the pituitary-adrenal system, but how it operates is still largely unknown (Levine 1971). This use of the word psychosomatic is so broad as to make it as indefinite as the term 'stress'. Thus a narrower definition may be more useful, although arbitrary. Psychosomatic could refer to specific physical illnesses in which psychological factors are thought aetiologically to be particularly important, for example, asthma and peptic ulcer. Lipowski (1968) urged that the psychosomatic approach should be focused on the relationship between specific psychological variables such as emotions and specific physiological consequences, rather than on disease entities per se.

Some of the abnormalities occurring in animals described by Schmidt (1968) and others were as follows: Anorexia nervosa was observed in dogs and cats; gastrointestinal ulcer was rare but occurred in some cats, dogs, pigs and cattle; vomiting and motion sickness were known to occur in dogs. Defecation was a common phenomenon during clinical examination of dogs, cats and cows. The baboon had been found to have cardiac disorders, but arterial hypertension was rare in animals.

Respiratory disorders were common, taking the form of polypnea and bronchitis in the dog, and allergic respiratory disorders in the guinea pig. There were a variety of disorders associated with the reproductive system. In the females, the ovarian cycle could be influenced by light, and emotional trauma could block ovulation. Nymphomania was common in Siamese and Persian cats. In the cow, fear could cause abortion and in the hen fear stopped egg laying. Pseudopregnancy, where most of the normal signs of gestation were present, has been known to occur in cats, rabbits, dogs, goats, horses and cows. In males, "psychological castration" could occur, for example, the male rooster had no sexual interest in the female when dominated by another male. Psychological factors were also hypothesized to play a part in the onset of diabetes, dermatological and neuromuscular disorders (Schmidt 1968). If vets could analyse the conditions of onset and appearance of these disorders, their exact symptomatology and associated behavioural changes, then animal studies could be important to medicine.

Chertok and Fontaine have carried out much of the work on abnormal animal behavioural reactions. They have noted "collective panic" in herds of horses and cattle and certain forms of animal aggression with a sexual syndrome. They described hysterolepilepsy among dogs. The animals showed convulsive symptoms which overlapped with certain epileptic elements (Chertok and Fontaine 1963).

Therefore, a large number of disorders which may have psychological concomitants have been observed in animals. But behavioural changes need quantifying in behavioural terms and although veterinary medicine and farms offer good opportunities for observing biological/behavioural illnesses, they are seldom exploited because of the lack of staff suitably qualified to record behaviour.

Stomach ulcers, artificially induced in animals, have been extensively studied and Lazarus (1966) considers this informative as the pathological symptoms arising in the animals are similar to those found in man. Work on gastric ulcers is reviewed in Chapter Six.

Sudden death, related to belief in witchcraft, sometimes occurs in primitive tribes; apparently the origin is psychological (Richter 1957). Some healthy boys and girls after slight stress, for example, a plunge into cold water, have died, although they had shown no previous symptoms warning that this could occur. Autopsy revealed no obvious physical disorder except that the adrenal cortex was small and the thymicolymphatic tissues were overdeveloped. It was suggested that the low stress resistance of these children was due to a deficiency in the adrenal cortex, but this has not been proved (Selye 1956). Cannon hypothesized that sudden death resulted from shock produced by continued production of epinephrine. Richter (1954, 1957) also considered aspects of sudden death in wild and domesticated rats. Wild rats were shown to have larger adrenal glands than domesticated ones (Richter 1954). The glomerulosa layer of the adrenal gland has salt regulatory functions in that secretions from this layer help to conserve salt. Richter (1954) took the fact that wild animals could survive on a low sodium diet much longer than domesticated ones, without visible effects, as evidence that the adrenal gland of the wild rat was more efficient than that of the domesticated variety. However, wild rats could not endure certain types of stress as well as domesticated ones.

Richter (1957) examined swimming survival times; many more wild rats died, than domesticated ones. A few died five to ten minutes after immersion but others survived 81 hours. Autopsy revealed that some rats had a large heart, distended with blood, which implied death may have been induced by over-stimulation of the parasympathetic system. Richter

explained this finding in terms of learning the temporary nature of the situation. If wild rats were held in the water for short periods and freed, they could withstand longer immersions. Domesticated rats did not need this learning to overcome the "hopelessness" of immersion (Richter 1957). Alternatively the difference between wild and domesticated rats may not be so much related to stress susceptibility but to a metabolic difference such as the assimilation of salt in relation to vigorous activity.

Ewing (1969) reported that subordinate cockroaches died after a fighting situation. Their movements were sluggish, the righting reflex disappeared and they showed a state of semiparalysis, but they did not show any signs of external damage. This resembles a situation of social stress in mammals. Barnett (1958) found that aggression in a rat pair could produce disease in the subordinate, characterized by the GAS and death, which could not be attributed to any external damage. Barnett, Eaton & McCallum (1959) found that this type of stress (that is, an aggressive encounter) raised the blood sugar content and that death was possibly due to non-specific failure of carbohydrate metabolism, although the very early deaths were more likely to be due to vagal syncope.

Why did attack produce such an extreme response? It could not be due to exhaustion alone, because although the attacking animals were equally exhausted, they were able to survive. This phenomenon of sudden death or death from shock in animals could have important parallels with a similar phenomenon which occurs, albeit rarely, in man. It is difficult to determine the causes of or the contributory factors to such human deaths with any confidence; thus it would appear that there might well be scope for using animals in the study of this phenomenon, with extensive autopsies, to reveal predisposing factors and ultimate consequences.

Some animals react to fearful situations with behavioural changes and others by somatic disturbances or even death. These different reactions are also apparent in man. A great deal of information about such reactions can be gained from the study of animals, thus permitting the different types of response to be analysed. It is only with animals that experiments investigating the neuroendocrine system can be conducted and well controlled genetically. Animals are used in studies of radiobiology, aerospace research, environmental physiology and psycho-pharmacology, all of which contribute to the voluminous stress literature.

Conclusions

Animal studies with regard to the development, organization and display of fear behaviour could aid understanding of the similar phenomenon in man principally in two ways:

1. The roles played by the brain and neuroendocrine systems in the production of fear behaviour, flight and immobility, and developmental factors affecting susceptibility to fear reaction could be sought in animals.
2. The relationship between the adrenocortical system and psychosomatic disorders may be elucidated in animals.

CHAPTER FIVE

PRENATAL AND POSTNATAL INFLUENCES ON ADULT EMOTIONALITY

A. MATERNAL INFLUENCES

In 1843 Little noticed the association of abnormal parturition, difficult labours, prematurity and asphyxia neonatorum with cerebral palsy. Since then neurological disorders of childhood, such as mental retardation, epilepsy and behavioural problems have been attributed to embryological and birth processes (Lilienfeld & Pasamanick 1955). A comprehensive study of prenatal and paranatal records of children born with cerebral palsy, epilepsy, mental deficiency and who develop speech disorders or tics, led Pasamanick and his colleagues to hypothesize a continuum of reproductive causality (Pasamanick & Lilienfeld 1955, Pasamanick, Constantinou and Lilienfeld 1956, Pasamanick & Kawi 1956). This suggests that, as obstetric complications are associated with foetal and neonatal mortality, a milder difficulty might produce a living infant who would develop neuropsychiatric disorders depending on the severity, type or location of damage. Anything from stillbirth to minor behavioural dysfunctions could occur (Pasamanick and Kawi 1956).

Sontag (1966) was concerned with foetal movement in response to stimulation, such as sound. In early observations he found that experiences of a pregnant woman could alter foetal activity. He has recorded several incidences that have dramatic implications. For example, a young woman carrying her first child fled to the Fels Institute, Ohio, (where Sontag works), alone and frightened as her husband had just suffered a psychotic breakdown and threatened to kill her. She complained of the kicking foetus, so Sontag and his colleagues recorded the activity level. It was ten times the level it had been in prior weekly sessions. The husband of another pregnant woman being studied was killed in a car accident. Her foetal movements increased markedly. They have managed to collect eight similar cases,

showing foetal response to maternal fear. Children born to mothers suffering late pregnancy traumas were found to have no morphological defect but tended to be irritable and hyperactive, with marked feeding problems.

These observations are to a large extent incidental, and human prenatal research has to be relatively uncontrolled, so there are many confusions and uncertainties in the findings. The previously mentioned Sontag study points out the importance of considering, not only variables directly affecting a given individual, but also those which affected his ancestors. The strength of any prenatal influence depends on a number of factors, such as genotype, ancestors, intrauterine experience, maternal experience from birth to pregnancy and parturition. After birth, maternal or foster mother behaviour towards the child and finally the child's own postnatal experience add to interaction possibilities and these variables could be confused with the prenatal influence. Therefore, the nature of maternal transmission to offspring is important - whether it is through the placenta, in lactation or in postnatal behaviour. In human studies, reviewed by Barrett (1971), it is unlikely that one design could differentiate genetic, prepregnancy, prenatal and postnatal influences. But when experimenters who use different techniques in varied situations, implicate similar findings and conclusions, interpretations may be justified, especially if reinforced by animal studies, which have few ethical problems (Barrett 1971). The converse is also true. Extrapolation from animals to man "is unwarranted unless supported by evidence in man" (Fraser 1964, p. 285). Human and animal studies mutually strengthen each other.

In the last ten years there has been an enormous upsurge of experimental animal work, gathering information on grandmother, maternal, prepregnancy, prenatal and postnatal effects, and their interaction with genotype (e.g. Denenberg 1962, Denenberg & Rosenberg 1967, 1968,

Denenberg, Karas, Rosenberg & Schell 1968, Deneberg & Whimbey 1968, Ottinger, Denenberg & Stephens 1972, Ressler 1963, 1966, Porter & Wehmer 1969, Wehmer, Porter & Scales 1970a, 1970b). Human studies could not be controlled in the way necessary to reveal the independent workings of these influences. Also, small rodents, commonly used in this kind of research, have short gestation periods and large litters, so the validity and reliability of patterns can be traced over several successive generations. It would probably take centuries to do the same in man (Barrett 1971).

In 1961 Broadhurst stressed that behaviour genetics studied in small mammals could be confounded with maternal effects, if not controlled for. He was interested in strain-specific effects, whereby an organism resembles its parents. He emphasises that this similarity can only be assumed to be caused genetically, if maternal and environmental effects can be excluded. Most earlier work does not consider the possible maternal influence, for example Hall in 1951, studying rat emotionality. Emotionality, especially, has been shown to be highly correlated with maternal influences, so omission of this factor was serious.

Maternal influence can operate postnatally, prenatally or before conception. I will follow a research pattern developed over the last ten years (which has seemed to work backwards), considering firstly postnatal variables.

Postnatal Effects

Cross-fostering between two or more strains is the most common procedure for differentiating postnatal and genetic effects. In this way, an offspring is reared by a genetically similar mother and an unlike mother. Postnatal effects can be observed by comparing the scores of the differently reared offspring. Cross-fostering itself should be controlled for, so that if two strains are being considered, there are six rearing possibilities:

1. Offspring of strain one are reared by their natural mothers, of strain one.
2. Offspring are cross-fostered to mothers of their own strain.
3. Offspring of strain one are cross-fostered to mothers of strain two.
4. Offspring of strain two are reared by their natural mothers of strain two.
5. Offspring are cross-fostered to mothers of strain two.
6. " " " " " " " " one.

There are three possible outcomes of this situation:

1. The pups resemble the foster mother more than their natural mother, so there has been a postnatal maternal effect.
2. They resemble their natural mother more than their foster mother, so postnatal effects are small, but prenatal and genetic effects are not separated.
3. The offspring score intermediately between foster and natural mother so there may be a weak postnatal effect or a balancing between pre- and postnatal effects (Broadhurst 1961).

Depending how the offspring behaviour is measured, and between which strains the young are cross-fostered, a "maternal buffering response" whereby the maternal environment moderates extreme genotypic tendencies of the offspring in response to prenatal stress¹ may be found, as recently described by Fulker (1970). Despite possible laboriousness of the cross-fostering procedure, it would seem to be an effective control of postnatal effects.

Ressler (1963) was one of the first workers to show the importance of parental behaviour in offspring reactions. He considered two strains of mice, Balb/c and C57BL/10. Foster parents of each strain could rear offspring of their own strain or the different strain. Parental handling of pups, offspring exploratory and manipulatory behaviour, body weight and survival to weaning were measured. The main result showed that postnatal genotype-correlated parental influences contribute to strain differences in visual exploration, body weight and viability.

¹ See note at end of chapter, page 53.

That is, offspring of Balb/c genotype engaged in more manipulatory behaviour than C57BL/10 regardless of their foster parents. Both strains engaged in more visual exploration, were heavier and more viable, if reared by Balb/c parents. Regardless of opinions about the effectiveness of the measures used, this study clearly demonstrates the need for caution in attributing behaviour to a genetic, rather than maternal cause. Previous work (Ressler 1962) had shown that Balb/c young received more handling than C57BL/10 young, from either strain of foster parent. In some way, offspring genotype and/or behaviour was affecting parental response, which may in turn have altered offspring behaviour.

Reading (1966) followed up this work, measuring adult behaviour in fostered and cross-fostered mice of strains Balb/c and C57BL/6, on a variety of tests. Again, validity of measures apart, he found that when reared by foster mothers of their own strains, there were marked behavioural strain differences compared to rearing by foster mothers of the different strain. Neither strain of pup showed complete resemblance to its cross-foster mother, but Balb/c pups showed more resemblance to C57BL/6 mothers than did cross-fostered C57BL/6 pups to Balb/c mothers. Reading did not comment on whether there was a greater correlation in behaviour between Balb/c young reared with Balb/c mothers, than for C57BL/6 pups reared with C57BL/6 mothers, that is, whether Balb/c pups were more inclined to resemble any parent, than were C57BL/6 pups, but the fact remains that young react differently to different maternal environments. This further complicates the genotype-environment question.

Lagerspetz and Wuorinen (1965) considered the relationship of maternal behaviour to aggressiveness. They picked two mice strains previously discriminated as aggressive and passive. Fostering was controlled for and each pup was reared by a mother of its own strain or a different strain. Maternal behaviour was measured for ten days

preweaning, by five behaviour categories and aggression was measured in males only, by a seven point rating scale at $4\frac{1}{2}$ months of age. The results showed that mice from the aggressive strain showed more aggression than subjects from the passive strain regardless of maternal strain. Also subjects of one strain reared by their natural mothers were more aggressive than cross-fostered subjects of the same strain, suggesting maternal care can modify aggression, but not mask the genetic effects brought about by selective breeding (Lagerspetz and Wuorinen 1965). However this anomaly reflects certain inadequacies of the fostering process.

Rosenblatt and Lehrman (1963) and Young (1965) emphasized the importance of the stimulus properties of the neonate. Rosenblatt and Lehrman (1963) have shown that maintenance of the mother's postnatal behaviour depends partly on stimulation from her litter. Several studies (Young 1965, Richards 1966, Meier and Schutzman 1968) stress consideration of the litter's effect on maternal behaviour.

Ottinger, Denenberg and Stephens (1972) take a slightly different angle. They state most research has been concerned with the effect of experimenter mediated stimulation, such as shocking or handling infants, on later behaviour. They wished to look exclusively at mother mediated stimulation, by rotating rat mothers between their own litters and another every 24 hours. Offspring reared in this way were more emotional in adulthood than controls.

Furthermore, little research has involved the effect of postnatal maternal events on offspring behaviour.

The studies cited indicate postnatal effects, but do not give a complete picture of maternal influences.

Prenatal Effects

Any experiment using different strains embodies a variety of prenatal effects. Females of differing genotypes produce different

intra-uterine environments (Joffe 1969). The usual control procedure for this is to carry out reciprocal crosses. If two strains are taken, a male of strain one is mated with a female of strain two, and a male of strain two is mated with a female of strain one. The hybrids of both crosses are compared, and any differences between them are thought due to prenatal maternal effects, assuming adequate control for postnatal effects (Broadhurst 1964, Joffe 1969). Sex linkage, delayed inheritance or extranuclear inheritance are genetic phenomena that could confound the separation of prenatal and heredity factors (Broadhurst 1964).

Most of the work in the field of prenatal experiences has dealt with maternal stress and offspring behaviour. The first study investigating trauma in pregnancy affecting offspring behaviour was by Thompson (1957). Female rats prior to pregnancy were conditioned to a buzzer sound, followed by an electric shock. They could avoid the shock by pressing a lever which opened a door to a safe compartment. During pregnancy they were exposed to a different situation in that the sounding of the buzzer was not followed by shock and they were prevented from opening the door to the safe compartment. It was assumed that inability to escape, after previous association of shock with the buzzer, would generate fear. Thompson did not foster any young. He tested the young for emotionality by use of the open field, at 30 days and 130 days and found young from mothers made fearful during pregnancy to be more emotional than offspring from control mothers. The implications of this study gave rise to a number of rigorously controlled experiments. The degree of generality of this finding was unknown because of the lack of empirical data (Denenberg 1962).

Weir and De Fries (1964) made it clear that the response of offspring to prenatal stress is a function of its genotype. To prove this, they took females of the C57BL/6J and Balb/cJ mouse strains, already certified as of high activity and low activity, respectively. The females were given prenatal stress in a swim tank, a tilt box and the open field, and the offspring were tested in the open field at 40 days of

age. ^{that} Assuming high ambulation indicates low emotionality, they found different open field activity scores in the offspring of the two strains. These findings differ from those of Thompson, Watson and Charlesworth (1962) who found no offspring differences when female rats of two strains, known to differ in activity were given maternal adrenalin injections. The results of both these studies imply that the effect of prenatal stress differs with genotype of offspring and mother, and that the two types of stress yield different behavioural outcomes. Weir and De Fries justifiably conclude that the species, strains within the species, activity level of the females within heterogenous strains and the type of stress administered, are all relevant variables when prenatal maternal influences on behaviour are considered.

Weir and De Fries did not cross-foster the offspring, so the effect could have been mediated prenatally or postnatally. Since then most workers have used the diallel cross to separate out the prenatal and postnatal effects.

The open field test has been used in much of the prenatal literature as a test of emotionality. Joffe (1969) cited an experiment using the diallel cross carried out on the Maudsley reactive and non-reactive rats. Females were placed in one of the conditions of pre-mating plus gestational stress, pre-mating stress only or no treatment (controls). The treatments did not significantly affect the mothers' open field scores, as tested before the experiment and after litter weaning. Litter sizes and offspring viability were similarly unaffected. Untreated control offspring gained more weight and were heavier at weaning than either of the prenatally manipulated groups. Offspring open field defecation was not affected by prenatal treatment. The expected strain differences were found, but the hybrids from reciprocal crosses behaved similarly. Regarding offspring ambulation, Joffe found a significant paternal strain by prenatal treatment interaction. This indicates, reported Joffe, the

importance of the foetal genotype in determining the response to prenatal maternal stress. Offspring of Maudsley nonreactive fathers and reactive mothers showed an increase in ambulation, by prenatal treatment.

Fulker (1970) takes up this problem. It appears that the paternal nonreactive genotype pulls the F1 in the direction of the low scoring inbred line, rather than the high scoring reactive mother, and vice-versa for reactive fathers and nonreactive mothers. It is possible, argues Fulker, to see how a reciprocal difference can be ascribed to paternal genotype statistically, but difficult to see how this could happen in reality since the fathers were hardly present at any time during the development of the foetus and not at all after birth. Fulker proposed a mathematical model to help explain this phenomenon, assuming that reciprocal differences are more plausibly ascribed to the mother. His analysis showed that maternal and additive genetic effects pull the phenotype in opposite directions and in so doing almost cancel each other out. Therefore Fulker proposed that genes determining the offspring's phenotype also act in a compensating manner to the maternal environment, hence buffering progeny against a large, unidirectionally imposed prenatal stress.

Similarly, Joffe (1969) concluded that offspring genotype determines the direction of changes in behaviour and postulated that changes will be toward an optimum level for adaptation and survival. If the optimum is a medium one, strains usually having extreme scores will be bidirectionally affected and differences reduced, whereas if the optimum level is high or low, effects will be unidirectional.

Denenberg is primarily responsible for bringing to the fore the 'handling' variable (Denenberg and Karas 1961). Handling usually means removing a pup from the home cage nest, placing in a container for a few minutes and returning it to its cage. Handling in infancy has been

shown to reduce adult emotionality in the open field as determined by defecation and activity scores (Denenberg et al. 1962). It has been shown also to affect growth rate and mortality in response to food and water deprivation (Denenberg and Karas 1961). Handling in infancy seems to affect behaviour normally measured as emotional reactivity. Up to a certain point handling in infancy should reduce adult emotionality. It is argued there is an optimum amount of early stimulation which results in efficient performance in adulthood and that stimulation leading to very high or very low emotionality results in impaired performance. An inverted U-function should be obtained between the amount of infantile stimulation and adult performance on tasks which involve a noxious element and which are of moderate difficulty (Levine 1969).

Denenberg and Whimbey (1963) found that the handling experience of a mother while she was an infant affected her offspring's weaning weight and open field performance. In this way the experience of one generation affected the behaviour of the next. This idea has broad implications for the evolution of behaviour, so Denenberg and Rosenberg (1967) asked how far into the future could such effects extend? They investigated this by determining whether experiences during the infancy of female rats could affect their grandpups. Females were handled or not handled in infancy. When they were pregnant they were assigned to maternity cages or "free environment boxes", weaned offspring were placed in laboratory cages or "free environment boxes" until 50 days of age, when free environment females were placed in laboratory cages. These females were the mothers of the animals investigated in this study. At weaning the young received an open field test and were weighed. Grandmother infantile experience interacted with maternal cage environment to affect grandpup open field activity and weaning weight. The interactive nature of the variables must be emphasized. If the female offspring of handled and nonhandled grandmothers had been kept in laboratory cages from birth

to adulthood, the most significant finding would have disappeared, that is, the free environment in the mothers early life was necessary for the effect of the grandmothers' handling experience to express itself in the grandpups. Denenberg and his colleagues have since tried to separate out such interactive effects by "programming life histories" in rats. They have considered handling or not handling the mother in infancy and providing a normal cage or a free environment at birth, at the time of weaning and postweaning. They have also considered these variables and the handling experience of the pups and the sexual and reproductive variable. However the report by Denenberg and Rosenberg in 1967 was the first to suggest that the early experience of a female animal could affect its descendents two generations away by a nongenetic mechanism.

Wehmer, Porter and Scales (1970a,b) followed up the possibility of nongenetic transmission of information. They were interested in whether prenatal stress, in the form of active avoidance, could, like infantile handling, affect the behaviour of more than one subsequent generation. One group of female rats, Group 1, were given pre-mating active avoidance trials in a shuttle box. During pregnancy they were given trials, but only allowed to escape on three randomly distributed trials (Wehmer, Porter & Scales 1970b). However, like Thompson's study (1957) they were not shocked. In a second group, females received pre-mating training only. Open field behaviour of grandpups was tested with the result that grandpups of the two groups of females had increased open field activity, compared to controls. On open field latency, grandpups of Group 1 females had the shortest ones. The data support the theory that stress before or during pregnancy, like infantile handling, can influence the behaviour of individuals two generations away.

The mechanism responsible for the transmission of information is not known, but a few ideas have been put forward. Ressler (1966) suggests

offspring behaviour may be affected by changes in quality or quantity of milk. Milkovic and Milkovic (1966) present evidence that the foetal adrenal pituitary axis is modified by maternal physiological states, produced by environmental interaction. For example, adrenalectomy of the mother (rat) was followed by foetal adrenal hypertrophy. They hypothesize that adrenal hypertrophy was caused by ACTH secretion from the foetal pituitary. Foetal adrenal hypertrophy is associated with a shorter than normal postnatal stress non-responsive period. In this way, it enables the organism to react earlier and protectively to stress (Wehmer, Porter and Scales 1970b). This method could account for transmission across one generation, but not two. It is possible to envisage that causes of physiological/biochemical change in a female animal which alters the pituitary adrenal axis of her female offspring, prenatally, by hormonal interchange across the placenta, and postnatally by her behaviour towards them, and/or milk content, could, by predisposing the offspring to fear reactions, in terms of ACTH secretion, similarly be transmitted to another generation. Here, the transmitting effects of handling and a complex preweaning environment are expected to produce different results from pre-mating or pregnancy treatments. In this way, either nonemotional or emotional behaviour could be passed on, as a result of the mentioned procedures, respectively. However, the amount or hormonal or other information that can be passed across the placental barrier is unknown.

From the foregoing it seems that prenatal and postnatal factors are significant in their contribution to offspring behaviour. In contrast, Broadhurst (1961) found little evidence for prenatal effects when the Maudsley reactive (MR) and non-reactive (MNR) strains of rats were reciprocally crossed. These results may seem surprising in view of the quantity of more recent studies showing a marked prenatal and postnatal maternal impression on offspring behaviour. However, it has already

been shown that the results of comparisons between strains in a species are doubtful and comparisons between rats and mice are even more uncertain. As regards studies on prenatal stress, I have not come across one, which like Broadhurst's, carries out a reciprocal or diallel cross between lines known to differ in emotionality based on the open field or any other situation, and tests the offspring adult behaviour without experimenter manipulation pre-mating, prenatally and postnatally. Therefore Broadhurst's findings (1961) are not comparable with many of the later studies.

Barrett (1971) summarized the main findings of the prenatal studies as follows:

1. In some mammals environmental events during pregnancy can alter the intra-uterine environment and, without obvious morphological effects, influence offspring behaviour.
2. The effects can be very wide and subtle, for example on emotional behaviour.
3. Offspring can be affected by experiences undergone by the grandmother or by the mother in infancy, before mating, or during pregnancy.
4. The extent to which the offspring are affected depends on a variety of prenatal interactions, for example with foetal genotype, stage of pregnancy and postnatal experience.

Joffe (1969) put forward the ultimate experiment controlling for all known variables. This would be to mate rodents from inbred strains in a diallel cross, with additional females receiving transplants of ova of all possible genotypes. They would be subjected to a variety of pregnancy stress and the litters delivered by caesarian section and handreared until testing. This experiment is feasible but there are difficulties and weaknesses. For example, the success of ova transplantation in terms of maternal responsiveness, is not known and hand rearing could confound by acting like the handling or stressful variables. More realistically, Archer & Blackman (1971), in a good review of prenatal stress, suggest important points for future work:

1. The strains and their behavioural characteristics must be a major variable in experimental design.
2. The responses of pregnant animals to any prenatal procedure should be specified. In this way it may be decided for any individual, how stressful the experience is.
3. Traditional measures of emotionality should be replaced by a more complete description of the animal's behaviour in a variety of situations.

In my experimental study, prenatal and postnatal maternal variables are controlled for, as recommended by Broadhurst, with no experimenter intervention until the offspring are weaned. Prenatal effects on pregnant females were not considered (which relates to point 2 above); point 1 was acknowledged as being important for any animal experiment; point 3 was accepted, especially in view of the doubtful validity of emotionality measures (c.f. Chapter Seven).

B. HOUSING EFFECTS

Experiments on the housing variable have been extensively carried out since 1959 (Winokur, Stern and Taylor). Housing refers to the way animals are caged, that is, the size of cage and number of animals per cage which are relevant issues in this thesis. It can also refer to the complexity of the cage environment.

Some human studies have reported that anxiety states and depression in human beings can result from solitary confinement or isolation (Ziskind 1958), and there is much work on children suffering maternal, social or sensory deprivation. Therefore, isolation in the rat has been presumed to be fear provoking and a series of studies have set out to show this. Some studies have used the term 'isolation stress' (e.g. Hatch, Wiberg, Balazs and Grice 1963, Weltman, Sachler, Sparber and Opert 1962, Weltman, Sachler and Sparber 1966).

Hatch, Wiberg, Balazs and Grice (1963) described rats housed

individually for three months as "nervous, aggressive, intractable." These workers (1963) found that after three months the individually housed rat had a great tendency to bite, so heavy leather gauntlets were worn to enable handling. Objective tests, that is open field and emergence (Ader and Friedman 1964, Hahn 1965, Stern, Winokur, Eisenstein, Taylor and Sly 1960), showed that isolated rats were more emotional than group housed rats. Moyer and Korn (1965) replicated these findings, using different measures. Rats were placed in individual cages for 16 weeks after weaning, and then rated on a five point scale of emotionality, for handling and startle response and in an open field and emergence test. The results confirmed the hypotheses that animals housed individually for a long period were more emotional than group housed animals. Two possible explanations are put forward by Stern, et al. (1960). One idea is that individually housed animals have restricted open field ambulation because of limited exploration in the home cage. This idea assumes that an individually housed animal is in a much smaller cage than the group housed ones; but what would happen if the cages were the same size so that exploratory possibilities were equal? The second idea is that the greater variety of sensory-motor experiences group housed animals receive, the greater the 'gentling' effect.

However Stern, et al. (1960) and Ader (1965) have shown that immobilization produces more gastric erosions in group housed rats than individually housed rats. The second hypothesis of Stern and his colleagues cannot account for this finding, so Moyer and Korn (1965) proposed an elaborated version of the first hypothesis. That is, immobilization by restraint is a situation which has greater similarity to an isolated subject's previous experiences, so similarity of the housing situation to the test situation may be a determining factor in an animal's response. Following this reasoning, it could be argued that placement alone in an open field is less disturbing for an isolated animal

used to solitary experiences, than for the group housed animal which is facing a greater change in its environment. Yet, most open field data are taken as indicative of less emotionality in group housed animals.

In 1956 Lubow & Marcuse suggested stress was a function of the unfamiliarity of the situation in which the animal was placed. They tested rats' response to auditory stimulation, individually or with their mother in an experimental cage, in the form of a convulsion or substitute behaviour. They assumed substitute behaviour was a response to a stressful situation, although there is no conclusive evidence on the significance of displacement activity. Presence of the mother did not alter the incidence of convulsive behaviour but it reduced substitute behaviour. They assumed presence of the mother in an unfamiliar situation reduced stress and hence responses associated with it.

Morrison and Thatcher (1969) went a step further and considered differential group housing in relation to placement in a testing situation in pairs. Morrison and Hill (1967) had previously shown by means of open field tests that animals tested in groups were less emotional than those tested individually. In the Morrison and Thatcher study (1969) the housing consisted of placing rats in populations of 1, 4, 16, or 32. The results showed that rats housed one or four per cage were described as less emotional in the open field when tested in pairs. The opposite was true for those housed in groups of 16 or 32, so that these subjects were less emotional when tested individually. This strange effect cannot be explained, but it exemplifies the complexity of the housing and emotionality problem.

There is conflicting evidence on the effect of housing on activity, emotionality, learning tasks and aggression. In rats and mice workers have shown group housing led to greater locomotor activity, for example, Stern, Winokur, Eisenstein, Taylor and Sly (1960), Thiessen (1963, 1964b), who favour the idea that the increased activity implies decreased

emotionality. Zimbardo and Montgomery (1957) reported greater activity for isolated rats and Bovard & Newton (1956) found grouped rats defecated and vocalized more during transportation. For mice the results are similarly controversial (Essman 1966). Essman considered a major factor responsible for these inconsistent results was that differential housing had been introduced at different ages, ranging from immediately postweaning to adulthood and different measures had been used to measure motor activity. The purpose of Essman's study was to investigate the development of activity differences in mice raised alone or in groups of 20 immediately after weaning. From 22 days of age their activity was measured for 22 days in an activity box. The results showed that isolated mice had greater activity over the 22 days. The difference in activity between isolated and grouped mice was revealed three days after testing began. Isolated mice tended to maintain their activity level whereas grouped mice began to show a decrease. Essman theorizes that either condition may be stressful and that activity differences may reflect the effect of stress. Isolation results in reduced sensory and social stimulation and could be regarded as stressful or groups of 20 may lead to crowding, competition and fighting which may be equally stressful. Therefore, Essman is considering the effect of two types of housing, namely, isolation and overcrowding on the development of activity differences. In the future workers should try to separate the interacting variables of population density, social stimulation, aggression and competition.

Archer (1969) carried out a considerably more controlled study on rats, investigating the effect of duration of housing, sex of the animals and the effect of different group numbers on subsequent open field performance. In the first experiment females from the age of four weeks were isolated for six weeks and then placed in cages, either on their own or in groups of three or eight. Similar cages were used for the isolated rats and the

groups of three. After two weeks they were tested in the open field and activity scores for the isolates were smaller than for grouped rats, but the difference was not significant. Therefore differential housing for two weeks in adulthood was not long enough to show up open field differences. However, the question remains as to whether differential housing could result in varied open field behaviour if introduced for two weeks only, immediately postweaning.

Archer's second experiment (1969) assigned females at the age of four weeks to one of these conditions: 1. isolation; 2. groups of three; 3. groups of five; 4. groups of eight. After 20 weeks they were observed in the open field. Males were treated in the same way. The results for the females showed isolated rats had lower activity scores in the open field than the grouped ones, although there were no significant differences between the groups. These females were ascribed housing at four weeks which was presumably near weaning time. The different results of isolated and grouped animals may have been apparent much earlier than 20 weeks later. For males, however, isolated and grouped rats did not differ, and Archer tentatively suggested that this may be related to differences in social behaviour between males and females. What would happen if males and females were randomly mixed in groups?

Thiessen (1964a) reviewed the effect of housing on aggression and concluded that generally increased aggression resulted from increased population size. From Thiessen's report (1964a) it seems that too often crowding is confused with group living. It is possible that isolation and crowding are extreme situations, even for domesticated laboratory animals, both of which could result in altered behaviour, compared to animals reared in small groups.

Group housing has been found to affect learning performance, for example, Marx (1956) and Dolger (1954). Griffiths (1960) found that group housed rats were better at learning a shuttle box escape response

than isolated ones and hypothesized that isolation is a stressful experience which activates the pituitary adrenal system, resulting in the rats' desensitization to pain from electric shock and hence an increase in escape threshold.

Physiological findings for animals in group or solitary housing seem less conflicting. Weltman, Sachler & Sparber (1966) carried out a comprehensive study of the metabolic and endocrinological alterations due to isolation, in female mice. Isolation, the authors report, was not complete because although partitions were placed at the sides of each cage to prevent vision of adjacent cages, the front was unobstructed. Control females were housed in pairs. Body weight, food consumption, oxygen consumption, locomotor activity, leucocyte and eosinophil counts were obtained regularly in the 16 week observation period prior to death. Significant differences in the measures were found between the isolated and control mice. Increases in food consumption in the isolates coupled with increased faecal weights were found. Weltman, Sachler & Sparber did not say how food intake was measured, but there were no significant increases in body weight in the isolated mice, which coupled with increased oxygen consumption, support the hypothesis that isolated animals have a higher metabolic rate. Investigation of thyroid function shows hyperthyroidism towards the terminal weeks, but neither state was accompanied by respective decrease or increase in body weight.

Increased adrenocortical function was deduced from decreased leucocyte and eosinophil blood corpuscle counts, and also from the increased weights for the adrenal gland and reduced weight in the thymus. These changes coincide with those occurring in Selye's adaptation syndrome and Thiessen (1964a) reviewed thoroughly work on adrenal cortical response to isolation and crowding, in several animal species. Hatch, Wiberg, Zawidzka, Cann, Airth & Grice (1965) showed similar findings for rats and suggested this was symptomatic of a hypercortical state in the isolated rat. This was more pronounced in the females which showed higher plasma corticoid

levels, greater adrenal cortical response to ACTH, increased adrenal weights and cortical widths.

Some inconclusive work has been done on housing in relation to the formation of gastric ulcers. Essman (1966) indicated that isolated mice were more susceptible to starvation induced gastric ulcers. Weltman and his colleagues (1962,¹⁹66) have shown that isolated animals consume more food than group housed animals. In view of the importance of food consumption in the formation of gastric ulcers, (discussed later) it is possible that deprivation of food is more stressful for the isolated animals, which consequently develop ulcers. On the other hand, among rats subjected to restraint stress (Hahn 1965), the isolated animals show more resistance in terms of ulcer formation, than group housed animals. This is thought to be the case because group housed individuals, used to a larger cage and greater exploratory possibilities, find immobilization more stressful than isolated ones.

The studies by Essman & Hahn are good examples of the diversity of variables incorporated in the housing literature: species, strain, sex, age at which differential housing is introduced, duration, number of animals per group, size of cage, objects in the cage, amount of food and water, and their accessibility - these and measures of behavioural and physiological effects must be consistently controlled for if any conclusions are to be derived from the many studies. The two experiments also exemplify the circular use of the term 'stress'. A situation, designed as stressful, for example, starvation results in ulcer formation in isolated mice. Therefore, ulcers must be indicants of stress. Another situation, immobilization, results in ulcer formation in group housed rats, therefore it must be stressful, and reasons for this are being sought. It seems likely that an isolated mouse develops ulcers in response to one kind of situation, whereas a grouped rat develops them in another. Weltman, Sachler, Sparber & Opert (1962), and Weltman,

Sachler & Sparber (1966) have extrapolated from clinical studies in man which tend to show isolation can lead to mental illness, thus presuming a similar effect occurs in animals. From the foregoing it should be clear that generalizations about housing effects cannot be made over sexes, strains or species, but it can be concluded that they affect the kind of behaviour I am interested in, and this thesis attempts to compare hamsters differentially housed, alone or in small groups for $2\frac{1}{2}$ weeks postweaning, on all recorded measures.

Seitz (1954) was one of the first researchers to test the theory that infantile experiences can affect an organism throughout its life. He tested the effects of litter size during infancy on adult behaviour in the albino rat. His findings generally showed large litter rats to be more emotional in adulthood on a variety of measures than rats from small litters. Priestnall (1970) has replicated some of Seitz's findings with mice. He found females rearing smaller litters attended their young more often. Pups reared in smaller litters grew faster and were heavier at weaning. In a modified open field animals reared in larger litters were more emotional. Priestnall felt it may be possible to account for the differences in smaller and larger litters' responses by the different maternal stimulation the young received. In a later study, Priestnall (1973) assigned mice at weaning to isolated living conditions or to a bisexual group of ten to twelve animals. When tested in a modified open field, isolated mice showed more activity and less defecation. This conflicted with other studies showing isolates were more emotional, and less active, in the open field (Stern, Winokur, Eisenstein, Taylor & Sly 1960), but it must be repeated that studies which use different species, strains, rearing conditions and behavioural tests are not strictly comparable.

Denenberg & Rosenberg (1968), Denenberg & Whimbey (1968), Denenberg (1969a) have shown an interaction of maternal emotionality

with preweaning and postweaning housing conditions (that is, maternity cage or free environment) on offspring reactivity. It is only one step from here to assume that litter size effects, possibly mediated by the mother, interact with postweaning isolation or group housing.

The need to control housing conditions and litter size has been shown. In view of the importance of housing conditions and litter size, it seems that genotypic consistency in the litter should also be checked, that is, sibling effects, in terms of number, genotype and sex. In the main study of this project, these factors are presumed to be randomly distributed in any one litter and are in this way controlled.

[NOTE. My preferred use of the term 'stress' was given in Chapter Two. However, the reader will note that it is applied somewhat differently in this chapter, in reference to studies carried out by other researchers who have used it primarily to describe prenatal treatments. In discussing their experiments, I have, of necessity, retained their usage of the term in the interest of accuracy of reporting their work.]

CHAPTER SIX

THE INFLUENCE OF STRESS ON GASTRIC ULCERATION AND PARASITIC INFECTION

A. GASTRIC ULCER FORMATION

An incidental observation in 1969 arising from dissection of a piebald hamster, led to the possibility of spontaneous (that which is not experimentally induced), gastric ulcer formation in this animal. Therefore, at the end of the series of experiments to be reported, every hamster was killed and dissected for notification of stomach ulceration. Any animals that died before or during experimentation were also examined for ulcers.

As ulceration is thought to be associated with aspects of emotional behaviour, its incidence and extent could be significant in a project attempting to measure the same aspects of behaviour, and a review of some of the animal work on ulcer formation seems fitting.

Ulceration develops uniformly in the rumen, less often in the antrum and infrequently in the body (corpus) of the stomach. It appears when unbuffered gastric juice is present in the stomach for a sufficient length of time (Shay, Komarov, Fels, Meranze, Gruenstein and Siplet 1945).

Ulcers are not known to occur spontaneously in domestic animals, except in pigs, when they are transported, (Chertok and Fontaine 1963). However, ulcers have been experimentally produced in two ways. Sawrey and Weisz (1956) first introduced the conflict method. Hooded rats were deprived of food and water for 47 hours and placed in a box with food at one end and water at the other. Every time a rat approached food or water it received a shock, which was supposed to induce conflict. They lived in the box for 30 days and every 48 hours the rats were able to feed and drink freely for one hour. A control group, food and water deprived for 47 hours, were placed in a similar box for 30 days, but did not receive electric shock on approaching food and water. In the

experimental group, many animals developed ulcers, compared to none in the control group. A second experiment was needed to separate the relative contributions of shock, hunger, thirst and conflict. A greater number of ulcers were found in animals subjected to conflict, hunger, thirst and shock, compared to those receiving only hunger, thirst and shock. The authors concluded that conflict contributed to ulcer formation, but that hunger and shock also made significant contributions. Sawrey, Conger and Turrell (1956) have posed questions that still form the basis of much research on ulcers. They questioned how:

1. Strain and sex differences affected ulcer susceptibility of rats.
2. Pre-experimental emotional differences within strains related to ulcer susceptibility.
3. Early life social experiences and the present experimental situation affected susceptibility.

The second method that has been used to induce gastric ulcers is restraint or immobilization (Hanson 1963). This technique involves keeping the animal in one position for a long period such as 24 hours. Hanson (1963) described a plain wire screen envelope fastened tightly around the animal as a method that is "quick, cheap and reliably produces gastric pathology in the rat."

Strain and Sex Differences in Ulcer Susceptibility in Rats

Sawrey and Long (1962), using the conflict method, induced gastric ulceration in four rat strains, Long Evans, Sprague-Dawley, Wistar and Nebraska Hooded. They found that Wistar females were more resistant to ulceration than females of any other strain and that females were mostly more resistant than males. Ader, Beels and Tatum (1960), using the restraint technique to induce ulcers found that Wistar females were more susceptible than Sprague-Dawley females and that females were less resistant than males. These conflicting results point to several factors that should be controlled for:

1. Members of a strain of any name, even if obtained from the same supplier may not be genetically identical, so the experimenter should ascertain the exact genotype he is using before making comparisons.
2. Procedure of inducing ulcers should be the same, as it is possible restraint is more stressful to some strains and females, and conflict less so and vice-versa.
3. Age of testing should be controlled for. Ader, Beels & Tatum restrained their rats at 90 days, whereas Sawrey and Long placed theirs in the conflict situation at 125 days.

Sines (1959) was the first worker to select rats for incidence of stomach lesions. He immobilized rats, noted ulceration and allowed the animals to recover and undergo breeding. He found 89 per cent of the F2 generation of lesion susceptible animals, showed ulcers following restraint, which was a significant increase over the F1 generation. He also found females had a higher occurrence and severity of ulcers, but this point may be related to: 1. Sawrey and Long's suggestion (1962) that there were sex differences in ulcer incidence after restraint and that many females would be in oestrus when they were more active and restraint produced frustration which could be more disturbing for females than males; 2. Broadhurst's finding (1957a) that females were more active in the open field. If heightened activity is a female tendency it is possible that they were more reactive to restraint, compared to males, especially as Sawrey and Long (1962) have shown the reverse for conflict situations with males developing more ulcers.

Sines (1961) found that lesion susceptible animals were lighter in weight. Also selectively bred generations of lesion susceptible animals tended to show increased activity when subjected to the open field, so that a higher activity level characterized animals most susceptible to ulceration. This is also supported by the sex difference in which females show a higher lesion incidence and greater activity. In addition, lesion susceptible animals showed smaller

litter size and increased probability of offspring death during parturition. There are indications that lesion susceptible females display less maternal behaviour toward their young. If ulcers are a stress response, accompanied by fear, yet lesion susceptible animals exhibit a greater amount of open field activity - a measure usually considered to indicate low emotionality, it is difficult to reconcile the correlation of increased ulceration with high activity in these rats.

Pre-experimental Emotional Differences

Sines and McDonald (1968) estimated the heritability of ulcer susceptibility in rats to be at least 50 per cent and concluded in view of this, that genetic and environmental factors must be taken into account. They commented on great individual variation in development of ulcers in reaction to stressful events.

Pare (1966) investigated the effect of stress, comprising shock following a CS tone for 20 hours a day for 22 days, on ulcer incidence and body weight in rats judged to be emotional and non-emotional on the basis of open field behaviour. The results showed no significant strain differences in ulcer incidence, although the reactives lost more body weight. Pare concluded that if reactive rats were more susceptible to stress, they demonstrated it as a loss of body weight. But this loss in weight is related to food intake as reactives consume less food than non-reactives when subjected to stress. There is conflicting evidence on weight loss in relation to ulceration, for example Weisz (1957) found no significant difference in weight loss between rats suffering severe gastric ulceration and rats with less severe ulcers. Sines (1961), Sines, Cleeland and Adkins (1963) on the other hand, found the weight of selected lesion susceptible lines to be smaller than that of the stock they were drawn from. Lack of food consumption has been shown to be important in the formation of ulcers (Mikhail 1972), but it did not affect the Maudsley strains. Although the reactive rats showed a greater weight loss, the deprivation did not distinguish the strains in ulceration.

Mikhail and Broadhurst (1965) subjected reactive and non-reactive rats to immobilization and again found no strain differences in ulceration, but did find a negative association between ambulation and lesion incidence, that is the less active animals were more likely to develop lesions. This contradicted Sines' (1962) findings and one reason put forward for this by Mikhail and Broadhurst was that genetically different strains were used. In view of these findings Mikhail (1969) employed a new method for inducing ulcers. MR and MNR rats were put in plaster of Paris and immobilized for 24 hours. Ulcers formed mainly in the antrum and there were significantly more in the reactive line. This result is taken as demonstrating the importance of genetic factors in gastric pathology.

In contrast to the examination of ulcers arising in artificial, experimentally induced stress situations, Berruecos and Robison (1972) carried out a study of ulcers occurring 'naturally' in swine. They reported that since late 1950's the frequency of diagnosis of gastric ulcers in swine has been increasing and is now recognized as a world wide disease. The aetiology of gastric ulcers has not been established. Bacteria and fungi are contributing agents but are not thought to be primary causes. Overcrowding, time before or following parturition, social ranking, confinement and transportation have all been reported as ulcerogenic agents. Nutritional factors have also been associated with a high incidence of ulcers. Once again food is seen to play a large part in ulcer formation. Breed differences have been inconclusively found and Berruecos and Robison undertook their study to evaluate heredity in ulcer incidence. They report a high heritability (0.52), and are inclined to think selection against ulcers would be effective. In the laboratory, Sines had relative success in selection for ulceration in the rat.

Early Life Social Experiences and One Experimental Situation

Prenatal, postnatal and housing conditions have been shown to be important determinants of an animal's later behaviour. Conger, Sawrey and Turrell (1958) investigated the role of social experience in the production of gastric ulcers in hooded rats. They made three predictions: 1. Animals placed in a conflict situation alone would be less resistant to ulcers than those placed in groups; 2. Animals reared in isolation would be less resistant than those reared in groups; 3. There would be interactions between the two conditions based on the assumption that the animal would find changes in its social experiences from rearing to the test situation. Prediction 1. was confirmed, but not prediction 2. although animals reared alone tended to lose more weight. No interaction effect was found. Ader, Tatum and Beels' results (1960) contradicted these, as they found no evidence that animals undergoing conflict in pairs were more resistant to ulceration than those facing the same conflict, singly. Ader and Belfer (1962) used albino strains and once again there was the possibility that strain differences masked the pair/solitary differences. Ader, Tatum and Beels (1960) also found that early separation from the mother resulted in animals gaining less weight and showing more susceptibility to ulcers, in so far as number of ulcers per animal can be accepted as an index of susceptibility. However, as they pointed out, the effect of early separation from the mother could be confounded by such variables as the temperature of the environment or mature condition of the animal. Until these variables were controlled for, no definite theory of early maternal separation could be made. Ader (1965) has also considered handling and housing in relation to gastric ulcer susceptibility in albino rats. Interestingly, he found prenatally handled rats to be more susceptible to ulcers from immobilization than control animals. If ulcers are a stress reaction and prenatally handled animals

are less emotional, as many previously cited studies have reported, then they would be expected to show less ulcer incidence following a stressful experience than controls. Ader & Plaut (1968) examined the prenatal treatment and housing interaction. Prenatally handled and control offspring were housed individually or in groups after weaning and later given restraint stress. No differences were found between the group housed individuals but in the animals housed alone, prenatal handling reduced emotional reactivity but increased susceptibility to stomach lesions. Winokur, Stern & Taylor (1959) varied handling in albino rats in infancy (postnatally) and group reared them till 79 days, when they were immobilized for 48 hours. Those that had been handled in infancy developed fewer lesions than controls. This difference seemed to be due to handling as housing was equal. If Winokur et al. had some handled and nonhandled rats also individually housed, it could be seen if a postnatal handling interaction with housing occurred, similar to Ader & Plaut's prenatal handling/housing interaction (1968).

Early experience in relation to gastric ulcers is another area with conflicting reports and contradictory findings.

As a result of the differences found between lesion susceptible (SUS) and normal Sprague-Dawley rats (Sines 1961, Sines and Eagleton 1961) Sines, Cleeland & Adkins (1963) investigated their acquisition of a learned response. The two groups of rats were tested for reaching water in a straight maze and in a Y-maze with black-white discrimination, after water deprivation. They were also tested in a Miller-Mowrer box for shock avoidance. Sines et al. found that SUS ran the straight alley and the Y-maze more slowly than controls, although they learned the Y-maze discrimination as rapidly as the controls, and they learned how to avoid shock more quickly. These results were interpreted as consistent with the tendency of SUS to be more active in the open field. In the straight runway and Y-maze, SUS were more exploratory and took longer to reach water.

The workers also suggested that SUS greater motor activity as seen in the open field, facilitated a gross motor response, as in shock escape. They hypothesized that SUS would be poorer where avoidance was passive or involved inhibition, for example, in CER.

Importance of Warning Signals

There have been several studies concerned with the significance of a warning stimulus in ability to cope with a fearful event. This concept may be important in view of Lazarus's idea (1966) that appraisal of threat is essential for effective coping responses.

Brady, Thornton and De Fisher (1962) and Pare (1964) presented rats with a warning tone followed by shock, shock only, or neither tone nor shock. They hypothesized that rats receiving a warning tone would find shock less aversive in terms of ulcer incidence, than rats receiving shock only. The hypothesis was not confirmed. This result could be due to the fact that the rats given the warning stimulus were unable to cope with the situation. Weiss (1968) has shown that rats with yoked controls, which were able to avoid or escape shock by jumping on to a platform thereby stopping shock to themselves and their yoked control, gained more weight and developed fewer ulcers than yoked control rats. Moot, Cebulla and Crabtree (1970) confirmed these results using a different shock paradigm involving conflict. Weiss (1970) reported stress reactions were more severe following an unpredictable stressor, than one predictable by a warning signal. He found rats presented with unpredictable shock developed more stomach lesions and showed a greater rise in body temperature, a higher plasma corticosterone concentration, a greater weight loss and more defecation, than rats presented predictable shock, whether the warning signal was auditory or visual. Seligman (1968) suggested the reason for this was that when shock was indicated by a signal, absence of a signal suggested no shock and therefore safety. The animals were only experiencing emotion during

the signal, not in its absence. When shock was unpredictable the animals experienced chronic fear, which resulted in more severe stress reactions. Seligman & Meyer (1970) report that animals chose predictable in preference to unpredictable shock, and humans reported that unpredictable shock hurts more. Maybe this ties in with man's desire to 'know where he stands' in many situations and the general feeling that certainty is preferable to uncertainty.

Weiss (1970) studied the relationship between shock predictability and coping response in rats with yoked controls. Both rats received a warning signal and one animal could prevent or terminate the shock to itself and its yoked partner by jumping on to a platform. The yoked rats' responses made no difference to shock onset. The yoked animals lost more weight than their counterpart avoidance rats, and developed more ulcers. These results conflicted with Brady, Porter, Conrad & Mason's findings (1958) for monkeys. They showed 'executive' or coping monkeys developed more lesions than yoked partners. Weiss (1972) proposed a theory for how coping behaviour can affect gastro-intestinal activity which accounted for the contradictory findings. He proposed that feedback from the coping response is relevant for ulcer formation, that is, if responses did not provide appropriate feedback, ulceration would occur. Monkeys were selected for good shock avoidance and yoked to a lower performance monkey. The feedback for correct responding was low, as it did not turn off a warning signal. Feedback came entirely from internal cues, that is, shock or no shock. Ulceration has been found to be related to the number of responses made (Weiss 1972), and the feedback was insufficient to counteract the stress of such a high response level, consequently executive monkeys developed ulcers and died. On the other hand, yoked controls made few coping responses and received few shocks due to the effective coping behaviour of the executives and so survived with small ulcer incidence.

Weiss tested rats in a similar situation and confirmed Brady's et al. results. He went on to test the effects of poor versus relevant feedback by shocking rats every time they performed a previously correct response to a warning stimulus. They had control over the stressor but response produced the wrong kind of feedback, the stressor itself. These rats developed severe ulcers. However, this situation is similar to Pavlovian development of experimental neurosis. A correct response becomes an incorrect one, so this does not seem a good test of the lack of feedback hypothesis.

Cause of Ulcers

Mikhail (1972) hypothesized that food consumption is related to the development of rumenal ulcers. Pare (1965) reported loss of body weight in rats subjected to shock, coincident with lower food and water consumption. Mikhail (1972) gave rats three 48 hour sessions of 47 hours of food deprivation followed by one hour of feeding. Many rats showed rumenal ulcers. He concluded therefore, that conflict caused ulcerogenic effects, partly through reduction in food intake and partly through direct physical damage caused by shock. The relevance of this elaborate procedure to gastric pathology is not clear, as rumenal ulcers can be obtained by direct starvation. Considering antral ulcers, Mikhail did not find anxiety treatment led to ulcer formation. He is sceptical about the relationship of fear and ulceration, as conflict and conditioned avoidance are associated with sympathetic activity which suppresses gastric acidity and presumably ulcers. He also found prolonged conditioned anxiety reduced the stomach acid level in pylorus ligated rats. The parts played by the sympathetic and parasympathetic nervous systems were also used to explain the differences in ulcer susceptibility of the MR & MNR rat strains, (Mikhail 1969). The parasympathetic system tends to promote defecation, so it is suggested that the MR rats have an especially

active parasympathetic system. However, gastric motility is inhibited largely by the sympathetic system, so if this too is more active in MR rats, they should show lower ulcer incidence; ^{but} this has ^{not} been confirmed by Mikhail (1969).

There is the suggestion (Weiss and English 1960) that gastric activity can be mediated by a hormonal pathway, independent of the autonomic nervous system. Injections of ACTH or cortisone have been shown to increase gastric activity, pepsin secretion and uropepsin excretion in vagotomized dogs (Weiss and English 1960). If research on how the ACTH system can affect the stomach is followed up, it may well be difficult to accept Mikhail's suggestion that fear plays little part in ulcer formation.

On looking at the ulcer studies, with the possible exception of Weiss's (1972) work, it becomes increasingly apparent that they offer little understanding of the relationship between ulceration and behaviour in animals or man. There are few reports of spontaneous ulcers, and the need to induce ulcers artificially in animals involves all the confounding variables of species, strain, sex, rearing and experimental situation. The questions posed by Sawrey, Conger and Turrell in 1956 (and given earlier in this chapter) are still unanswered since:

1. Studies of strain and sex differences show conflicting results.
2. Pre-experimental emotional differences between strains in relation to ulcer susceptibility, as studied in the MR and MNR rats, has led to confused findings.
3. Early life social experiences affecting susceptibility have not been studied in great detail, yet a profound effect is expected in view of the early experience literature.

Most of the studies were based on only two methods of ulcer induction with a scattered array of results, reported from simple behavioural tests, and a few physiological or biochemical recordings. If an elaborate study similar to the programming of life histories in rats carried out by Denenberg and others (1968, 1969a) was

undertaken for investigating onset, duration and recovery of ulcers in any mammalian species, more understanding of this apparently fairly nonspecific disorder may be achieved.

B. STRESS-LINKED PARASITISM

This concept links parasitic infection with stress, so that the behavioural state of an animal can determine susceptibility, onset, duration and recovery from parasitic infections. In this way, a mild infection could be fatal in an animal under severe stress, yet almost inconsequential in another. As this idea may be relevant to the understanding of the low viability of the piebald hamster, it is briefly discussed.

Stress in vertebrates is followed by complex hormonal changes concurrent with less resistance to infection. This is caused partly by ACTH release from the pituitary gland and consequent adrenal output of corticosteroids, which lower the white blood cell count. Stress has been shown to be related to population density, sexual cycles, the circulatory system, antibody formation, alimentary tract, tissue damage and many other bodily reactions, but few studies have linked stress with parasitic infection, (Noble 1961).

No parasite can live in a host causing no effect, but the effect could be small enough to escape notice. This kind of parasite could have a more severe effect if its host is under stress (Sheppe & Adams 1957). These workers have shown that *Trypanosoma duttoni* injected into the house mouse had more harmful effects if the mice were partially starved and kept at a low temperature. Robinson (1961) subjected mice to electric shock, bright light and white noise before and after injecting with *Trichinella* and found enhanced parasitic population. Robinson recommended the use of stressed mice for the study of immunity. Nelson (1962) found injection of acetylsalicylic acid and ACTH broke down lambs' resistance to keds, that is, ked numbers increased and ked mortality decreased. Noble (1961) compared wild Ground squirrels with those captured and given the stress

of caging and crowding. In the time they were caged they were also subjected to a variety of stressful stimuli, although it was found that caging, without additional procedures, provided enough stress to be reflected in the parasitic density. In a second experiment, Noble (1962) investigated presence of coccidia oocytes and Trichomonas in Ground squirrels. They were placed in pairs in cages. One of each pair was subjected for two hours each day, to crowding stress, where fighting ensued. No valid conclusions could be made with regard to the coccidia parasites, but Trichomonas numbers increased in fighting animals, and when these squirrels were prevented from fighting the numbers returned to normal for field populations. Tuberculosis infection was more severe in crowded mice (Tobach & Bloch 1956).

The concept of stress-linked parasitism has important connotations for many animal studies and human medicine. The studies I have cited would have needed a much more thorough psychological approach if the relation between so called stress and disease were to be clarified. I have been unable to explore recent work in this field. Investigation of parasitic infections have the advantage that their severity can be easily diagnosed (by population number). Many infections are not fatal, and it could be informative to determine their frequency of onset and severity in relation to the environment and behaviour of the organism.

C. MEDICAL GENETICS

A brief consideration of the concept of medical genetics is placed here because it may have relevance to the increased disease susceptibility and low viability shown by piebald hamsters.

Medical genetics is a new term. Geneticists view disease as a maladjustment between an individual and his environment. Genes may play a subordinate role, in cases where aetiology is caused by chemical, physical or infective environmental agents; or a determinate role, in cases of illnesses due to genetic complications and defects (Bartalos 1968a).

Contagious and infectious diseases, although having high environmental components, are influenced by genetic variation and susceptibility. Identical twins, for example, show a great concordance for tuberculosis and poliomyelitis and a lesser one for measles and scarlet fever. It seems likely that variations in susceptibility to many contagious diseases are due to genetic variation (Osborn 1968). The essence of medical genetics is the study of the ways genes influence the interaction between an organism and its environment, which is the basis of all disease (Bartalos 1968b).

If genes and the environment predispose the organism to stress responses and the stress affects disease resistance, it seems that genes and environment may affect onset, duration and recovery from illness via the intervening variable of stress. A study of the interaction of genetics, behaviour and disease would seem to be a worthwhile research area.

CHAPTER SEVEN

STUDIES AND MEASURES OF FEAR AND EMOTIONALITY

A. INTRODUCTION

Forty years ago, C.S. Hall wrote that "no valid and objective measure of individual differences in emotionality has been devised either for animals or human beings" (Hall 1934). Hall looked for an objective measure of so-called emotionality and designed what is now widely known as the open field test. Hall's early work was reviewed by Broadhurst (1960a).

It can still be asked what emotionality is, and whether there are valid measures of it.

B. THE CONCEPT OF FEAR/EMOTIONALITY

Gray (1971a) suggested that an animal was frightened if it displayed freezing, fight or flight, accompanied by autonomic activity in a situation.

Archer (1975) agreed that fear behaviour was either immobility or escape, but that the relationship of fighting behaviour to fear was, in his opinion, a somewhat separate issue. This will be discussed later in this chapter. In a review on tests for emotionality, Archer (1973) noted that fear responses were of four types:

1. Undirected escape, for example, running following a startling stimulus.
2. Avoidance of a specific stimulus or area, for example escape following electric shock, avoidance of a shock area, orientation towards the periphery of an open field.
3. Immobility or freezing in an open field or after a startling stimulus.
4. Sympathetic activity, for example, heart rate, basal skin resistance and possibly defecation in the open field.

These agree with the intuitive assumption that although fear/emotionality are hypothetical constructs, they can be shown behaviourally by immobility or escape, with altered activity of the autonomic nervous

system. One attraction of this delineation of fear is that the behaviour can be observed easily in experiments.

C. MEASURES OF FEAR/EMOTIONALITY

Both Gray (1971a) and Archer (1973) recommended the same way of measuring emotionality, which was to develop a series of tests, based in Gray's terms (1971a) "on common sense beliefs" (p.36), about which situations could cause fearful behaviour. At present, this is the only basis on which diverse tests for emotionality can be built.

A situation could be considered fear provoking only if it induced fear behaviour as represented by immobility and escape. Other behaviour which correlated well with freezing or flight may then provide additional valid indicators of fear. Also, further behaviour patterns which correlated with these new valid indicators would also be measures of fear in this situation, and may in turn be directly or indirectly associated with immobility or escape.

Observation of the occurrence of immobility and escape behaviour in any experimental situation is the preliminary and essential step towards the validation of other behavioural measures as indicators of fear since their validity depends on the extent of their correlation with these two central fear behaviours. However it cannot be assumed that a valid measure of emotionality in one situation will be a valid measure in another, as the occurrence of fear behaviour, defined as freezing or flight, must be tested first.

Establishing validity is usually a difficult procedure because of a lack of external criteria against which to test any measure. To overcome this limitation the procedure most commonly adopted for validating measures of emotionality has been to design test situations that are a priori fear provoking and to correlate responses recorded with each other, on the assumption that they therefore measure similar aspects

of behaviour. However, it is then a conceptual leap to regard this aspect of behaviour as emotionality (as opposed to anything else), unless the occurrence of fearful behaviour, exhibited as immobility or escape, has been demonstrated.

The suitability of various situations and consequent behavioural responses as measures of emotionality, similar to ones used in my experiments, will now be discussed.

D. THE VALIDITY OF BEHAVIOURAL MEASURES OF FEAR/EMOTIONALITY

Validity of Open Field Defecation

The open field test for rodents was originally designed by Hall (1934) to measure the number of faecal boluses excreted, taken as the defecation score, in a fearful environment. Defecation was chosen as a measure of fear because on a priori grounds it seemed to be a response to frightening conditions. It was noticed that it occurred readily in rodents by laboratory workers and has been observed in man (Stouffer, Guttman, Suchman, Lazarfeld, Star and Clausen 1950).

This test, developed by Broadhurst (1957a, 1960a) has since been frequently used to measure rodent emotionality. It consists of a brightly lit arena marked off into squares and with white noise turned on. Animals are placed in the arena and their defecation score noted together with the number of lines crossed which is taken as a measure of ambulation. Occasionally other measures, such as rearing, grooming and entries to the middle squares are also recorded.

Hall (1934) suggested two validation processes. Firstly, he assumed that measures of emotionality would decrease with repeated exposure to the test situation, as familiarity was thought to reduce fear. Defecation has been shown to decrease over trials in rats (e.g. Broadhurst 1957a), although increases have been observed on occasions in mice (e.g. Nagy and Forrest 1970). Secondly, Hall thought that if

defecation was a measure of emotionality, it should occur at higher rates in the fearful experimental situation than in the home cage. This was confirmed by Candland and Campbell (1962).

Therefore, defecation in the open field occurred at a higher rate than in the home cage and diminished with repeated exposure to the field, at least in rats. However, emotional responses are not the only ones that habituate over trials and this criterion has been used to define exploratory behaviour.

A more satisfactory procedure for the validation of emotionality measures was again based on a priori grounds, and it was reasoned that increased stimulus intensity would increase emotional behaviour (Broadhurst 1957a, Ivinskis 1970, Livesey and Egger 1970, Blizard 1971a) in rats and mice. Generally, defecation was found to be higher and ambulation lower at high stimulation levels, for example, with increased noise and light in the open field, and can therefore be said to describe loosely emotional responses in rats and mice (Archer 1973).

It could also be expected that other responses dependent on autonomic activation would correlate with defecation. Candland, Pack and Matthews (1967) correlated heart rate with defecation frequency, considering differences between intertrial and intratrial heart rate. They found heart rate and defecation frequency changed consistently between and within trials but the two measures were not correlated with each other. One major difference was that defecation adapted over trials but heart rate showed no adaptation, although adaptation occurred in the course of any one trial. As reaction to a novel environment resulted in increased heart rate and defecation compared to replacement in the home cage, but without a correlation between heart rate and defecation score, Candland, Pack and Matthews (1967) suggested that use of the defecation measure on its own neglected other autonomic changes

that occurred in apparently emotional situations. Both measures showed emotional arousal but they were not comparable indices of emotional adaptation.

However, conflicting evidence on the relation between heart rate and defecation frequency does not necessarily invalidate defecation as a measure of emotionality, because as Archer (1973) pointed out, heart rate is not simply an effector system controlled by sympathetic activation. Specific sympathetically innervated reflexes often occur simultaneously although not necessarily activated by precisely the same sets of stimulus conditions and they may show different rates of habituation and different temporal response patterns. Also, when locomotion is involved, heart rate may be more closely related to this activity than to defecation, which is usually either not correlated or negatively correlated with ambulation in the rat (cf., Snowden, Bell and Henderson 1964, Candland, Pack and Matthews 1967).

Blizard (1968) directed attention to some of the limits of the defecation response, one being related to the scale of measurement. A score of zero was supposed to indicate that the animal was not emotional, but if defecation was exhibited at very high levels of arousal only, a zero score could represent considerable variation in autonomic activity. Blizard therefore tried to correlate defecation in the open field with other autonomic measures, predominantly heart rate, on a finer scale of measurement. He confirmed the results of Candland et al. (1967), and found no correlation between defecation and heart rate. However, in comparing the Maudsley reactive and non-reactive rats, significant heart rate differences between the strains were found, which were not apparent in random bred animals (Blizard 1968). This suggested that for the Maudsley rats, two autonomic measures thought to be related to emotionality showed reliable differences between strains.

It has been suggested that open field defecation may be a form

of scent marking, especially in mice. In some cases with mice, open field defecation has been found to increase rather than decrease, as is usually found for rats, over the first five to six daily trials (Nagy and Forrest 1970, Candland and Nagy 1969, Nagy and Glaser 1970) and this response pattern has been found to occur in males, but not in females (Collins 1966). This would correspond with evidence indicating that male mice more readily form territories than females (Mackintosh 1970). As males, but not female mice may tend to show territorial behaviour in a novel environment, it is not unreasonable to suggest that odor deposition, including defecation, is one step towards this (Archer, in press).

By contrast, there is little evidence from the temporal patterning and sexual dimorphism of defecation in rats to suggest that it is a marking response in this species (Archer, ¹⁹⁷⁵ ~~in press~~).

It has therefore been suggested that defecation occurs in some species in novel situations as an autonomic response to any fear evoked, to establish territorial rights or so that animals may give strange objects and areas an odor like their own with which they are familiar (Candland and Nagy 1969).

In conclusion, it would seem that defecation by rats in the open field is a reliable and valid emotionality response (Broadhurst 1957a, Gray 1971a, Ivinskis 1968, 1970) but not necessarily in mice. However, defecation has not been strictly validated by its association with freezing and escape in the open field. This test situation has seldom been designed to allow escape, as well as freezing, but it would not be difficult to incorporate a design which effectively demonstrated any association between central fear indices, escape and immobility, and defecation.

The next concern is whether other aspects of behaviour produced by rats in the same experimental situations correlate consistently with

the defecation score and can consequently also be considered fear responses.

Correlation of Defecation and other Open Field Measures

1. Ambulation

As ambulation, with defecation, is a frequently recorded score from the open field, its correlation with defecation will be discussed.

Archer (1973) reported that generally open field defecation and ambulation were negatively correlated, although the relationship could show dissociation when factors such as small sample sizes, strain differences, sex differences and early experience were included.

Ambulation was thought to be a measure of exploratory activity and it has long been accepted that fear inhibits exploration (e.g. Hinde 1966, Russell 1973), thus high defecation accompanied low ambulation and vice-versa.

There is, however, much controversy as to whether open field ambulation constitutes a form of exploration. Evidence that it does was given by Whimbey and Denenberg from a factor analytic study (1967a,b). Sixteen groups of rats were tested in a variety of experiments and two factors were found with regard to open field scores. One had significant loadings for day one ambulation and days one to five defecation and the other for days one to five ambulation. The factors were orthogonal to one another and called emotionality and activity respectively.

Other workers have been sceptical about the relationship of ambulation to fear and whether it represents a kind of exploration. Blizard (1968) reasoned that if ambulation represented exploration, so did rearing and certain stationary activities, such as head turning and sniffing. In experiments with rats in the open field, Blizard found that ambulation and defecation decreased with time. Both were highest initially. Rearing increased from trial one, then levelled out, so temporally it was negatively related to ambulation. Stationary activities also increased over trials.

If ambulation, rearing and certain stationary activities are all forms of exploratory behaviour, their different temporal patterns need to be explained. Blizard (1968) considered that the high initial ambulation was not a valid indicator of exploration and in view of its correlation with high initial defecation, more nearly represented "high drive or panic".

Welker (1957, 1959) supported the idea that high open field ambulation on trial one may indicate escape behaviour. As animals may be initially timid when faced with a novel situation, and given choice of entry do not approach and explore it until after some exposure to it (Montgomery 1955, Welker 1956), it was reasoned by Welker (1957) that animals arbitrarily placed in such a situation were possibly searching for escape. He then examined activity by rats under conditions of forced entry to a novel environment and choice of entry. The results showed there was greater activity in the forced sessions than the free ones. Activity decreased over forced sessions but showed no change during free ones.

These results are difficult to explain. Fear may be associated with the hesitant (low activity) behaviour at the beginning of the free session, but in the forced sessions the animals do not initially show the lack of activity normally correlated with emotionality. It was suggested that the animals were searching for an escape route in the forced session, hence high activity, and the subsequent decrease represented fear, as familiarity of the situation increased. From the data it would seem that ambulation could indicate avoidance of, as well as an approach to, a situation and unless the animal can make this choice the significance of ambulation cannot be established.

Hayes (1960) considered activity differences between rats forced into a novel environment on one day and free to leave it on the next.

Activity was lower in the latter situation, but that they had already had one trial could have confused the results. However, those rats most active in one test were also most active in the other and Hayes concluded that as those rats which avoided the novel environment most were the least active when confined to it, their activity was exploratory and inhibited by fear.

Halliday (1966) suggested that mild fear motivated exploration and Lester formalized Halliday's ideas and findings into a theory (1967a,b, 1968a,b,c, 1969) based on Mowrer's suggestion (1960) that although fear can lead to avoidance of situations, it can, in some circumstances, motivate exploratory behaviour. Lester proposed a U-shaped relationship between the fear aroused by a novel stimulus and the probability of approach by the animal to it, and presented several papers which purported to show this.

Russell (1973) did not feel that much of the literature supported Lester's hypothesis and that most findings could be explained by a theory which supposed that exploration was the outcome of competing tendencies to approach and to withdraw. Some researchers have been unable to support Lester's findings, for example, Aitken (1970) and Russell (1971).

In an open field validation study, Ivinskis (1970) found that although defecation decreased over trials, rearing and ambulation did not increase, as they were expected to if they signified exploration and were therefore negative indices of emotionality. Montgomery (1953) found that exploration decreased with repeated trials by satiation, so if rearing and ambulation were considered to be exploratory measures, their scores in the Ivinskis study could be explained. Ivinskis (1970) concluded that a decrease in open field behaviour could be due to lowered emotionality or a satiation of exploratory behaviour or a combination of both, but could not verify a causal relationship.

On a priori grounds, increased stimulus intensity could be expected to increase positive indices of emotionality, and this has generally been true for defecation (Broadhurst 1957a, Ivinskis 1970). However, the effect on ambulation and rearing is variable, as shown in studies by, for example, Ivinskis (1970), King (1970) and Broadhurst (1957a).

Added doubt regarding the significance of open field ambulation and rearing were given by Masur's findings (1972). Rats were divided into high and low groups, therefore emotional and non-emotional, depending on their open field defecation scores. Masur found that ambulation seemed more closely related to an animal's sex than to its emotionality. Zero defecators, whether male or female, still showed sex differences in ambulation, with females ambulating more. The negative correlation between ambulation and defecation found in many, but not all studies (reviewed by Archer 1973), can become dissociated when sex differences are also considered.

Two questions have been posed in the foregoing.

First, is ambulation a form of exploration? There are several studies which show that exploratory behaviour can occur without ambulation as in sniffing, whisker movements or head turning (for example, Bindra and Spinner 1958, Woods 1962, Woods and Davidson 1964), and also that high ambulation may be related to escape behaviour, a primary fear measure (e.g. Walker 1957, Livesey and Egger 1970). Therefore ambulation may be specifically exploratory in some cases but can represent other modes of behaviour, for example escape.

Second, is the measure of ambulation consistently related to emotionality? Freezing behaviour or immobility have been reported as animal reactions to novel environments (e.g. Bindra and Spinner 1958, Woods 1962). Denenberg (1969b) considered that the observation that many

mammals froze when exposed to novel stimuli was the logical basis for design of the open field test and described an emotional animal as one that froze and defecated in the open field. However, freezing or crouching have been shown on occasions to occur little in open field tests (e.g. Streng 1971), and escape behaviour, exemplified by high ambulation, in the alternative fear behaviour to freezing in a novel situation. The possibility that either fear reaction can occur, that is, freezing or escape, both of which invoke the extremes of ambulatory activity, renders low ambulation an unreliable measure of emotionality.

2. Other measures

Correlation of defecation with other behaviour in the open field, was firstly carried out by Hall, who thought a fearful animal would not eat in a strange environment and subsequently found a negative correlation between defecation and readiness to eat in the open field.

Archer (1973) summarized findings which correlated defecation and other open field measures. Defecation was unrelated to grooming, orientation towards the periphery, rearing and latency in studies where it was also unrelated to ambulation, and there was insufficient evidence to support a different conclusion when ambulation and defecation were related. Smith (1972) found freezing, a measure often used as a direct measure of emotionality (e.g. Denenberg 1969b), was unrelated to ambulation and negatively related to defecation in mice. This questions the validity of defecation as a measure of fear in mice, especially as it has been shown by several workers (e.g. Nagy and Forrest 1970) to increase over trials.

Grooming is commonly thought to be a positive index of emotionality (Archer 1973), that is, more grooming accompanies greater fear. Grooming was found to be higher in the Maudsley reactive, as opposed to the non-reactive rats, when placed in a novel environment (Gray, Levine

and Broadhurst 1965). If grooming is a positive measure of fear it should decrease over trials (as fear diminishes) and although Streng (1971) found it decreased over a 20 minute session, other workers have shown it to increase over trials (e.g. Bolles 1960), and this weak validation suggested that grooming is a negative index of emotionality.

Hughes (1968) found that male rats groomed more than female rats and also froze more in a novel environment, and other studies have shown males to defecate more. This correlation of grooming is evidence that increased grooming is indicative of emotionality in these circumstances.

Doyle and Yule (1959) examined grooming and freezing behaviour in rats over 12 trials and thought that emotional responses should decrease with trial. (It will be recalled that it was stated earlier that emotional responses were not the only ones which habituated over trials). These workers used one group of rats whose mothers had been subjected to stress before and during pregnancy and another as a control group. The former group showed a non-significant trend towards increased freezing. Grooming behaviour did not occur until trial seven for the control group and trial nine for the experimental group, after freezing, urination and defecation had ceased. Doyle and Yule thus concluded that grooming was not correlated with other emotionality measures. They made an interesting analogy with eating in the open field, suggesting that if this kind of behaviour was a sign of adjustment and non-emotionality, so also may be grooming. However, they were careful to point out that their results did not necessarily imply that grooming was not a measure of emotionality in some circumstances.

This is probably true for many peripheral, occasionally scored open field measures, such as rearing, grooming, latency and entry to the middle squares. That is, they may be positive or negative indices of emotionality in some test situations, but the conflicting data throw doubt

on the validity of the measures across tests, species, strains, sexes and animals from differing early environments.

Correlation of Open Field Defecation and Behaviour Considered Emotional in Other Situations

Defecation, itself, has been found to be a behavioural response in a variety of situations, designed a priori to be fearful. Parker's work, described by Hall (1941) showed high rat defecation in six situations; the open field test, a buzzer, sudden dropping, a tilting box causing the rat to slide down, swimming, and immobilization.

It was shown by Anderson (1938) that defecation and emergence correlated in the Maudsley strains of rats. The MR rats (high defecators) had a faster speed of escape to an exit than MNR rats (low defecators) and also greater response suppression in a CER situation (Gray 1971a).

But correlation of open field defecation and other measures in different tests are also conflicting. For example, Thompson (1957) showed that prenatal stress decreased open field ambulation and increased defecation, and significantly increased latency to emerge from the home cage, but Ader and Belfer (1962) found a similar treatment decreased open field ambulation although it had no effect on emergence times. Hunt and Otis (1953) found no correlation between defecation and emergence time.

Satinder (1968) found little evidence of correlation between open field measures (defecation, ambulation, urination, rearing, grooming) and escape avoidance conditioning. Wilcock and Broadhurst (1967) found that defecation was not associated with measures of avoidance learning in five inbred strains of rat, and Tobach and Schnierla (1962) could reveal few significant correlations between defecation and rate of avoidance learning in mice with different sets of early experience.

Reading (1966), studying mice reared by foster mothers of their own strain or a different one, found no correlation between open field

ambulation and defecation and escape latency in a water escape test.

Evidence from the correlations between defecation and behaviour in emergence, avoidance learning and water escape tests shows no consistent trend, so that defecation may not be a measure of fear, or the other behavioural measures may not be emotional responses, or a complex of patterns of fear behaviour may be shown over experimental situations, thus masking simple relationships between responses. This last suggestion most easily explains the conflicting findings.

Behavioural responses occurring in different fear provoking situations must be validated by their association with freezing or flight, not with defecation, whose validity as an emotionality measure, even for rats, is not absolutely certain.

Most behavioural measures of emotionality have not been subjected to this rigorous validation procedure.

Validity of Reaction to Handling as a Measure of Emotionality

Some workers have used resistance to handling as an indicator of emotionality. As a handling experiment, by its nature, allows the occurrence of freezing or flight, which in essence are fear responses, the need to validate resistance to handling as an indicator of fear is not so great as for more indirect measures.

However, reaction to handling has been correlated with other test situations purported to measure emotionality. For example, Stern, Winokur, Eisenstein, Taylor and Sly (1960) differentiated isolated and group housed rats in the open field test and in reaction to handling. The individually housed rats were considered to be more emotional in the open field, that is, defecated more, and showed greater resistance to removal from the cage. Moyer and Korn (1965) rated rats for emotionality observed in a modified open field, an emergence test and response to shotgun stimuli. These two studies, claiming a correlation between resistance

to handling and emotionality in the open field, strengthen the likelihood that defecation in the open field is a valid measure of emotionality.

Contradictory evidence was provided by Corman and Biondo (1969). Correlations between open field latency to leave the start square, ambulation and time in the centre squares, and ratings of emotionality based on reaction to handling in rats, were not significant. However this may have been because Corman and Biondo used open field measures that have not been satisfactorily validated and are not necessarily aspects of the same behaviour as are measures of reaction to handling.

With regard to vocalization (which may occur in response to handling) Richter (1954) described the wild rat as having a high pitched squeak or squeal when frightened.

Vocalization was used by Stern et al. (1960) and King (1958) as an indicator of emotionality. A human being, on hearing an animal vocalize (squeal) would tend to consider this animal to be in pain. Information concerning the relationship of vocalization to pain and fearfulness, or actual validation of vocalization as a fear response is scarce (Berryman 1974). Although many papers dealing with rodent social, sexual, aggressive, parental and play behaviour give some indication that vocalization occurred, comparatively little is known of the structure and function of acoustic behaviour and most experiments carried out have been confined to the study of ultrasounds (Berryman 1974).

The response of vocalization could be easily validated in a reaction to handling test by its association with immobility or escape, which can readily occur.

Validity of Avoidance Learning as a Measure of Emotionality

Fear can be learned (Singh 1959) and fear can disrupt learned behaviour (Estes and Skinner 1941). Avoidance learning is thought to be fear motivated, so there is much work on the relationship between emotionality and avoidance conditioning.

Positive evidence that avoidance learning is fear related can be found from studies which showed no behavioural differences between the two Maudsley lines under circumstances which logically were not expected to arouse fear, such as the problem-solving Hebb-Williams maze (Gray 1971a). However, the possibility remains that this was a characteristic of the Maudsley strains and needs to be considered in other high and low defecating rats.

Various types of avoidance learning have been considered in relation to emotionality. Active avoidance situations demand that a particular behavioural response be emitted to deter punishment. By contrast, in passive avoidance situations, inhibition of desired behaviour is required to prevent punishment. The conditioned emotional response (CER) was introduced by Estes and Skinner (1941). They trained an animal to press a lever for food or water reward in a 'Skinner box'. It was then repeatedly presented with a warning stimulus, such as a tone, followed by an electric shock in another environment. The CER would then be the suppression of lever pressing on hearing the tone subsequently in the Skinner box.

1. Active avoidance learning

Tests of this nature have been carried out on the Maudsley rats, already discriminated on defecation.

Broadhurst and Levine (1963) tested the Maudsley reactive (high defecating) and non-reactive (low defecating) rats in active avoidance and conditioned emotional responding. They discovered that the MR rats showed greater response decrement in CER, that is, learned more effectively, but that the MNR rats were significantly better at active avoidance, acquiring and executing the response more quickly. Post-hoc reasoning was used to account for these results and it was hypothesized that as the CER was acquired outside the Skinner box where lever pressing took

place, the greater emotionality of the MR rats, illustrated by freezing, would be advantageous if it encouraged reduction in behavioural responses such as lever pressing. By contrast, active avoidance learning demands a motor response; this would be impeded in the MR rats, which readily freeze, so MNR rats would perform better.

Other studies have provided inconclusive evidence regarding the relationship between defecation and active avoidance, mentioned earlier in this chapter. For example, Wilcock and Broadhurst (1967) based emotionality in open field behaviour in five inbred strains of rats and tested them on avoidance learning. They found significant strain differences, with a positive correlation between ambulation but not defecation, and number of avoidances. Strain one (of the five inbred strains) showed fast avoidances and slow escape latencies characteristic of the MNR rats, but differed from them in showing a relatively high defecation score. Similarly, strain two resembled the MR rats in showing low ambulation, low avoidance score and high avoidance latency, but differed in showing little open field defecation. Therefore, active avoidance learning did not occur in a way predictable from open field defecation or compared to MNR and MR rat defecation and avoidance behaviour.

Wilcock (1968) found no strain differences in the Maudsley rats in motor response to shock, although the MNR rats showed a higher skin resistance, implying the MR rats were more reactive. He concluded that differences in active escape learning did not depend on differences in the motor reaction to shock.

Broadhurst and Levine (1963) recommended that shock intensity should be controlled for, as it was possible an optimal shock level, without too much fear arousal, was necessary for speedy acquisition of conditioned responses.

In an experiment by Imada (1972), involving the Maudsley reactive and non-reactive and the Roman high and low avoidance rats (referred to as MR, MNR, RHA, RLA respectively), the degree of emotionality was assessed by the suppression of drinking behaviour shown after repeated presentation of an unsignalled electric shock in a drinking situation. The strains were then matched on basal emotional level (BEL) as indexed by the degree of suppression of drinking. The shock intensity was adjusted so that average suppression was equal for all four strains. It was assumed that for suppression of drinking behaviour to be equal in strains differing in emotionality, a stronger shock would be needed for a less emotional group than for a more emotional one. Conditionability was measured by the rate of recovery of drinking behaviour when unsignalled shock became signalled.

With respect to emotionality, there was an increase from the MNR strain to the RHA, with the MR and RLA rats being the most emotional. A more intense shock was required for the MNR than for the MR rats, indicating that the former strain was less emotional. The difference in shock required for equal performance by the RHA and RLA strains, if any, was not mentioned. The RLA strain was poorer at conditionability than any of the other three. Despite indications that the RLA rats were more emotional than the RHA, there were no differences in open field defecation, or in defecation during the shock experiment.

If correlation between measures of emotionality is necessary for their validation, then either or both of the methods used by Imada (response suppression and defecation) are invalid. Imada (1972) considered that his experiment indicated that defecation was an insensitive measure of emotionality and of little predictive value.

The issue is further complicated by Sines' work on ulcer susceptible rats (SUS). Sines, Cleeland and Adkins (1963) tested their selected

SUS rats, thought a priori to be more emotional, and the Sprague-Dawley rats from which they were derived, on acquisition of avoidance responses. The SUS were superior on active avoidance learning tasks but inferior, compared to controls, where inhibition of responding was demanded, as in CER. In these two types of learning situation, SUS compared to control rats were behaving as MNR rats were to MR rats. Both SUS and MR, thought to be more emotional strains, defecated more in the open field, but whereas the MR rats were less active than the MNR rats, SUS were more active than controls.

Once again, as shown by these four rat lines, activity seems more closely related to active avoidance responding than is open field defecation.

A somewhat different proposition was put forward by Denenberg and Karas (1960), which was based on a study of infantile effects. They hypothesized that an intermediate amount of emotionality was optimal for learning. They studied the effects of handling in infancy thought to be fear reducing and found that rats handled for 20 days and unhandled controls both showed poor active avoidance learning, compared to rats handled for a few days. They suggested that the two groups performed badly for different reasons. The unhandled controls were so distressed by the shock that they were wildly active in the situation, whereas handled rats were so 'casual' in their response to shock, that some even sat on the grid before escaping. The former group was too disturbed by the shock to learn the task, and the latter was not motivated enough by shock to learn. Emotionality was thought to decrease as infantile handling increased, so that as rats receiving an intermediate amount of infantile handling learned best, it seemed that some fear was essential for avoidance learning. Therefore, it was claimed that stimulation giving rise to very high or very low emotional reactivity resulted in impaired

performance, although by different processes. Levine (1969) qualified this theory as descriptive for adult behaviour in an open field or learning situation, but indicated that it did not discuss how infantile stimulation acted to produce such effects.

The extent to which this theory is defensible could be tested. If high and low defecating animals are taken as emotional and non-emotional, respectively, then both these groups would be predicted as showing poorer active avoidance learning than an intermediately defecating group.

It is clear that defecation and active avoidance behaviour are not related in a consistent direction across strains of rats and mice (Broadhurst and Levine 1963, Wilcock and Broadhurst 1967, Tobach and Schnierla 1962, Imada 1972). Active avoidance conditioning demands an active escape response which may partially explain the greater correlation between open field activity and avoidance responding that is often found, in contrast to the lower correlation shown by open field defecation and active avoidance (e.g. Sines et al. 1963, Levine and Broadhurst 1963, Broadhurst and Bignami 1965, Wilcock and Broadhurst 1967).

However, active escape is only one of the basic fear responses. The other is immobility and occurrence of this response could confound any judgement of emotionality level based on active avoidance behaviour. The primary step of observing and recording the two fear responses, escape and immobility, in an active avoidance situation may indicate the usefulness of avoidance responding as a general indicator of emotionality. At the present time, it seems likely that for some animals in some conditions active avoidance may be a measure of degree of emotionality but not generally so across species, strains, sexes and regarding animals with differing early environments.

2. Passive avoidance learning

To turn to passive avoidance learning, Mowrer (1960) hypothesized that if fear generated by a particular stimulus was sufficiently great, further responding would be inhibited, which is necessary for effective passive avoidance learning.

Carran (1967) tested this hypothesis, reasoning that strain differences in emotionality should produce similar strain differences in passive avoidance. He chose two mice strains, C3H/HeJ, more fearful and predicted to be better at passive avoidance, and C58/J, supposed to be less fearful. Skin resistance was used as the index of fear, which was induced throughout a two minute period by foot shock. C3H/HeJ mice remained fearful throughout the time whereas C58/J mice quickly lost their fear, that is, showed heightened skin resistance. Mice were deprived of food and trained to remove a cover from a bin to obtain food reward. Then they were given air-puffs every time they approached the bin. The number of air-puffs each mouse received was recorded. The time to open the bin was the same but the non-fearful C58/J were faster at approaching it and the C3H/HeJ mice received fewer puffs (because they had learned). Carran repeated and confirmed the results of this experiment using water deprivation and water reward, and offered this experiment as some support for Mowrer's theory.

Carran (1967) considered skin resistance to be a valid measure of fear, and if it is, his findings provide some evidence that fear enhances passive avoidance learning. More studies, using other indices of fear are needed to confirm the generality of Carran's finding.

Riccio, Rohrbaugh and Hodges (1968) considered maturational variables in relation to avoidance learning. Rats were given a single training trial. Each was placed in a white compartment and after ten seconds a guillotine door was raised and their latency to pass through

the doorway recorded. When the rat had crossed, the door was lowered and a one second shock was administered. The rat was removed for a retention interval and replaced in the white compartment. Its latency to move into the black compartment was taken as a measure of its learned passive avoidance. Learning markedly improved with age, although retention over a 24 hour interval was complete for all groups. By contrast active avoidance did not significantly differ with age. The workers suggested that response inhibition was selectively influenced by maturation.

Conclusions. Passive avoidance situations, like active ones, must be observed for the occurrence of freezing and escape behaviour. Response suppression, compatible with immobility, is demanded in passive avoidance situations. If escape is the common response to fearful situations for any one animal, passive avoidance learning would be impaired but the animal may in fact be just as fearful as one which, freezing in the situation, showed good passive avoidance. Alternatively, the animal inclined to escape would be expected to show good active avoidance learning but would not necessarily be more fearful in this situation than an animal showing freezing behaviour. Therefore, in active and passive avoidance situations, effective learning may relate to expression of emotionality, but not necessarily.

The Relationship of Fear to Aggression

In a review on population density and behaviour, Thiessen (1964a) suggested that many studies indicated that increased aggression and emotionality were associated with increased population density (e.g. Barnett 1963, Rosen 1961, Ross, Scott, Cherner and Denenberg 1960, Calhoun 1952, Denenberg 1962) although there were exceptions among strains and species.

Christian (1959) found no correlation between number of scars shown by grouped mice and the increase in adrenal weight resulting from the grouping and which was thought to be a measure of emotionality. Fighting was mutual, but increased adrenal weight was greater in the subordinate animal. Davis and Christian (1957) showed that when mice were marked from most dominant to least dominant in 14 populations, adrenal weight was least in the dominant animals and greatest in the most subordinate mice, while animals with intermediate ranks had intermediate weights. Davis and Christian suggested that the reason for this was that the subordinate mice were subjected to more stressful stimuli.

Other workers, for example Welch and Welch (1965) have suggested that emotionality, rated by open field performance, may be correlated with aggression as isolated mice displayed both these behaviours to a greater extent than non-isolated individuals. Geller, Yuwiler and Zolman (1965) found isolated mice were more aggressive and had higher levels of brain norepinephrine and heavier adrenal glands, both considered to be indicators of emotionality, than non-isolates.

There is conflict between the primate and rodent isolation data in relation to aggression. Workers in both primate and rat studies largely agree that isolation in young animals results in high fear, but whereas rat studies have shown that isolated individuals are more aggressive (e.g. Welch and Welch 1965, Geller et al. 1965) than group raised animals, primate studies, such as Harlow's work with monkeys, have shown that isolated monkeys, apparently in great fear, never threatened companions when placed with them, despite frequent threat displays.

There seem to be few generalizations that can be made across species and the differences in aggressive behaviour resulting from solitary rearing in the two species are not altogether unexpected, especially as many factors are involved, such as age of separation from the mother to

isolation, length of isolation and species-specific social behaviour.

The importance of genetic and maternal effects in relation to aggressive responding has been studied. For example, Lagerspetz and Wuorinen (1965) carried out a cross-fostering experiment with mice selectively bred for aggressiveness and non-aggressiveness, to determine how much of their antagonistic behaviour is due to genetic variables and how much to maternal care. Maternal behaviour was observed for ten days preweaning. After weaning the males were reared in isolation and tested for aggression. The results showed that offspring of the aggressive strain displayed more antagonistic behaviour than the offspring of the non-aggressive strain, regardless of cross-fostering. Mice reared by their own mothers were more aggressive than cross-fostered offspring. Lagerspetz and Wuorinen (1965) suggested that this showed maternal behaviour could modify aggressiveness but could not mask the genetically predetermined variation. It could be asked at this point whether anyone has considered cross-fostering alone as a variable in aggressiveness.

Southwick (1972) carried out a study similar to Lagerspetz and Wuorinen's. He chose two mice strains differing in aggressiveness. All mice were reared by their own mother, fostered to a mother of their own strain or cross-fostered to a mother of the other strain. At weaning, the animals were isolated and the males tested for aggressiveness at 43 days. They were placed in groups for seven days and frequent observations of their social interactions were made. Significant strain differences were found with the aggressive strain scoring higher than the non-aggressive one. The results also indicated that cross-fostering the passive strain to the aggressive strain resulted in their increased aggression but the reverse did not hold, that is, the aggressive strain cross-fostered to the passive strain did not show less aggression.

Neither of these studies considered females. Despite female mice apparently showing little aggression (Lagerspetz and Wuorinen 1965), the nature of their behaviour could be instructive. Cross-fostering, as a procedure for studying strain differences in maternal effects, should be supplemented by reciprocal crosses.

Hamsters have been used for studying intraspecific aggression (Lawlor 1963, Payne and Swanson 1970, 1971, 1972). Lawlor (1963) compared social dominance of the sexes in the two strains of golden hamster. Having established that dominance hierarchies were formed in these rodents, she found that females showed more dominant behaviour than males, and a higher general level of activity. She also found strain differences.

Payne and Swanson (1970) felt that the golden hamster differed from other laboratory rodents, as both sexes were aggressive, with the females being larger than and dominant to the males. They investigated social encounters between pairs of hamsters, of the same or opposite sex. Behaviour was categorized and scored. There was no sex difference in any one component, implying the sexes interacted similarly. Payne and Swanson (1970) therefore suggested more controversially, that the females were not "naturally more aggressive than males", but they conceded that females were dominant to males. They also found a positive correlation between body weight and aggressive success in both sexes. This has also been found in other rodents. Mutual investigation was low and usually the animal which investigated more, became dominant. When males were paired with females, they first attempted to mount the females. When in oestrus the female responded with lordosis but on other days they usually won the encounter. Murphy (1973) noticed the power of female vaginal discharge to inhibit male aggressiveness. He showed the discharge did not give the male information regarding the female's receptive state and

Payne and Swanson (1970) suggested it may be responsible for enabling females to become dominant to males.

To return to discussion of the relationship between fear and aggression, the problem was partly tackled by Moyer (1968) who classified aggression and reviewed its physiological bases.

He tentatively proposed the following classes of aggression: territorial, maternal, instrumental, predatory, intermale, irritable and fear induced. Moyer indicated that fear induced aggression was preceded by attempts to escape and this distinguished it from all other types of aggression. If an animal was unable to escape, a basic fear reaction, it attacked the antagonist.

Irritable aggression can be induced by a variety of stimuli and although it is distinguishable from fear induced aggression, in that there are no escape attempts, in much of the literature the type of aggression elicited cannot be determined because it is unknown whether the animal would have escaped if it had had the opportunity (Moyer 1968).

Pain and the resulting fear are likely to result in aggression. If two rats are caged together, a shock to the feet will elicit fighting between them and this applies to many other animals (Gray 1971a). Gray (1971a) cited three experiments showing the relationship between frustration and aggression. In one, for example, pigeons were trained to obtain food by pecking a key. Another pigeon was restrained in the chamber. When the pecking pigeon was no longer rewarded for its responses, it attacked the restrained pigeon. Gray suggested that fear was equivalent to frustration in the sense that punishment had the same effects on an organism as frustrative nonreward. In his view both fear and frustration depended on activation of the same physiological system in the midbrain and stop maladaptive behaviour, either because it leads to punishment or because it no longer leads to reward (Gray 1971a).

However, frustration is a factor commonly thought to induce irritable aggression (Moyer 1968), yet it is clear that fear and frustration in some cases may be linked and confused, so that fear induced and irritable aggression may not always be distinguishable.

Similar to Moyer's fear-induced aggression category is Archer's suggestion (personal communication) that almost any situation could lead to either fear or aggression. Fear would be displayed by immobility or escape and aggression by attack. If, for an animal that would normally show fear in a situation, escape is prevented and immobility hastens disaster, that animal attacks. This would seem to be fear-induced aggression, preceded by either or both fear responses, escape and/or immobility.

Aggression in these circumstances would be a well validated emotionality measure.

Although there is some early work implying that timidity was correlated with lack of aggression in a conflict situation (e.g. Arnold 1944) there seem few, more contemporary studies correlating aggressive responding with the fear reactions, escape and freezing, or with indirect measures of emotionality, such as defecation.

It remains largely a hypothetical a priori assumption that fearfulness is associated with low aggression and subordination, but even this may be species, sex and circumstance specific.

In conclusion, attack on a conspecific or a predator, by any animal, preceded by escape attempts or immobility, could be considered a fear reaction. In the aggressive experiment to be reported, escape and immobility were not recorded although other behaviour occurring in the encounter which may be linked to these was noted. Agonistic behaviour or lack of it, in conjunction with other behaviour in the situation, was then regarded in terms of emotionality.

E. THE VALIDITY OF NONBEHAVIOURAL MEASURES OF FEAR/EMOTIONALITY

The validity of nonbehavioural measures of emotionality, similar to the ones I used, will now be discussed.

Body Weight

Loss of body weight has, on occasions, been associated with emotional behaviour. Weiss (1968), for example, in a study relating occurrence of stomach lesions to inability to cope with a stressful situation, used weight loss as his main indicator of emotionality and considered it to be a sensitive measure.

Pare (1966) also used weight loss as an indicator of rat susceptibility to induced chronic environmental stimulation which consisted of a four second 2000cps tone followed immediately by a 1.5 second two milliamp shock, presented on average every four minutes. Rats were ranked for emotionality from an open field test and half of them subjected to the conditioning procedure. He found that rats rated emotional lost more weight in response to the situation than those labelled non-emotional, so this study represented some validation of weight loss as an emotionality measure.

A measure of body weight is commonly used in studies evaluating the effects of various drugs, herbicides, pesticides and other substances on animals (own observations). An effect is considered detrimental if treated animals show a lower average body weight than controls.

Males of most species are larger and heavier than females and this has been shown to be related mainly to hormonal effects (Bell and Zucker 1971). The weight difference, by itself, suggests no related behavioural effects. Similarly, animals showing lowered body weights may behaviourally be no different, although a pituitary-somatotrophic hormonal relationship having repercussions for the other hormonal systems, is a possibility.

Few animal studies have described any relation between body weight and aspects of behaviour, although the Maudsley reactive (emotional) rats have been demonstrated to be heavier than non-reactives.

In my study, there will be a search for consistent genotype differences in body weight, as well as in behaviour.

Adrenocortical Function

Now there is considerable study of the causative and feedback mechanisms between areas of the brain and organs of the body. It has been established that the hypothalamus, continuously receiving nerve impulses, regulates the release of pituitary hormones, which in conjunction with the autonomic nervous system, affect the internal environment of the bodily cells and many aspects of emotional behaviour (Feuer 1969).

Feuer (1969) therefore proposed the hypothesis that animals displaying genetically determined differences in the hypothalamus and pituitary gland, reflected in different types of emotional behaviour, may also show the differences in activity of the peripheral hormonal systems. Some evidence for this viewpoint has been reported. For example, Brown-Grant, Harris and Reichlin (1954) found that restraint or sudden changes in ambient illumination, considered stressful, caused inhibition of thyroid activity in rabbits, and Harris and Woods (1958) showed that thyroid activity could be increased by electrical stimulation of the hypothalamus and pituitary glands.

Adrenal weight is thought to be a measure of ACTH activity in response to acute or chronic stress. Christian (1963) described adrenal weights as the "best available index of adrenocortical activity in many studies" (p.245). Many measures are labile and reflect rapid changes in adrenal function of the moment, such as, changes in adrenal ascorbic acid, lipids, cholesterol, the production of plasma corticosteroids or circulating

eosinophils, so that adrenal weight is more useful for the assessment of longer term changes.

Selye (1946) described enlargement of the adrenal cortex as a response by rats to the injection of toxins and this has since been considered a stress reaction.

There is some evidence that increased adrenal weight is associated with psychological stressful stimulation. Eranko and Muittari (1957) found that rats suffering from induced experimental neurosis, showed significantly increased adrenal weights compared to controls and concluded that the adrenal glands reacted to very slight stimuli. Of course, it is possible that so-called experimental neurosis may affect adrenal weight more reliably than other types of fear provoking situations.

Yeakel and Rhoades (1941) searching for correlations between body weight, adrenal, thyroid and pituitary gland weight in rats labelled emotional and non-emotional by C. S. Hall, found the thyroid gland alone showed significant weight differences between the strains. Male emotional rats had heavier adrenals than non-emotional males but adrenals in the females showed no correlation with emotionality.

Feuer (1963) found reactives had larger adrenals than non-reactive rats, and followed up this study by showing that reactive rats had a high corticosteroid level and an elevated ACTH level (Feuer 1969). This author suggested that the increased adrenal activity of the reactive rats was associated with a variety of emotional conditions, and reflects a subtle reaction by the animals, although his grounds for this statement are not clear.

Pare (1966) subjected rats to severe stress (described under body weight, pg. 95) and found that they showed greater adrenal hypertrophy than those not subjected to the stimulation. However, within the stressed

and unstressed groups, rats rated as emotional and non-emotional from open field responsiveness could not be differentiated on adrenal hypertrophy. This is an indication that open field defecation and enlarged adrenal glands do not necessarily reflect emotionality equally in animals.

Findings that give rise to scepticism that adrenal weight and other measures of adrenal activity are indicators of emotionality are provided by Ader, Friedman and Grota (1967) and Ader (1969). A reaction-to-handling experiment and open field test were carried out (Ader et al. 1967), using two strains of rats. The hooded strain was described as more emotional, based on their greater tendency to show a startle response and greater vocalization and resistance to being picked up, than the albino strain. However, open field defecation did not differentiate the strains, although ambulation was higher in the hooded line, and the authors suggested that in view of the results in the reaction to handling test, it seemed reasonable to question the validity of open field scores as measures of emotionality. As the reaction to handling experiment incorporated measures of startle and resistance to being picked up (escape), which are central measures of fear, it would seem to be a more valid indicator of emotionality in this case, than the open field scores.

The strains did not differ in plasma or adrenal corticosterone taken soon after each experiment but the hooded strain showed a positive correlation between adrenal weight and open field activity. The larger adrenals of the hooded rats were consistent with the hypothesis that they were more emotional, as judged by the reaction to handling test. However, their increased open field activity, often considered indicative of lowered emotionality, confused any interpretation of the significance of adrenal weight.

Ader et al. (1967) carried out a separate analysis of the adrenal weights of albino and hooded rats that did and did not display behaviours

recorded in the reaction-to-handling experiment. They observed no significant differences and concluded that their data provided no evidence of a relationship between emotionality as measured by the open field and reaction to handling, and adrenocortical activity given by adrenal weight or plasma and adrenal corticosterone.

It would seem that a relationship between adrenocortical activity and emotionality displayed behaviourally, cannot be discovered by considering one or two adrenal measures in response to one or two behavioural tests. For example, Christian and Davis (1956) found that adrenal weights of rats related positively to population density; yet contrary to expectations, adrenalectomized rats were more emotional in the open field and the emotional features for differentiating two strains of mice were not affected by cortisone or adrenalectomy (Pare and Cullen 1965).

Thiessen and Nealey (1962) tested five strains of mice for eosinophil level (related to adrenocortical activity), adrenal weight and for time taken to pass from one compartment of a box to another through a hole in the wall. These measures differentiated the strains although they did not show concordance, that is, the rank order of strains on any one measure did not correspond closely to the rank order on any other measure. Therefore, strain differences in adrenal response may depend upon the particular measure utilized.

Pare and Cullen (1965) tried to correlate open field behaviours and adrenal weight and adrenal ascorbic acid (AAA) in the rat. Defecation was not correlated with adrenal responses although there was a positive correlation between latency in the open field test and adrenal weight. These researchers interpreted this finding in terms of the behavioural differences shown by emotional and non-emotional rats in escape avoidance and CER situations, in some studies. Pare and Cullen (1965) suggested that if emotional rats acquire the CER faster, but show impaired

escape avoidance due to freezing (Broadhurst and Levine 1963), this was reflected in the correlation between latency and adrenal weight they found.

In the past, ideas regarding the relationship between autonomic activity and emotional behaviour have been oversimplified (Pare and Cullen 1965).

Measures of adrenocortical activity, like all other behavioural and nonbehavioural indices of emotionality, should be validated as such by their association with the only direct fear responses, escape and immobility. Considering their correlation with indirect or species, strain and sex specific measures of emotionality would seem likely to lead to conflicting results, which makes it difficult to assess the generality or specificity of the adrenal measure.

Stomach Ulcers

The relationship of stomach ulceration to emotionality was discussed in the last chapter (Chapter Six).

F. SUMMARY AND CONCLUSIONS REGARDING THE VALIDITY

OF BEHAVIOURAL AND NONBEHAVIOURAL MEASURES OF FEAR/EMOTIONALITY

This chapter has so far discussed the validity of various behavioural and nonbehavioural measures of emotionality, (which are similar to those used in my experiments).

Probably the most widely validated measure of emotionality is open field defecation in rats, considered to be an autonomic response to a novel environment. However, there is little evidence in support of the assumption that this is therefore a valid measure across species, such as mice (cf. Nagy and Forrest 1970) or in fear provoking experimental situations other than the open field, such as active avoidance learning (e.g. Imada, 1972, Tobach and Schneirla 1962).

Open field ambulation had varying degrees of relationship to defecation, although it has generally been shown to be negatively correlated (c.f. Archer 1973). However, the meaning of ambulation is unclear as it may be a form of exploration, locomotion or escape seeking behaviour, depending on the individual, its developmental history and experimental circumstances. Exploration in any given situation is hard to decipher, as it may be carried out in the form of locomotion or as stationary activities, such as sniffing, so may need to be broken down into components including different types of ambulation.

Other open field measures have been validated by their correlation with defecation and weakly by their change over trials. A measure may be a positive index of emotionality if it decreases over trials or a negative one if it increases, assuming of course, that emotionality decreases with familiarity of the situation (brought by trial). This weak validation procedure (because it could be applied to other measures besides those of emotionality) could be used for indices in other situations, such as response to handling or avoidance learning.

The most satisfactory validation technique considered the level of defecation and ambulation scores in response to increased open field intensity, that is, increased light and noise. However, only defecation and latency have been shown by this procedure to be valid measures (Ivinskis 1970).

Measures from other situations have been validated by their correlation with open field defecation with varying success. These are reaction to handling, avoidance learning, ulcer formation and adrenal weight.

Therefore validation of measures of emotionality is, on the whole, incomplete.

It has been emphasized repeatedly in this chapter that two behavioural patterns can be defined as fear responses, namely, escape and immobility. Therefore, to search for the relationship between any proposed measure of emotionality and the occurrence of these responses leads to the best method of validation, yet this has seldom been carried out. Experiments have not often been designed to allow both escape and immobility, but they could be. For example, exploratory or novel situations allow freezing behaviour, but they should also be designed to allow escape, especially if freezing is not a common characteristic in the behavioural repertoire of the species studied.

A measure thus validated may have generality across experiments, species and sexes, although not necessarily. Strictly, this should be tested.

G. IMPLICATIONS OF THE FOREGOING SECTIONS

In the experiments to be reported, measures of emotionality were not validated in this way, although in the future this would be recommendable. I chose a series of tests comprising measures of body weight, food intake to the cage, reaction to handling, open field, novel situation, aggressive encounter, passive avoidance learning, home cage activity, adrenal gland weight and notification of gastric ulceration, to predict, based on common sense beliefs and previous work, that emotionality would be displayed in certain aspects of behaviour.

The independent variables of the experiment are the genotype of the hamsters, their sex and postweaning housing conditions. Behavioural responses are the dependent factors. If over the variety of experimental tests, any group of hamsters behave prima facie more fearfully than other groups, then emotionality or fearfulness will be used as the intervening variable to describe the hypothetical state of the brain and nervous system of this group.

To describe animals as emotional/fearful is useful, but these concepts have limitations. They implicate a general predisposition to certain aspects of behaviour, so that most animals of the category labelled as such, are expected to show greater emotionality in every test situation. When this is not the case, that group cannot be qualified as having greater emotionality or fear than any other group.

If animals are shown to differ unpredictably in their degree of emotionality across tests (as measured ideally by the occurrence of escape and immobility), emotionality is involved, not as a unitary construct as presumed by many workers (e.g. Broadhurst 1969, Denenberg 1969b, Gray 1971a), but as a complex of related states (Hall 1934, Archer 1973).

Despite inadequate validation of the emotionality measures used in my experiments, if one group of hamsters does not show greater fear overall compared to other groups, then they could not be described as more emotional and I would not have evidence in support of the idea that emotionality comprises a unitary state in these hamsters. Rather, the data would suggest that a follow-up study, using well validated measures should be carried out to prove this point.

H. SEX DIFFERENCES IN FEAR/EMOTIONALITY

As sex differences form a major issue in this thesis and as they have been constantly noticed in experiments, some findings, especially in relation to rodents, will be discussed.

The adrenal and sexual hormones are closely linked biochemically and as the adrenal system has been associated with fear reaction, it is not surprising that emotionality is related to the sex of an animal.

Stress and sexual activities seem to be antagonistic to each other (Gray 1971a). Richter (1959) for example, has shown that with domestication and presumably stress-free living, the adrenal glands of the rat have become smaller and the gonads larger. The animals mated

more easily and reproduced more often.

Early evidence for the importance of fear in sexual behaviour is provided by Anderson (1938). He tested male rats for fear, sexual activity, learning, general activity, hunger, thirst and exploratory behaviour, and measured emotional defecation in the open field and in two types of maze. The sum of the scores from these three tests were correlated with seven separate measures of sex drive, such as number of copulations and speed of running to reach a receptive female. He found that all seven measures correlated negatively with defecation score, considered to be a measure of fear. He also found that animals with lower emotionality scores had a higher sex drive. It is possible to bring female rats into oestrus by injecting them with oestrogen and this treatment reduced open field defecation (Anderson 1938, Gray and Levine 1964). Burke and Broadhurst (1966) found that in female rats which had entered oestrus spontaneously, open field ambulation scores, considered to be a negative index of emotionality, increased.

There were indications in male and female rats, therefore, that fear was antagonistic to efficient sexual activity. It may be asked how fear contributes to the common occurrence of sexual disorders in animals, such as female frigidity, nymphomania, abortion, lactation problems, pseudopregnancy (Schmidt 1968), embryo resorption (Conaway, Baskett and Toll 1960), or male impotence (Schmidt 1968) and the similar disorders that are found in man.

Animals typically show sex differences in behaviour in a number of tests.

The Open Field Test

Male rats have often been found to defecate more than females (e.g. Broadhurst 1957a, Snowdon, Bell and Henderson 1964), although some studies have reported nonsignificant findings (e.g. Thompson, Watson

and Charlesworth 1962, Levine and Broadhurst 1963, Ader 1965). In mice, on occasions females have been shown to defecate more than males (e.g. Candland and Nagy 1969, Nagy and Forrest 1970).

Genetic and early experience factors may explain some of the conflicting findings. However, Gray (1971b) presented the increased male open field defecation (in some cases) as evidence that male rodents were more emotional than female rodents.

The inverse relationship between open field defecation and activity found, for example, by Denenberg and Morton (1962) and Walden (1968), in rats, has been used as further substantiating evidence for Gray's proposition. However, there are some findings that do not indicate that such a relationship exists, especially for mice (e.g. Bruell 1969, Brain and Nowell 1969).

Non-reactive rats have been found to defecate less and ambulate more than reactive rats and Gray, Levine and Broadhurst (1965) pointed out that the behaviour of reactives to non-reactives was similar to that of males to females, and used this as confirming evidence that males were more emotional than females.

In a study of sex differences in three strains of rats in open field behaviour, Archer (1974) recorded a number of measures. He found no clear cut sex differences in emotional behaviour throughout the three strains. The only two significant sex differences found for all three rat lines were stationary sniffing and latency to enter the inner circle. Males showed more stationary sniffing which is consistent with findings that they ambulated less in the open field (Gray 1971b), but on other measures males showed no indication of greater emotionality. Archer's finding that males entered the inner circles sooner than females, despite lowered ambulation, is strong evidence against Gray's interpretation of the sex differences in activity being due to heightened male emotionality.

In one strain, three measures (latency to enter the inner circle, open field defecation and defecation following the sounding of a bell) indicated lower values for males than females and hence less emotionality.

Emergence Tests

Female rats and mice generally emerged sooner than males from a familiar to a novel environment or from a sheltered to an exposed situation (e.g. Saylor and Salmon 1971, for mice) although Harrington (1971) has shown the reverse to be the case in some strains of rat.

Swanson (1966) has found higher female ambulation in the open field and faster emergence times into a novel environment, in hamsters. (The hamster does not generally defecate in the open field so this measure had to be excluded). However, Swanson did not conclude therefore that females are less emotional than male hamsters.

Avoidance Learning

Female rats have been shown to learn active avoidance more quickly than male rats (e.g. Savage and Eysenck 1964, Levine and Broadhurst 1963, Denti and Epstein 1972, Beatty and Beatty 1970).

Female rats have been shown to have greater suppression ratios in a CER situation than males (Leshner, Brookshire and Stewart 1971, Savage 1960). Passive avoidance measured by retention of a learned response has been shown to be superior in male rats (Denti and Epstein 1972).

Thus, females learn active avoidance responses more quickly than males, yet are inferior with regard to retention of passive avoidance learning. If the assumption that both types of learning situation are fear evoking is correct, the findings do not easily implicate one sex as being more emotional in both situations. Furthermore the significance of greater female suppression ratios in CER with regard to emotionality, is unclear as this situation is similar to passive avoidance ones, where males are superior.

Therefore, what do the sex differences in active and passive avoidance learning signify in terms of emotionality?

It was proposed by Gray (1971b) that the superior active avoidance performance by females is linked with emotionality level as determined by defecation scores, because in a strain of hooded rats where defecation was higher in the females there was male superiority in active avoidance (Gray 1971b, Gray and Lalljee 1974). Furthermore active avoidance learning was more successful in rats selectively bred for low emotionality (Owen 1963, Levine and Broadhurst 1963) and in rats made less fearful by experiences during infancy (Levine, Chevalier and Korchin 1956, Levine and Wetzel 1963).

A different viewpoint was suggested by Archer (¹⁹⁷⁵~~in press~~). If the behaviour of the two sexes in active and passive avoidance learning situations is observed, it would seem that the sexes show individual types of response, each related to emotionality, rather than different degrees of the same response, on a continuum of emotionality.

For example, Beatty and Beatty (1970) showed that the sex difference in active avoidance was associated with the generally more rapid escape behaviour of female compared to male rats. They also showed that female rats had lower thresholds, in terms of flinching and jumping, to electric shock, than males. Wilcock (1968) showed that females responded with more running when administered electric shock.

Denti and Epstein (1972) ~~reported~~ ^{replicated} previous findings that showed females learned an active avoidance response more efficiently than males but were inferior on a passive avoidance reaction. Although in some studies, females may have been found to show greater sensitivity to electric shock, this did not account for their superior active avoidance learning and inferior passive avoidance in Denti and Epstein's study, as shock intensity was equal in the two cases. Measurement of exploratory

activity in the two-way avoidance box showed that although females did not spend significantly longer than males in either compartment, they crossed between compartments more often and this is taken to represent more activity in this situation (Denti and Epstein 1972). In the passive avoidance situation, the compartments were differentiable in terms of illumination, and intention movements, defined as approaches toward the dark compartment or incomplete crossings into it, and grooming during post-shock trials, were recorded. Intention movements were found to occur more often in females and the authors (Denti and Epstein) interpreted these behaviours as resulting from conflicts in an avoidance situation between tendencies toward and against movement.

Denti and Epstein (1972) concluded that as correct responding in the two types of avoidance situation demanded differential movement of the rats, sex differences in behaviour in these experiments may be related to sex differences in activity. Therefore, males with low open field ambulation and few intention movements in passive avoidance conditioning, learned this type of avoidance more quickly than females; in contrast females with greater open field ambulation and more intention movements during passive avoidance learning, responded more effectively in an active avoidance situation.

Recently Gray and Lalljee (1974) have presented alternative evidence (briefly mentioned earlier) attempting to show that the sex differences in active avoidance performance were associated with emotionality, rather than with activity. Females of a strain of hooded rats showed higher open field ambulation scores (in agreement with a number of previous findings regarding sex differences) but a higher defecation score than males (contrary to many reports on sex differences). Gray and Lalljee (1974) reasoned that if efficient active avoidance depended on activity, females should show their usual improved performance, as

they were more active according to open field ambulation scores. If, however, lowered fearfulness was responsible for successful active avoidance, the males should learn better, as their lowered defecation scores in the open field indicated lowered emotionality. The performance of this hooded strain was investigated in a two-way active avoidance situation.

Males of the hooded strain conditioned more quickly in the active avoidance learning experiment and it was concluded that this must be due to their lesser fearfulness. In addition, females of this strain showed greater activity in the shuttlebox, measured by the initial number of crossings, but did not learn to make effective crossings as quickly as males.

The evidence that active avoidance is impaired by high emotionality is provided by data from selectively bred strains, which showed that non-reactive rats learned more easily than reactive ones (Broadhurst and Levine 1963, Levine and Broadhurst 1963); from early handling experiments, where rats made less fearful during infancy performed better in active avoidance in adulthood (Levine, Chevalier and Korchin 1956, Levine and Wetzel 1963); from experiments on the effects of a fear reducing drug, aminobarbitol (Miller 1964, Kamano, Martin and Powell 1966); and from studies on the effects of lesions to the limbic system (McCleary 1966). These also support Gray's and Laljee's findings for sex differences and the proposed cause, that is, emotionality.

This conflicts with Archer's type of interpretation, where type of activity and emotionality are related. Gray seems to regard them as separate phenomena so that males of the hooded rat strain actively escaped more quickly than females (due to fear), despite low open field activity. Further, more diverse studies with this strain of rat may clarify the unusual relationship of higher female ambulation with higher

defecation compared to the male pattern.

Adrenocortical Function

Gray (1971b) cited a number of studies showing that the resting levels of both plasma and adrenal corticosterone were higher in female than male rats. The corticosteroid response to stress is initially more intense in the female but returned more rapidly to the pre-stress level. The two sexes also show different patterns of diurnal variation in corticosteroid secretion.

Gray (1971b) reviewed studies which showed that oestrogen reduced fearfulness in open field and emergence tests, although androgens had no effect, and used this as additional evidence for his theory that male rodents were more fearful than females. Gray (1971b) also pointed out that the sex difference shown in open field defecation and emergence by rats and hamsters persisted after adult castration, implying that hormones alone are not responsible for the differences.

In rats, females showed heavier adrenals and in hamsters the reverse was true, with males having heavier glands (Zieger, Lux and Kubatsch 1974). This difference has been demonstrated cytologically and morphometrically in rats as occurring in the outer fasciculata of the gland, with the individual cells of the female displaying relative hypertrophy (Zieger et al. 1974). By contrast, the sexual dimorphism in the hamster was in the zona reticularis layer of the adrenal gland and was apparent from the fourth week of life. However, the importance of the species difference (between rats and hamsters) in adrenal area responsible for sexual dimorphism is not clear at present (Zieger et al. 1974), but the hamster findings increase scepticism about Gray's theory that male rodents are more emotional than females on the basis of adrenocortical response.

A question that might be asked is whether any sex differences in

emotionality altered or reversed in hamsters compared to rats, is related to the species-specific sexual dimorphism in the adrenal gland.

Susceptibility to Gastric Ulcers

It was found that when enforced immobilization was used to induce stress, females developed more ulcers than males (Ader, Beels and Tatum 1960), although this has been explained by the greater female tendency to struggle during immobilization. If males tend to freeze in any given situation and females to escape as tentatively proposed by Archer (¹⁹⁷⁵~~in press~~), this may partially explain some of the ulcer findings. Thus, immobilization, as an ulcer inducing technique would be less stressful for males than for females which may well therefore struggle more. In a conflict experiment males were found to be more susceptible to ulcers (e.g. Sawrey and Long 1962), which may tie in with their preferred tendency to freeze, compared to the more active responses shown by females.

These conflicting reports of sex differences may relate to strain of animal used, type of stimulation to induce ulcers or age of testing (mentioned in Chapter Six), in which case Gray's supposition that greater male ulcer susceptibility in conflict situations represents a general trend of increased emotionality in males would seem to be on shaky ground.

Sex Differences in the Intensity and Duration of Fear Responding

Archer (¹⁹⁷⁵~~in press~~) has considered sex differences in the intensity and duration of fear responding.

In response to the open field, male rats and mice were found to have shorter latencies for movement from the peripheral to the central area. Female mice showed more periods of freezing than males during the initial two minutes of exposure and also moved further during their flight response to the sudden sounding of a bell in the open field (Archer, ¹⁹⁷⁵~~in press~~). In addition, female rats showed more ambulation

than male rats during the first 30 seconds in the open field (Broadhurst and Eysenck 1964).

Although females have been found to display an initially more intense adrenal corticosterone response to stressors they have returned more rapidly to pre-stress levels than males (reviewed by Gray 1971b). In the hamster species, the male showed greater adrenal weight and higher steroid secretion than the female (Zieger, Lux and Kubatsch 1974).

It has been shown that females had higher heart rates than males after open field testing (Snowdon, Bell and Henderson 1964) and higher heart rates during handling (Blizard 1971b, c). Blizard (1971b, c) also found that heart rate increases during light and noise exposures were greater in males than females.

As regards passive avoidance learning, initial suppression ratio was greater in female than in male rats. It was on retention of the response that males were superior.

It was pointed out earlier that the female response to shock was more intense than that of the male.

It was on the basis of this evidence that Archer (1975) proposed that females showed more intense initial responses to fearful situations than males.

Conclusions

Gray (1971b) presented a case for greater male emotionality among rodents based on results from a number of test situations, namely, the open field, active and passive avoidance learning, the corticosteroid stress response and ulcer susceptibility.

Archer (1975) considering a larger sample of tests, found only some produced sex differences in the direction of Gray's hypothesis. In addition, if initial response rates only, were considered, there was evidence that females were more fearful than males.

In view of this, Archer (¹⁹⁷⁵~~in press~~) argued that sex differences in behaviour in fear provoking situations were related to different types of response rather than to quantitative emotionality. Male and female rodents differed in their most readily emitted fear behaviour, with females tending to escape and males to become immobile. This type of interpretation seems to have greater concordance with the literature than does Gray's theory.

Archer (¹⁹⁷⁵~~in press~~) also found that testosterone injected male chicks became immobile in response to a bell in the open field whereas oil injected controls showed more active avoidance responses, such as looking away from the bell or jumping. If testosterone exerted a similar effect in rodents, males would respond with immobility rather than escape, a characteristic of some of the studies reported earlier. Archer emphasized that this was a tentative but testable hypothesis.

J. SEX DIFFERENCES IN AGGRESSION

Aggressiveness has been observed to be greater in males than females in many mammalian species (Gray 1971a, b).

Although male rats and mice have been shown to be more aggressive than female rats and mice, Payne and Swanson studying hamsters (1970) found no sex differences in any of the behaviour categories they used for measuring an encounter, although females tended to be dominant.

Here therefore is a species difference. Male rats are more aggressive than female rats but female hamsters are dominant to male hamsters. In fact, this correlated with body weight. Although weight was controlled for in pairing, female hamsters were on average heavier than males whereas male rats were heavier than female rats (Swanson 1967).

There seems to be little research on how the sex difference in rodent aggression relates to purported sex differences in emotionality. In view of the reversed sex difference in the hamster species for

aggression, variations in sex differences in measures of emotionality will be looked for closely in the experiments to be reported.

Gray's Hypothesis on Rodent and Primate Sex Differences in Fear and Aggression

Gray (1971b) reviewed rodent and primate sex differences in fear and aggression, and his principle conclusions can be summarized as follows: in rodents, males are more aggressive than females and also more fearful; in man, males are likewise more aggressive than females with the reverse being true for fear, that is, women are more fearful than men.

With respect to the reported findings that sex differences in hamsters are not the same as those in rats on aggression scores, body weight and adrenal weight, my research seeks to confirm these, and in addition, explores sex differences in all experiments carried out, calling in to question Gray's hypothesis that male rodents are more fearful than female rodents.

K. CONCLUSIONS ON SEX DIFFERENCES

It has been shown in sections H and J of this chapter that sex differences in rodents do not fall consistently in the direction of one sex being generally more fearful than the other. On the contrary, results are conflicting and hard to interpret in terms of degree of emotionality.

Archer's suggestion (¹⁹⁷⁵ ~~in press~~) that there is a 'sex-typical fear response' in the direction of female escape and male freezing behaviour in reaction to novel/frightening situations, seems to comply with much of the data.

Archer's hypothesis thus indicated that as a result of any one fear provoking situation, male and female responses were different. There was also some evidence that females showed heightened initial responding on some occasions. Reactions overall may have been equal in intensity

for each sex or they may not have been but it would probably be difficult to differentiate them on this.

It should be clear by now, that a unitary emotionality concept cannot describe the diversity of sex differences. In any experiment, a variety of factors, for example, species, strain and early experience, affect the intensity of fear behaviour shown by either sex.

With regard to the probable sex difference in form of fear responding it may not be possible to establish that one sex behaves quantitatively more emotionally than the other in any experiment. But even if it was, the unitary adjectives, emotional and fearful, cannot be attributed to one sex, because they would lead to the expectation that a particular behavioural tendency would be shown by that sex over a variety of tests.

In view of the evidence considered, this would seem unlikely to be the case.

CHAPTER EIGHT

PILOT STUDIES

A. OBJECTIVES

These early studies were carried out to determine whether:

1. piebald and non-piebald hamsters, males and females, reacted differently to two test situations, the open field and one called the novel situation;
2. the direction of any differences observed could be considered to fall under the terms 'fear' or 'emotionality';
3. such differences would justify a more detailed investigation of piebald behaviour in aggressive and learning paradigms as well, and its relation to caging conditions, body weight, adrenal gland weight, ulcer formation and viability.

B. SUBJECTS AND MAINTENANCE

Eleven female and five male golden hamsters four to five weeks old were obtained from a commercial breeder at Basingstoke. They matured and bred in the psychology department at Leicester University. The offspring were used for the behavioural tests. In view of the piebald poor viability and high infant mortality, they are not bred commercially, but Pat Sturdy, a botanist interested in genetics, provided me with 21 piebald females and 18 piebald males, of varying ages and uncontrolled background genes. The combination of many infertile matings and high death rate in young and adults, resulted in several of this original stock being used for the behavioural experiments. The golden and piebald lines will both be called strains, although Pat Sturdy's line was not inbred.

When the animals arrived they were placed individually in polypropylene cages, measuring 17.5" by 10" by 5" with a barred metal top. An external food hopper and water bottle provided ad. lib. diet 41B and tap water. All hamsters were also given a supply of fresh green vegetables once a week. Twenty cages were kept in one rack. Wood shavings were put in

every cage and wood wool and newspaper added for nest material.

Cages were cleaned every three weeks. All animals received routine handling only. The temperature of the room was maintained at 24° C and as hamsters are nocturnal they were subjected to reversed light cycles. An automatic light schedule provided 14 hours of white light from 18.00 - 8.00 hours, and no light for the rest of the day. Eight 40 watt red light bulbs were turned on whenever the experimenter was in the room.

15 males and 15 females of golden and piebald hamsters were subjected to the two behavioural tests, the open field and novel situation. Three days elapsed between completion of one test and start of the next and hamsters began the first test after reaching maturity, at ten weeks of age. Half the subjects completed the tests in one order and half in the other.

C. CHOICE OF THE OPEN FIELD AND NOVEL SITUATION TESTS

The open field test was chosen as many rat studies in the past have based descriptions of animals as 'reactive' or 'non-reactive', 'emotional' or 'non-emotional', on behaviour in this situation. As Priestnall (1970) found the open field test failed to differentiate between mice which had been group reared from those which had been isolated, he designed a modified arena, supposedly less fear provoking. In case the open field did not differentiate between the hamster strains, I too developed a modified open field, similar to Priestnall's, and called it the novel situation.

In these pilot studies, the results from behaviour on these tests are not compared with those from other work employing similar tests, as these early investigations are reported primarily to give an impression of piebald hamster behaviour compared to normal and to indicate that in the writer's opinion this hamster was worth further study.

D. APPARATUS AND PROCEDURES

Open Field

Apparatus. The apparatus, housed in a sound proofed room, consisted of a 40" square hardboard base painted white and marked by black lines into 10" squares. Each square was numbered. The 12" high walls were also painted white. The arena was lit by a 500 watt lamp placed 3 feet above its centre. Illumination was therefore less intense at the walls and least in the corners. A loud speaker hanging just above the light emitted white noise generated by a Dawe white noise generator and amplified to 80 db. as measured by a Dawe sound level meter placed in the centre of the field. (See Figure 2. for floor plan of the open field arena).

Procedure. A mobile rack was used to transport animals from the basement animal room to the sound proofed laboratory on the second floor via a lift. Each animal was placed individually in the open field for four minutes per day for four consecutive days. All hamsters remained in their cages on the rack outside the laboratory until each individual had completed the test. Order for taking part in the test was randomized for every trial (day). The white noise was turned on and an animal placed in square 13 for a four minute trial. After each trial the arena was swabbed down with a mild disinfectant. Time (in seconds) was recorded only when the length of bout lasted ten seconds or more. The following measures were recorded:

1. Latency to leave square 13, that is, when the hamster's hind legs had crossed the lines of the square.
2. Total number of lines crossed, that is, ambulation score, measured by recording every square the animal entered. Entrance to a square was recorded when the hamster's hind legs had crossed the lines surrounding that square.
3. Number of times the middle lines were crossed, that is, entrance into squares 6, 7, 10 or 11.
4. Time spent on behaviours lasting more than 10 seconds in corner squares, that is, squares 1, 4, 13, 16. (Hereafter simply referred to as: 'time spent in corner squares').
- 5.) Number of bouts and length of time spent sniffing.
- 6.) Sniffing was recorded when the hamster had its nose to the ground, its vibrissae twitching.

7. Number of crouching bouts. Crouching took place in one of the four corners and occurred when, with front legs raised, the hamster pressed its ventral surface against the corner, tucked its head under and remained motionless.
8. Number of rearing bouts, that is, the hamster standing on its hind legs only with its forepaws off the ground (or against the side of the arena).
9. Number of scratching bouts. Scratching took place predominantly in the corners and the hamster scratched the base of the wall with its front legs.
10. Number of grooming bouts, that is, the hamster cleaning its body.
11. Number of freezing bouts, that is, the animal standing on four legs, motionless.
12. Number of faecal boluses deposited, that is defecation.

Novel Situation

Apparatus. This test is a modified version of the open field.

A black hardboard arena 24" by 36" by 12" high was placed on a black hardboard floor marked off at 6" intervals by white lines. The floor was covered with wood shavings and food pellets of diet 41B. Placed in the arena, along three of the walls were a water trough (5" by 5.5"), an activity wheel (5" diameter, attached to a metal frame), and a hardboard box (7" by 3.5" with an opening at one end and wire mesh covering a one inch slit across the middle of the top surface). The arena was in the animal room and the hamsters were observed in this situation under red light. (See Figure 3. for a diagram of the novel situation arena).

Procedure. An animal was placed individually in the arena for six minutes per day for four consecutive days. Order for placement in the test was randomized on every trial. Animals were placed in the starting square and their behaviour recorded for six minutes. The following measures were recorded (where no definition of a behaviour category is given it is the same as that used in the open field tests):

1. Latency to investigate, that is, sniff with nose and vibrissae the first object, either trough, box or wheel.

Figure 2. Floor plan of open field arena.

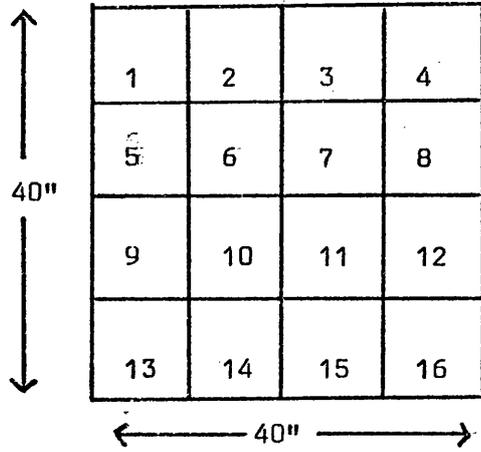
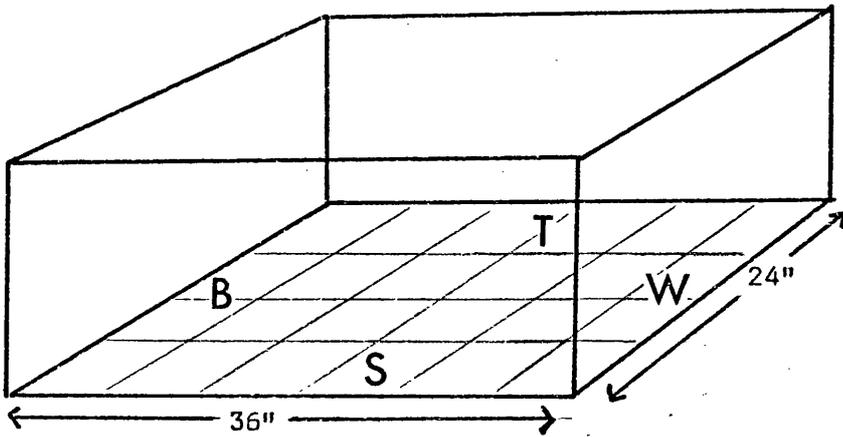
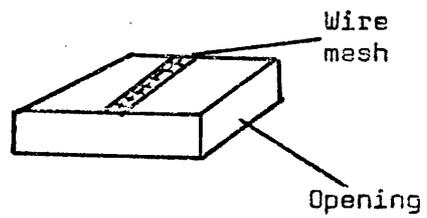


Figure 3. Novel situation arena.



B = Box
T = Trough
W = Wheel
S = Starting square

Box



2. Number of lines crossed, that is, ambulation, recorded by a digital counter. Hamsters were considered to have crossed a line when their fore and hind limbs had passed over it.
- 3.)
- 4.) } Number of bouts spent sniffing trough, box or
- 5.) } wheel.
- 6.)
- 7.) Time spent sniffing trough, box or wheel.
- 8.)
9. Time actually in the box.
10. Time actually on the wheel.
11. Number of food bouts, that is, sniffing, picking up or eating food pellets.
12. Number of pouching bouts, that is, pouching of food.
13. Number of rearing bouts.
- 14.) Number of sniffing bouts and length of time of
- 15.) each.
- 16.) Number of grooming bouts and length of time
- 17.) of each.
- 18.) Number of scratching bouts and length of time
- 19.) of each.

Recording and Timing

A small Philips cassette tape recorder was used to record a verbal commentary on any type of hamster behaviour that occurred. Behaviour fell into one of the categories already mentioned. The tapes were later played back and the relevant information (number of bouts and length of time) transferred to paper. This method of recording behaviour was used for every experiment in this thesis. It was chosen in preference to the pen recorder technique as with it, the order of behaviour could be determined, incidental observations outside the behaviour categories could be noted; and, when transferring to paper, any section could be played back a number of times for accurate information.

Events were timed with a stopwatch.

E. RESULTS

Treatment of Data

Each test consisted of four trials, so for each hamster there were eight sets of data. On any trial the number of bouts and total time were calculated for every behaviour category which was being examined. Each measure (behaviour category) was analysed separately.

15 hamsters of two strains and two sexes had four trials on the two tests. There were three factors, that is, strain, sex and trial, with repeated measures on one factor, trial. This case can be presented diagrammatically as follows:

Test: (Open Field or Novel Situation)

Strain	Sex	Trial			
		1	2	3	4
1.	Male				
	Female				
2.	Male				
	Female				

Each hamster was observed under all levels of the trial factor but is assigned to only one combination of strain and sex. Therefore every hamster falling into one of the four strain-sex combinations, was observed over a number of behaviour categories (called measures) for four trials. Each measure was analysed separately using a 3-way analysis of variance, to give the significance of strain differences, sex differences, trial differences, strain x sex, strain x trial, sex x trial, and strain x sex x trial interactions. The 5% level of significance or higher was considered acceptable.

Open Field

Of 12 measures, eight showed significant strain differences, four showed significant sex differences and three showed a significant strain x sex interaction. The golden hamsters had a longer latency before leaving square 13 than piebalds, a lower ambulation score, fewer sniffing bouts but longer sniffing time, spent longer in the corner squares, had fewer grooming bouts, fewer crouching bouts and much less defecation. Of 30 piebalds taking part in the open field test, 18 showed defecation on one or more trials. Only two golden hamsters out of 30 showed any defecation. Therefore, 60 percent of the piebalds defecated as against 7 percent of the golden hamsters. Males showed a longer latency, longer sniffing time, spent longer in the corner squares and had fewer crouching bouts than females. Strain x sex interactions occurred on ambulation score, with piebald males crossing the most lines (highest score) followed by piebald females, golden females, with golden males scoring the lowest. A similar interaction also occurred for time spent sniffing with golden males spending the longest time and piebald females the least, and for time spent in the corner squares; which shows the same pattern as for sniffing.

The measures which showed a significant difference over the trials were ambulation, rearing bouts, sniffing bouts and grooming bouts; those which showed a significant strain x trial interaction were ambulation, entrance to the middle squares and crouching bouts; while crouching bouts also showed a significant sex x trial interaction.

Novel Situation

Of 19 measures eight showed significant strain differences, four showed significant sex differences and four showed a significant sex x strain interaction. The piebalds crossed more lines (higher ambulation) than the golden hamsters, as did females compared to males. Females also had more rearing bouts than males. Golden hamsters showed fewer

sniffing bouts but a longer wheel time. They also spent longer time on the box, but the piebalds showed more grooming bouts.

Strain x sex interactions occurred for latency to exploration with piebald males showing the largest latency and golden males the least, and on the ambulation score, with piebald females crossing the most lines and golden males the least.

The measures which showed a significant difference over trials were ambulation, sniffing bouts, rearing bouts, wheel bouts, box bouts, grooming bouts, grooming time and feeding bouts; ambulation, rearing bouts, box bouts and scratching bouts showed a strain x trial interaction, while ambulation showed sex x trial interaction.

Summaries of Results

The results of the analysis of variance tests carried out on measures of the open field and novel situation trials are summarised in Summary Tables I and II

F. DISCUSSION OF RESULTS

The open field test showed significant strain differences on more measures than the novel situation. Although Priestnall (1970) considered it too fearful to distinguish mice, it was more effective in differentiating hamster strains, than the novel situation.

In both the open field and novel situation, piebalds showed a higher ambulation score. In the novel situation females crossed more lines and both tests showed a strain x sex interaction, with golden males having the highest score in the open field and piebald females in the novel situation. The novel situation sex differences agree with previous reports that females ambulate more than males (Gray 1971a). Ambulation is often considered to represent non-emotionality and a high score usually correlates with low defecation. However, piebalds ambulated more than golden hamsters in both test situations, and showed high defecation in the open field, so high ambulation here accompanied

SUMMARY TABLE I - OPENFIELD

Measures, analysed by three-way analysis of variance, with significant strain or sex differences, or strain x sex interaction.

Degrees of freedom are 1 and 56.

Measure	Source of Variation	F	Significance of F
Latency of leaving first square.	Strain	12.11	0.001
	Sex	4.11	0.05
	Strain x sex	3.29	NS
Ambulation	Strain	9.72	0.01
	Sex	1.91	NS
	Strain x Sex	6.08	0.05
Sniffing time	Strain	32.80	0.001
	Sex	20.70	0.001
	Strain x Sex	4.13	0.05
Sniffing bouts	Strain	20.50	0.001
	Sex	0.32	NS
	Strain x Sex	0.67	NS
Time in corner squares	Strain	17.02	0.001
	Sex	5.61	0.05
	Strain x Sex	4.58	0.05
Grooming bouts	Strain	8.84	0.01
	Sex	0.56	NS
	Strain x Sex	0.05	NS
Crouching bouts	Strain	13.70	0.001
	Sex	4.60	0.05
	Strain x Sex	3.94	NS
Defecation	Strain	10.11	0.01
	Sex	0	0
	Strain x Sex	0.09	NS

SUMMARY TABLE II - NOVEL SITUATION

Measures, analysed by three-way analysis of variance, with significant strain or sex differences, or a strain x sex interaction. Degrees of freedom are 1 and 56.

Measure	Source of Variation	F	Significance of F
Latency to exploration	Strain	0.83	NS
	Sex	0.67	NS
	Strain x Sex	7.12	0.01
Ambulation	Strain	31.64	0.001
	Sex	22.08	0.001
	Strain x Sex	19.68	0.001
Rearing bouts	Strain	0.08	NS
	Sex	24.87	0.001
	Strain x Sex	0.07	NS
Sniffing bouts	Strain	37.40	0.001
	Sex	3.72	NS
	Strain x Sex	0.29	NS
Sniffing time	Strain	5.03	0.05
	Sex	16.71	0.001
	Strain x Sex	1.16	NS
Wheel bouts	Strain	4.98	0.05
	Sex	0.04	NS
	Strain x Sex	3.07	NS
Wheel time	Strain	19.26	0.001
	Sex	0.02	NS
	Strain x Sex	0.04	NS
Box time	Strain	18.50	0.001
	Sex	0.25	NS
	Strain x Sex	0.03	NS

Summary Table II continued

Measure	Source of Variation	F	Significance of F
Grooming bouts	Strain	14.40	0.001
	Sex	3.67	NS
	Strain x Sex	3.12	NS
Scratching bouts	Strain	1.19	NS
	Sex	8.21	0.01
	Strain x Sex	7.44	0.01
Scratching time	Strain	2.07	NS
	Sex	3.72	NS
	Strain x Sex	6.43	0.05
Feeding bouts	Strain	6.88	0.05
	Sex	1.55	NS
	Strain x Sex	0.60	NS

much defecation. This conflicts with much previous rat work.

Piebalds also showed more bouts of various behaviours. They showed more sniffing bouts, grooming bouts and crouching bouts in the open field and more sniffing bouts, wheel bouts and grooming bouts than non-piebalds in the novel situation. In each test they showed less sniffing time, that is, many short bouts. By contrast, golden hamsters had a longer latency and spent more time in the corner squares in the open field and longer investigating the wheel and box in the novel situation. Furthermore, as piebald was to golden, so female was to male on latency to leave the first square, sniffing time, time spent in corner squares and crouching bouts, in the open field, and ambulation and sniffing time in the novel situation.

The picture can be summed up as follows: placed in a new environment the golden hamster becomes familiar with the situation (latency in the open field), and explores it systematically (low ambulation and long sniffing bouts, and long wheel and box bouts). The piebald hamster, by contrast, rushes off (short latency and high ambulation), exhibits short bouts of a variety of behaviours, and defecates in the open field. The impression is not one of greater ambulation and hence more exploration, but of greater ambulation and erratic behaviour. In the open field, the piebald hamster did not spend long enough in any one position to allow it to become more familiar and less frightening, and similarly in the novel situation, it did not spend time investigating the exploratory objects, the wheel and the box. Lester (1968b) emphasized the importance of orderliness in exploratory behaviour, suggesting orderliness increases as emotionality decreases.

The impression gained from these two experiments is that piebald hamsters could differ from non-piebald ones, in the direction of what might be called emotionality. Differences between the sexes are more difficult to interpret. There were no significant differences in defecation response and the absence of this major measure of fear in the

open field makes it possible to interpret the data on sex differences in a variety of ways. Females, however, tend to show the same relationship to males as piebalds do to non-piebalds (see figures 4 and 5) and as this kind of behaviour comprised low exploration in piebalds, which in conjunction with high defecation, implicated fear, it could also represent low exploration in females. However, this would not necessarily be accompanied by high emotionality, although it may.

Finally, it should be mentioned that the large proportion of piebalds defecating in the open field was an unusual finding, as normally very few hamsters show this open field response (Swanson, 1966).

These early studies will not be examined and interpreted further, as they were not strictly controlled. Firstly, the hamsters' genetic constitutions were uncontrolled. The two types were from different colonies, so their genetic backgrounds were different, and owing to the lack of inbreeding, backgrounds within either colony were different. Golden hamsters were bred easily in the psychology department here, whereas piebalds had to be obtained from Pat Sturdy in Warwick, and travel could be an important variable that should be controlled for.

Secondly, maternal environment was not controlled. Golden pups had golden mothers and piebalds were born of piebald mothers. Judging by the experimental evidence cited in Chapter Five, this could result in larger strain differences than if all mothers were of the same strain. Sibling environment also was not controlled. Piebald pups had piebald siblings and golden pups had golden siblings.

Thirdly, some females had one litter or more and others proved infertile. Offspring born of fertile piebalds are already subjects of selection. Infertility may be related to behavioural problems, as illustrated in Chapter Three, and piebald offspring born to piebald mothers are likely to continue the 'fitness' trend shown by their mothers'

Figure 4. Mean open field latency. Relationship of piebalds to golden hamsters, and males to females.

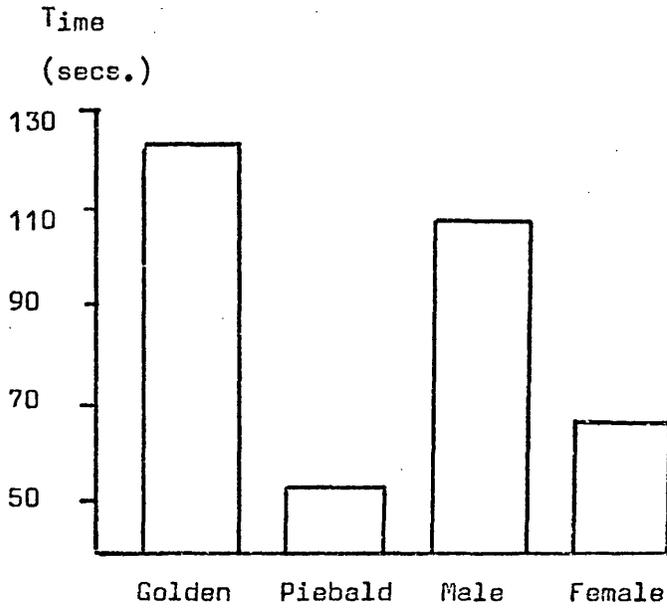
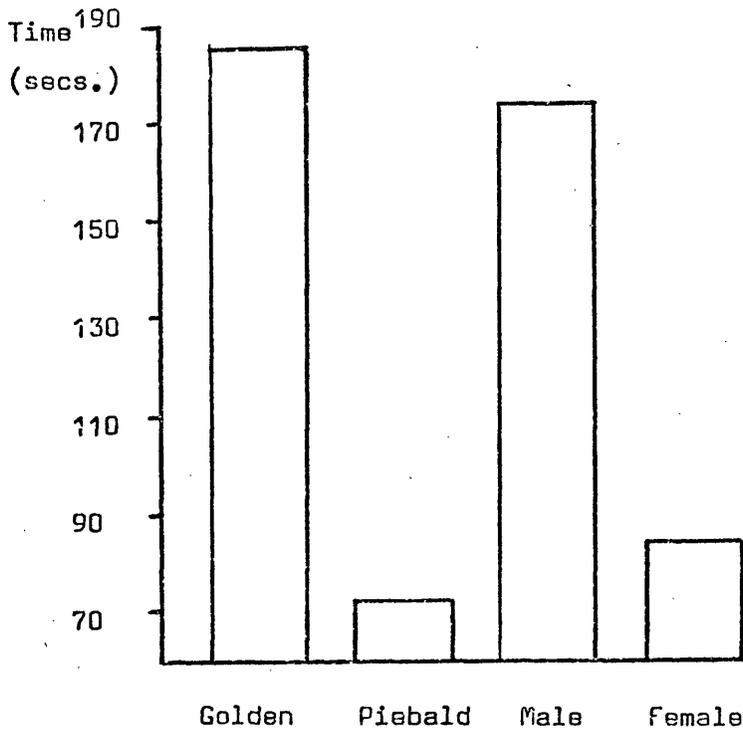


Figure 5. Mean open field sniffing time. Relationship of piebalds to golden hamsters, and males to females.



breeding ability. Males were placed with females for mating, so this meant that some males, especially 'stud' ones received much more handling than other males and females. Dealing with reproduction and birth would seem almost inevitably to lead to unfair treatment of animals and possible contamination of results.

G. CONCLUSIONS

The ideas put forward are tentative, based on evidence too slight to be conclusive. However these two experiments and other findings of fertility and birth rate not reported here, aroused my interest in the piebald hamster for research investigating its behaviour in various situations, examining the validity of measures used, and which results reveal the trend that piebald behaviour is affected and complies with that shown by other rodents in similar situations, which has led their being described as emotional or fearful.

I, therefore, decided to elaborate and expand the experimental design, including controlling for genetic, maternal and sibling effects and using a greater variety of behavioural tests and measures.

CHAPTER NINE

APPROACH TO THE MAIN STUDY

A. BACKGROUND

Reasons for Choice of the breeding Programme

The low viability and poor fertility of the piebald hamster posed serious hazards to the continuation of this project. One way of partially overcoming the fertility problem was the breeding of piebald offspring from non-piebald heterozygote mothers and piebald fathers. Piebald embryos would thus have a greater chance of reaching successful parturition and hopefully a greater chance of survival afterwards, under the superior care of a non-piebald mother.

In 1972, a meeting with the geneticist Roy Robinson, a worker with hamsters interested in the behaviour of the piebald type, led to the suggestion that a colony of piebald hamsters could be bred from a double heterozygous golden mother and double homozygous brown piebald father. The genetic cross and offspring that would be produced are shown diagrammatically below:

male		female	
bbss	x	+b+s	
	+b+s	golden	+ = golden
	+bss	golden piebald	b = brown
	bb+s	brown	s = piebald
	bbss	brown piebald	

It can be seen that the four genotypes of offspring which would be produced are golden hamsters, brown hamsters, golden piebald hamsters and brown piebald hamsters, all occurring in equal proportion in any litter. All the background genes would be randomly distributed among the offspring of differing coat colours, so that each animal has equal potential for inheriting any combination of background genes.

It was proposed that if Robinson carried out this breeding programme he could use the results for genetic data and send the offspring to me, postweaning, for subjection to a range of psychological tests.

The crucial factor is the piebald gene and I wished to examine behavioural effects which may be related to this major gene. Reasons for choosing to study these effects were given in Chapter One and advantages of single gene studies were discussed in Chapter Two. The pilot studies indicated that there was a behavioural change in the predicted direction associated with the piebald gene. In the main study, as a result of the cross shown previously, two piebald genotypes were compared with two non-piebald genotypes (as opposed to golden piebalds compared only with golden hamsters), as in this way, behaviour attributable to an effect of the piebald gene should occur in both the golden piebald and brown piebald hamster, but not in either the golden or the brown type.

There are two methods (Merrell 1965) which indicate that behavioural differences are due to the major gene, when one is involved. One of these is to achieve, through inbreeding, isogeneity at all loci except the one in question. A second procedure involves randomization of the rest of the genotype with respect to the locus under study, which can be useful when the main interest is in the behaviour rather than analysis of gene pathways (Merrell 1965). This procedure is utilized in this project.

Another great attraction of Robinson's proposed genetic cross was the simplicity in the way in which many variables were controlled for without experimenter intervention beyond the mating of the hamsters. Consequently it was decided to adopt this arrangement as it seemed to offer the following considerable advantages:

1. The mutant recessive (s) gene occurred at a single locus and the family which produced it would normally have been inbred to retain it, so the subline containing the mutant may have been more homozygous for genes in addition to the mutant, than the line from which it was derived. This kind of subline would also not necessarily hold a representative sample of other background genes, so that behavioural differences between the original line and mutant line could be due to: a. the mutant gene; b. the subline being more homozygous; or c. the different genetic background of the mutant subline. Having obtained two genotypes and two suitable mutant sublimes, Robinson chose a mating that discarded possibilities b and c as causes of behavioural differences.
2. This cross was less subject to the disadvantages inbreeding, repeated backcrossing and selection almost invariably lead to. The genes b and s, as represented by phenotypes golden, brown, golden piebald and brown piebald were systematically controlled and the inheritance of all background genes was random, hence individuals were unlikely to be genetically identical.
(these two points should make it clear that observed behaviour differences are likely to be due to a pleiotropic action of the piebald gene, although the possibility of genes closely linked to it, as causal agents, cannot be dismissed).
3. The important genes are those responsible for golden, brown and piebald coat colour. Every mother has the same combination of these genes and so has every father. This procedure controlled maternal effects without cross-fostering, or ova/ovarian transplant, to produce four genotypes which experienced the same prenatal and postnatal environments, without necessitating hybridization (as a diallel cross would have done). The cross, of course, does not control for offspring genotype x maternal genotype interaction, as a reciprocal cross would have done, but in view of the poor piebald breeding ability, it would not

have been practical to carry out a reciprocal cross.

4. The ratio of each genotype per litter was equal, as was the chance of any hamster pup having any other genotype as its litter mate. Each genotype was easily detectable by its coat colour, which controlled for sibling effects without split litter or complicated marking techniques.
5. By use of a golden double heterozygote mother, there was no longer the problem of lack of maternal care to pups, shown by piebald mothers. The possibility of infertile matings was much reduced, as only one parent, the father, was piebald. Once conception had taken place, there was a high chance the female could retain the embryos to parturition. Piebald viability could still be a problem, but their production would be enhanced.
6. With the acceptance by Robinson of the time-consuming task of breeding hamsters, it was possible to subject the animals to a greater variety of tests and observe more dimensions of their behaviour.

The hamster types will not be referred to as strains, because a strain consists of a group of animals genetically very alike, resulting from consecutive brother-sister matings. The colony was composed of animals, which differed consistently for the coat colour genes only, with the background genes being randomly distributed throughout the offspring, which were categorized into genotypes, according to coat colour.

Some Factors Affecting Choice of Test Situations

Emotionality has been used to describe and explain animal behaviour in a variety of situations, such as novel environments and avoidance learning, and related to such nonbehavioural measures as adrenal weight and gastric ulceration as illustrated in previous chapters.

The applicability of 'emotionality' to behaviour occurring in many experimental circumstances implies that it is general and pervades many

aspects of behaviour. In Chapter Three, it was stated that it would not be used as an explanatory concept, but as a label for animals showing consistent differences over a number of reasonably valid measures. Reaction by certain animals in the same direction, that is increased fearfulness, over a variety of experimental conditions, is crucial if they are to be attributed greater emotionality or fearfulness than other animals.

A single test would seem unable to offer much credible information about emotionality.

Therefore, it was decided to search for emotionality systematically in a variety of behavioural and nonbehavioural test situations controlling for genotype, sex, pre- and post- natal experiences and postweaning housing conditions.

It was predicted that hamsters carrying the piebald gene would behave in a variety of tests in a way that could be described as more fearfully, than would the two genotypes without the piebald gene. These predictions were based on earlier unsubstantiated ideas regarding the behaviour of the piebald genotype (e.g. Robinson 1958, Searle 1968) and pilot study findings, which, predominantly as a result of open field defecation, indicated that greater emotionality may be an attribute of piebald hamsters compared to other types.

No predictions were made about the way the golden and brown genes may be related behaviourally; nor about sex differences, differences resulting from housing conditions or any interaction effect as contradictory findings are abundant in the literature. However, significant results will be examined and contribute to conclusions about the validity of attributing descriptions of differential emotionality to any class of hamster.

B. SUBJECTS AND MAINTENANCE

The subjects were the offspring of the stated genetic cross. The golden hamster is the one which occurs in Syria, the natural habitat for this species. It has been used as a laboratory animal for over 40 years. The fur of the golden hamster is dorsally a rich brown and ventrally pale cream. Feet, nose and tail are white, while the eyes are dark. The brown homozygote is a rich cinnamon orange, while the ventral fur remains cream. The eyes are rich red in colour, which may make them more sensitive to light than the wild type. The piebald recessive gene (Foote 1949, Orsini 1952, Robinson 1958) causes a variable amount of white spotting. There appear to be effects on the reproductive and nervous systems, although there is uncertainty about the extent and nature of them. Piebalds also tend to have urinogenital abnormalities and reduced viability (Searle 1968). The brown piebald hamster combines the effects of the brown and piebald conditions, at least morphologically.

The number of hamsters received and used in experiments are given in Table I.

Table I

Genotype/Sex	Number received	Number used in experiments
golden males	26	20
golden females	19	17
brown males	37	23
brown females	18	17
golden piebald males	17	10
golden piebald females	25	16
brown piebald males	6	3
brown piebald females	32	21

A small number of golden and brown hamsters were observed initially in the experimental situations, which allowed categories of behaviour to be formed and gave practice in recording them. Six golden males and

13 brown males were killed or given away to make laboratory space available.

The animals travelled from London to Leicester by overnight train, when they were three to four weeks old, in large biscuit tins containing five to six individuals. Each hamster was identified, for genotype, sex and litter number. During the first three months of experimentation, hamsters on arrival, were weighed and placed individually in cages like those described in Chapter Eight and given tap water and diet FFG(M) supplied by E. Dixon and Sons. These hamsters were called isolates and involved five golden males and females, four brown males, five brown females, five golden piebald males and females, three brown piebald males and five brown piebald females.

After the first three months of experimentation, newly arrived hamsters (also three to four weeks old) were sorted and placed in groups of three or four wherever possible, but occasionally in groups of two, in cages identical to those for isolates. Genotype and sex of the groups depended on the hamster types received, but within this limitation, group consistency was random. These hamsters, called 'group housed' were kept in groups until aged six and a half to seven weeks, when they were placed in separate cages.

Every hamster was moved to a clean cage at seven weeks of age, whether it had been isolated or housed in a group. Behavioural differences between hamsters isolated or group housed on arrival will be referred to as housing differences.

C. BEHAVIOURAL TESTS

Hamster treatment took place from their arrival at four weeks of age to 14 weeks. The experiments carried out were called body weight, food intake to the cage, reaction to handling, open field, novel situation, activity, aggressive encounter, passive avoidance learning and dissection

(which included recording of gastric ulceration and adrenal weight). Methodological details of these experiments are given in Chapters Ten, Eleven and Twelve.

The experiments were chosen to represent a fairly wide cross-section of behaviour. If emotionality is considered to be a general descriptive term, attributable to certain classes of hamster, then diversity of behaviour experiments is essential. Without this, use of the term may be unreliable and invalid (cf. Chapters Two and Seven). All tests were expected, on the basis of previous findings and a priori grounds, to relate to emotionality.

The reasons for the choice of open field and novel situation were given in the chapter discussing the pilot studies (Chapter Eight). The activity experiment was carried out to give a measure of basal activity in relatively 'stress-free' conditions.

A measure of avoidance learning was taken because of the large body of material on the relationship of emotionality to this kind of behaviour and reaction to handling involved an especially convincing procedure that allowed the occurrence of a core fear behaviour, that is escape. Finally aggressive encounter was examined as hamsters have been used extensively in studies on aggressive behaviour and some measures recorded, such as mutual avoidance, which are more or less directly associated with the defined fear responses.

Measures of gastric ulceration and adrenal weight have often been linked with emotionality, so they too were recorded. Limited post-mortem observations of piebalds that died before taking part in experiments were also made.

Body weight and food intake to the cage were measured throughout the experimental period, and reaction to handling recorded every week from eight weeks of age.

The four behavioural tests labelled Open Field, Novel Situation, Activity and Aggression were carried out during the four weeks the hamsters were aged from eight to twelve weeks. Every animal took part in each test. It was hoped that sequence effects would be small relative to treatment effects, but so that sequence effects were spread over treatment effects, the order of administration of the tests was balanced by use of the Latin square.

Table II. Latin Square

	Order 1	Order 2	Order 3	Order 4
Group 1	Open Field	Novel situation	Aggression	Activity
Group 2	Aggression	Open Field	Activity	Novel Situation
Group 3	Activity	Aggression	Novel Situation	Open Field
Group 4	Novel Situation	Activity	Open Field	Aggression

Each test (treatment) occurs in every row and every column in a different position. This controls for order effects in a limited way. The animals were placed into four groups and received tests in the order given by the Latin square. Group 1 consisted of 32 hamsters, groups 2 and 3 of 30 and group 4 of 28.

There were two remaining experiments; passive avoidance learning was carried out when the hamsters were 13 weeks of age and they were dissected at 14 weeks.

All experiments, except passive avoidance learning, were performed between 9.30 a.m. and 12.30 p.m. The learning trials took place between 2.00 p.m. and 3.30 p.m. but the retention trial was carried out 20 hours later on the following morning.

Behaviour was recorded on to a Philips cassette tape recorder

(as described in the pilot studies, Chapter Eight) and events were timed by a stopwatch.

D. GENERAL TREATMENT OF DATA

There was a large body of data for many measures from a variety of behavioural and nonbehavioural tests. The results were for hamsters of four genotypes, each with two sexes, from two different housing conditions and repeated over trials in some cases.

As this study explored behaviour of different hamsters in a variety of situations, a statistical test was needed which could scan the data to give initial, but general information on genotype, sex and housing differences. One-way, two-way, three-way and four-way analyses of variance were carried out, depending on the number of factors involved, which were genotype, sex, housing and number of trials. The analysis of variance test was chosen as it gave not only significant differences, but also interactions, which could be important in this type of study.

The experiments were planned for an equal number of hamsters of each genotype and sex to take part in every experiment. Unfortunately, due to piebald death rate, the groups finally were not equal. Also, brown piebald males had to be kept by Roy Robinson for breeding and I therefore received few of them. Twenty golden males, 17 golden females, 23 brown males, 17 brown females, 10 golden piebald males, 14 golden piebald females, 3 brown piebald males and 21 brown piebald females completed all experiments.

Although there are procedures for the examination of unequal groups by analysis of variance, the capacity of the Leicester University computer would not have been large enough and programming would have been extremely complicated in this case. Even if programming had been feasible, the discrepancies in size between the groups of three brown piebald hamsters and 23 brown male hamsters, 21 brown piebald females

or 20 golden males, would have been too great to allow meaningful comparison. The assumptions behind analysis of variance of unequal groups do not permit such a large difference between the groups.

In view of the small number of brown piebald males, it was decided to exclude them from statistical analysis.

The groups had to be equal in size for analysis, which meant that only half the data could be used on any one occasion. As maximum information from the restricted data was desirable, analysis of variance was carried out on some of it, then part of that combined with new data and another analysis of variance performed. Therefore, the data for any one measure ~~were~~ were arranged in various ways and different analyses of variance carried out, which were not wholly independent of each other.

A number of golden males and females, brown males and females, golden piebald males and females, and brown piebald females were available for comparison, providing they were equal in number. Equal numbers of both sexes of the golden, brown and golden piebald genotypes could be compared and equal numbers of females from the four genotypes (golden, brown, golden piebald and brown piebald). On occasions, the differential housing variable was added, separating both sexes of the golden, brown and golden piebald genotypes into two groups, and the females from the four genotypes into two groups. Each hamster belonged to one genotype, sex and housing combination, called a group, and the different combinations of groups compared in any one analysis of variance led to the data being arranged in various ways. In some arrangements the two housing groups were not separated and in others, only females were compared. The way the data ~~was~~ ^{were} split and the number of subjects per group was not identical over all behavioural tests, but throughout the experimental chapters, I have shown the arrangement of the data, that is, listed the factors involved. The individuals comprising any group were chosen randomly

from the selection in the data.

As sex differences are an important aspect of this thesis, the data arrangements of three genotypes, two sexes will be considered more closely than data arrangements allowing analysis of only females from four genotypes.

It is hoped that a reading through the experimental results, where exact data arrangement for any one test has been given, will clarify the way the data ~~has~~ ^{have} been organized and analysed.

When analysis of variance showed that more than two groups were significantly different from one another, a multiple comparison test was carried out to determine which groups were significantly different from each other.

Although each genotype can be represented phenotypically (for example, ++ = golden) the following abbreviations were used throughout this thesis to facilitate reading: G = golden(s), B = brown(s), GP = golden piebald(s) and BP = brown piebald(s).

E. ORGANIZATION OF EXPERIMENTAL CHAPTERS

It seemed logical to place the methods, results and discussions of the nonbehavioural measures in one chapter, as they were likely to be related to one another, so they form Chapter Ten.

Of the behavioural tests, the open field and novel situation would seem fairly closely related, as the novel situation was designed, from the experimenter's viewpoint, to be less fearful than the open field, although measuring similar indices. They comprised also the main experiments in the pilot studies.

The activity experiment was designed to measure hamster activity in almost non-fearful conditions to give a baseline measure of activity. In so far as the open field and novel situation measured activity, in more emotional and less emotional conditions, respectively, the activity experiment giving an activity measure in the least fearful

circumstances fits with these to form Chapter Eleven.

Reaction to handling and the aggressive encounter could both be viewed as types of social situation. The former tested reaction to the experimenter and the latter tested reaction to a conspecific of the same genotype. The passive avoidance learning experiment tested vocal response to electric shock, as well as an aspect of learning, and in this respect has some similarity to reaction to handling, which measured vocalization. The passive avoidance learning experiment, reaction to handling and aggressive encounter therefore comprise Chapter Twelve.

CHAPTER TEN
NONBEHAVIOURAL EXPERIMENTS

A. INTRODUCTION

These consisted of measurements of body weight, food intake to the cage, adrenal gland weight and investigation of the low piebald viability.

Body weight was thought to be possibly related to food intake and was needed to calculate proportional adrenal weight.

The low piebald viability demanded attention in terms of autopsy but only limited results could be obtained.

The main aim of the nonbehavioural experiments was to determine whether they gave results which agreed with those from behavioural tests, that certain classes of hamster could be described as having greater emotionality.

B. BODY WEIGHT

Method

Each hamster was weighed once a week (every seven days) from arrival in Leicester, on a Gallenhamp balance, which measured in grams. Body weight was recorded throughout the experimental period.

Arrangement of Data, Treatment and Results

As explained in Chapter Nine, groups were unequal in size and brown piebald males had to be excluded from analysis. Nevertheless, wishing to obtain maximum information from the data, it was divided into what will be referred to as arrangements. The body weight data comprised two arrangements, each of which involved the recording of one measure only, that of body weight. When genotype differences were significant, and as there were more than two genotypes a multiple comparison test was carried out to determine which genotypes were significantly different from each other, and this is what is presented

in the results.

First arrangement of data

1. This consisted of:
 - a. 2 housing conditions, isolated and grouped.
 - b. 3 genotypes, G, B and GP.
 - c. 2 sexes, male and female.
 - d. 8 trials (weights) over 10 weeks.
 - e. 4 subjects per group.
2. Treatment of the data: by 4-way analysis of variance.
3. The results were:
 - a. Housing differences showed that animals grouped from four to seven weeks weighed more than isolated ones ($p < 0.001$).
 - b. Genotype differences showed that G and B hamsters weighed significantly more than GP hamsters ($p < 0.001$).
 - c. Sex differences showed that males weighed more than females ($p < 0.01$).
 - d. Trial differences indicated that all hamsters showed an increase in weight over 10 weeks ($p < 0.001$).

Second arrangement of data

1. This consisted of:
 - a. 2 housing conditions.
 - b. 4 genotypes, females only, G, B, GP and BP.
 - c. 8 trials.
 - d. 5 subjects per group.
2. Treatment of the data: by 3-way analysis of variance.
3. The results were:
 - a. There were no housing differences.
 - b. Genotype differences showed that G and B were heavier than GP or BP ($p < 0.001$).
 - c. Trial differences showed that all animals increased in weight over 10 weeks ($p < 0.001$).

For summaries of the analyses of variance carried out on body weights

see Summary Tables III and IV.

Summary Table III

Four-way analysis of variance carried out on body weights in first data arrangement.

Variation	SS	MS	DF	F	Significance level
Housing	4823.75	4823.75	1	15.25	0.001
Genotype	53937.25	26968.62	2	85.25	0.001
Housing x Genotype	1233.33	616.67	2	1.95	NS
Sex	3819.07	3819.07	1	12.07	0.01
Housing x Sex	2012.09	2012.09	1	6.36	0.05
Genotype x Sex	1480.58	740.29	2	2.34	NS
Housing x Genotype x Sex	487.00	243.50	2	0.77	NS
Trial	109978.10	15711.16	7	715.77	0.001
Housing x Trial	2713.98	387.71	7	17.66	0.001
Genotype x Trial	4248.12	303.44	14	13.82	0.001
Sex x Trial	615.41	87.92	7	4.01	0.001
Housing x Genotype x Trial	264.12	18.87	14	0.86	NS
Genotype x Sex x Trial	780.62	55.76	14	2.54	0.01
Housing x Sex x Trial	398.73	56.96	7	2.60	0.05
Housing x Genotype x Sex x Trial	113.13	8.08	14	0.37	NS

Summary Table IV

Three-way analysis of variance carried out on body weights in second data arrangement.

Variation	SS	MS	DF	F	Significance level
Housing	369.80	369.80	1	0.89	NS
Genotype	43533.94	14511.31	3	35.01	0.001
Housing x Genotype	942.80	314.27	3	0.76	NS
Trial	64367.19	9195.31	7	369.76	0.001
Housing x Trial	3268.90	466.99	7	18.78	0.001
Genotype x Trial	5021.86	239.14	21	9.62	0.001
Housing x Genotype x Trial	328.30	15.63	21	0.63	NS

Discussion

Piebalds, males and females, weighed less than golden and brown hamsters of both sexes, when eight weights were measured over a 10 week period. This agrees with earlier studies of the piebald hamster (e.g. Foote 1949, Robinson 1971).

Males of the G, B and GP genotypes weighed more than females of the same genotypes. This conflicts with Swanson's findings (1967), who found female hamsters tended to be heavier than male hamsters, but the sex differences in the results presented here are similar to the rat findings where males weigh more than females. Foote and Foote (1950), in a study of normal and piebald hamsters, found weight decreased from normal males, to normal females to piebald females, with piebald males being the lightest. My weights for G and B agree with Foote and Foote's for normals but among the piebalds, males showed a heavier weight than females consistently throughout trials. One reason for the conflicting findings of weight differences for males and females reported by Foote and Foote (1950) and by Swanson (1967) could be that the hamsters were obtained from different stocks, and different lengths of time after the original mutation, first described by Foote (1949). The combination of both these procedures could produce contradictory evidence, and the former reason could be an explanation of my findings compared to Swanson's (1967).

Housing differences were significant, with group raised animals weighing more than isolated ones. Winokur, Stern and Taylor (1959), studying differential housing over a 38 day period found that it produced no weight differences in rats. Hatch, Wiberg, Balazs and Grice (1963) found a short isolation of 10 days led to a lower body weight in mice. Differential housing in my experiment was short, from 15-20 days, with the result that isolates weighed less, concordant

with Hatch's et al. mice findings.

Many studies have suggested that rats and mice reared in isolation were more emotional as adults than animals kept in groups (Priestnall 1970). This is not necessarily expected in hamsters as almost nothing is known about their behaviour in the wild (Murphy 1971), and there is little basis for hypotheses regarding the impact of isolated or grouped living.

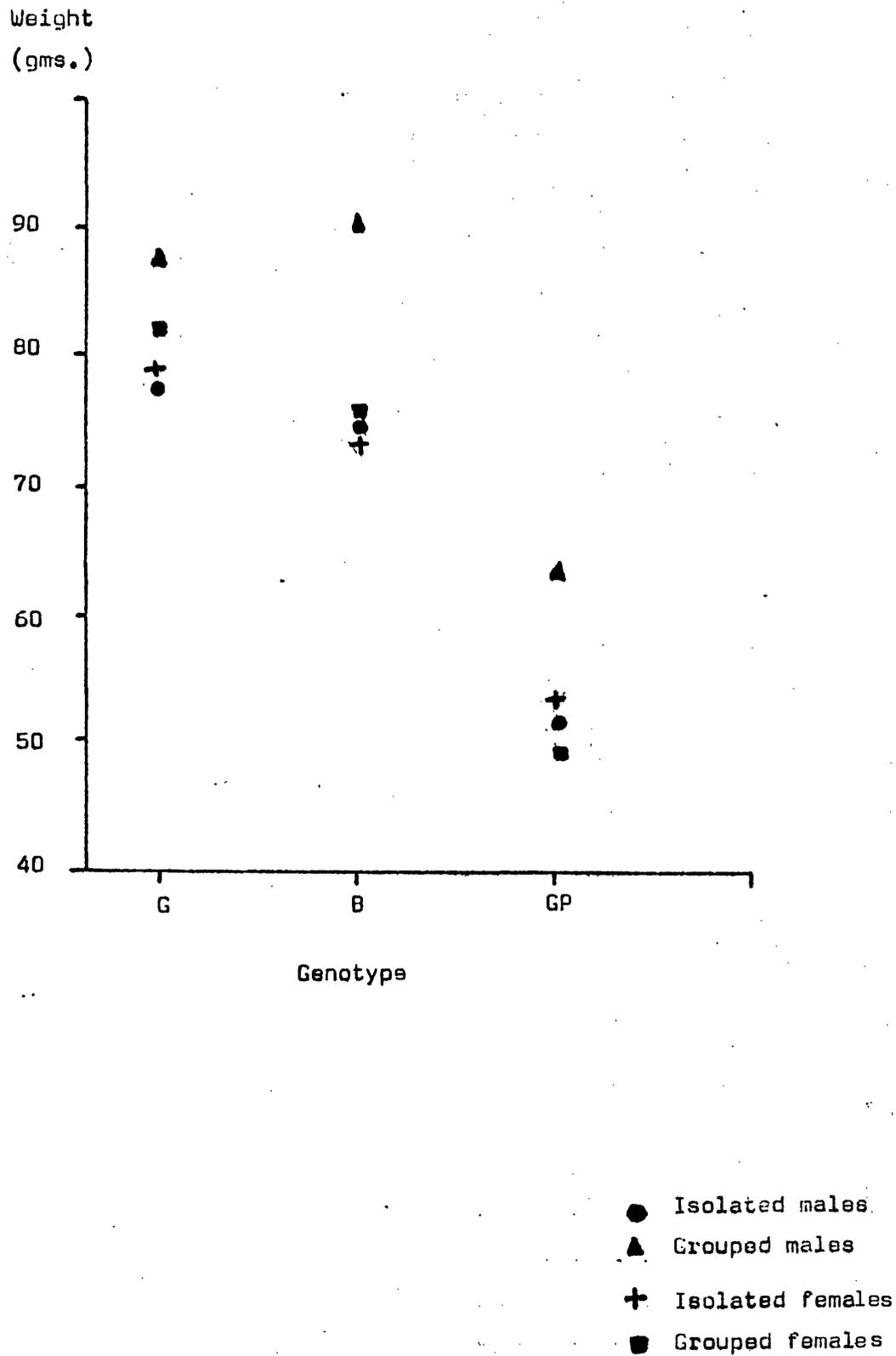
GP were shown to weigh less than G or B, isolated animals weighed less than grouped ones and females weighed less than males. Therefore, it can be predicted that grouped G and B males will be the heaviest, followed by grouped G and B females, isolated G and B males, isolated G, B females, grouped GP males and females, with the lightest animals being isolated GP males and females. Although the housing x genotype x sex interaction was not significant, trends of this sort were indicated (figure 6).

Weight increased over trials with piebalds weighing less than golden or brown hamsters on every trial, including trial one (genotype x trial interaction). Females weighed less than males on every trial (sex x trial interaction) and grouped hamsters weighed more than isolated ones until trial 6 when they became equal (housing x trial interaction).

Piebalds, females and isolates therefore weighed less than golden or brown hamsters, males and group housed animals respectively.

There is some indication that increased levels of glucocorticoids produced by the adrenal cortex (thought to occur in response to stress) resulted in decreased growth (De Wied 1966) and that corticosteroids produced by the adrenal gland depress growth in hamsters (Swanson 1967). Lowered growth is also mentioned as part of the general adaptation syndrome (Selye 1946).

Figure 6. Mean body weight: housing x genotype x sex interaction, data in arrangement one.



Therefore a low body weight resulting from depressed growth may be linked with emotionality, but the way in which this happens needs to be ascertained. The piebald hamster showed increasing weight discrepancies with age (trial) compared to the golden and brown type. This may be due to:

1. deficiencies in the somatotrophic (growth) hormone which relate to effects of the adrenocortical system (thought to be associated with emotional behaviour).
2. deficiencies in the growth hormone linked with changes in areas not specifically linked with emotionality.
3. the possibility that the piebald hamster is genetically smaller than the wild type, which may relate to physical coping and survival, but not to behaviour.

It cannot be determined, at this point, whether the genotype weight differences shown in the study, reflect differences in susceptibility to emotionality.

C. FOOD INTAKE TO THE CAGE

Method

Isolates were given 50 food pellets of diet FFG(M), in their food hopper when they arrived, and the amount they took into their cages, in terms of number of pellets, every week, was recorded.

Group housed animals were given a random amount of food pellets, while housed in groups, and only when they were isolated at seven weeks were pellet numbers controlled and individual intake to the cage recorded.

Water consumption was not measured as hamsters drink little water.

The food intake score was measured for all animals when they were living alone (not in groups) but they were labelled according to

whether they were isolated or group housed for $2\frac{1}{2}$ weeks after arrival. As isolated hamsters lived alone from arrival, the first five recordings of their food intake would be from their ages of four to nine weeks, and the first five recordings from the group housed animals would be from eight to 13 weeks of age. The first five recordings of the isolated and group raised hamsters have been compared, and their ages ignored. These form the data under the heading: Food Intake to Cage; First Five Recordings; Age Uncontrolled.

Recordings taken between the ages of eight and 13 weeks for isolated and group reared animals were also compared and comprise data under the heading: Food Intake to Cage; Age Controlled Recordings.

Arrangement, Treatment and Results of Data from Food Intake to Cage,
First Five Recordings; Age Uncontrolled

First arrangement of data

1. This consisted of:
 - a. 2 housing conditions, isolated and grouped.
 - b. 3 genotypes, G, B and GP.
 - c. 2 sexes, male and female.
 - d. 5 trials.
 - e. 4 subjects per group.
2. Treatment of the data; by 4-way analysis of variance.
3. The results were:
 - a. Housing differences showed that isolated animals took more food into their cages than grouped ones ($p < 0.001$).
 - b. Genotype differences showed that GP took in less than G or B ($p < 0.001$).

Second arrangement of data

1. This consisted of:
 - a. 2 housing conditions.
 - b. 4 genotypes, females only, G, B, GP and BP.
 - c. 5 trials.
 - d. 5 subjects per group.

2. Treatment of the data: by 3-way analysis of variance.
3. The results were:
 - a. Housing differences showed that isolated animals took more food into their cages than grouped ones ($p < 0.001$).
 - b. Genotype differences showed that G took in more food than B, GP or BP ($p < 0.001$) and B took more in than GP or BP ($p < 0.001$).

Arrangement, Treatment and Results of Data from Food Intake to Cage;

Age Controlled Recordings

First arrangement of data

1. This consisted of:
 - a. 2 housing conditions.
 - b. 3 genotypes, G, B and GP.
 - c. 2 sexes.
 - d. 5 trials.
 - e. 4 subjects per group.
2. Treatment of the data: by 4-way analysis of variance.
3. The results were:
 - a. Housing differences showed that isolates took more food into their cages than grouped hamsters ($p < 0.001$).
 - b. Genotype differences showed that G took in more than B and GP, and B took in more than GP ($p < 0.001$).
 - c. A housing x trial interaction ($p < 0.001$) showed that isolated animals took more food into their cages on all trials than grouped individuals, but they showed a decrease over trials. Grouped hamsters showed the opposite tendency with a small increase over trials. By trial 5, the two differentially housed groups showed similar intake of food to the cage.

Second arrangement of data

1. This consisted of:
 - a. 2 housing conditions.

- b. 4 genotypes, females only, G, B, GP and BP.
 - c. 5 trials.
 - d. 5 subjects per group.
2. Treatment of the data; by 3-way analysis of variance.
 3. The results were:
 - a. Housing differences showed that isolates took more food in than grouped animals ($p \leq 0.001$).
 - b. Genotype differences showed that G took in more than B, GP and BP; B took in more than GP and BP, and GP took in more than BP ($p < 0.001$).

For summaries of the analyses of variance with significant housing, genotype and trial differences, and housing x trial interactions see Summary Table V.

Discussion

Whether or not age was controlled the results showed the same trends. Piebalds took less food into their cages than G or B and they have been shown to weigh less. However, isolates took in more food than group housed animals, but have also been shown to weigh less. Isolated piebalds took in more food than grouped piebalds, although these amounts are less than those for G or B.

It should be emphasized that here the measure taken weekly was number of food pellets left in the food hopper. It would be possible for an animal to take into its cage an amount of food but actually ingest only a portion of it. Number of faecal boluses were not recorded, and the cages were not searched for remnants of food pellets so actual amount eaten is unknown.

Regarding housing differences, these food intake results agree with the findings of Weltman, Sachler and Sparber (1966) for mice, who observed albino female mice under differential housing conditions for 16 weeks from one month of age. The workers measured food

Summary Table V

Analyses of variance carried out on food intake to cage data showing housing, genotype and trial differences, and housing x trial interactions.

	Variation	SS	MS	DF	F	Significance level
First Five Recordings, Data in Arrangement One	Housing	3352.54	3352.54	1	62.91	0.001
	Genotype	3368.32	1684.16	2	31.60	0.001
	Trial	563.06	140.76	4	8.22	0.001
	Housing x Trial	244.27	61.07	4	3.57	0.01
First Five Recordings, Data in Arrangement Two	Housing	3672.25	3672.25	1	94.44	0.001
	Genotype	3988.70	1302.90	3	33.51	0.001
	Trial	574.55	143.64	4	7.39	0.001
	Housing x Trial	130.53	32.63	4	1.68	NS
Age Controlled Recordings, Data in Arrangement One	Housing	2281.67	2281.67	1	48.26	0.001
	Genotype	3116.61	1558.30	2	32.96	0.001
	Trial	369.73	92.43	4	5.92	0.001
	Housing x Trial	751.50	187.88	4	12.04	0.001
Age Controlled Recordings, Data in Arrangement Two	Housing	2820.01	2820.01	1	57.34	0.001
	Genotype	3577.30	1192.43	3	24.25	0.001
	Trial	234.22	58.56	4	4.16	0.01
	Housing x Trial	691.22	172.80	4	12.29	0.001

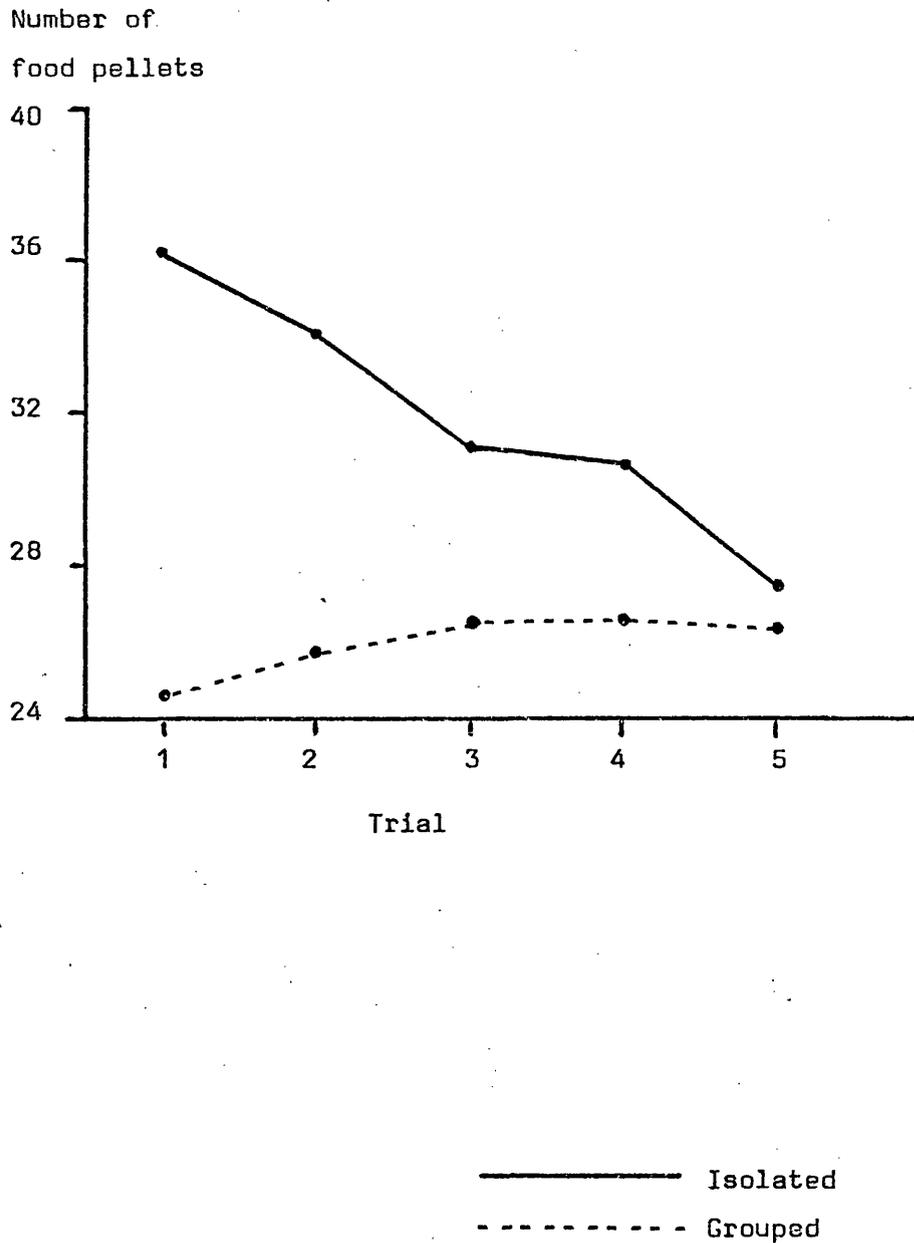
consumption, but did not mention how this was taken and reported that isolated mice showed increased food consumption compared to mice housed in pairs, despite a trend toward decreased body weight. In an earlier study Weltman, Sachler, Sparber and Opert (1962) found differences were only significant until the tenth week. Weltman et al. (1962, 1966) could not account for the differences in food consumption other than suggest that "isolation stress" resulted in various endocrinological changes and increased metabolic rate, so that despite increased food consumption, isolates showed a lower body weight.

An increased metabolic rate and food assimilation in isolated rodents could be responsible for the hamster findings, but this needs to be tested, especially as it was stated earlier that there was little evidence to give rise to hypotheses on the reactivity of hamsters to different types of housing.

There is another possible reason for this particular finding. On looking at the housing x trial interaction (figure 7) it can be seen that variation between trials is small for grouped hamsters but larger for isolates. On trials one to three isolates collected more food than grouped animals, but by trial five, their intake decreased to equal that of grouped hamsters. It therefore seems unlikely that the extra food taken in by the isolates was needed to encourage growth or other metabolic processes, as the grouped animals should have taken in as much, especially as they weigh more. The difference may relate to hoarding behaviour, so that isolates take more food in than grouped hamsters, but hoard more initially. Over trials, isolates learn that food is constantly accessible, so no longer take in excessive amounts, thereby equalling the rate of grouped hamsters by trial five.

The validity of this kind of suggestion will depend on results from observation of hamster hoarding behaviour.

Figure 7. Mean number of food pellets taken into the cage; age controlled recordings: housing x trial interaction, data in arrangement one.



It is relevant at this stage because previous workers have shown an association between hoarding and emotionality. For example, Seitz (1954) suggested that rats from large litters were more emotional than rats from smaller ones and showed that the former hoarded significantly more food pellets at two and nine months of age.

Two rat strains, the black-hooded and brown-hooded, have been shown to be emotional and non-emotional, respectively, in the open field test (Broadhurst 1958), yet Stamm (1954) showed that food deprived black-hooded rats hoarded sooner, hoarded more and hoarded for a longer period of time, than brown-hooded rats, even though food pellets were supplied in the cage.

It could be postulated that isolation in hamsters may lead to hoarding behaviour via the intervening variable of emotionality. However, hamster hoarding behaviour in conjunction with records of body weight, metabolic rate, faecal number and weight, as well as behaviour more generally of isolated individuals, must be studied first.

Piebalds and isolates, although showing less weight gain compared to non-piebalds and grouped hamsters respectively, reacted differently to their environments in terms of collecting food for the cage (cf. Results). If increased emotionality is to be used to describe the state of the piebald hamsters, it cannot be used also to describe that of isolated individuals who behaved differently from piebalds, in this experiment, unless it is suggested that piebalds and isolates display different patterns of emotionality, of which food intake is a single measure.

The findings of this experiment reinforce the view that emotionality is complex, and can too easily be invoked as responsible for a

variety of behaviours by different animals in one test situation. The experiment reported did not allow direct measures of fear, escape and immobility, and the indirect measures are difficult, at this stage, to interpret in terms of emotionality.

Therefore, it is concluded that this experiment offers little regarding factors affecting emotionality differences in hamsters of four genotypes, two sexes and reared in two types of postweaning housing conditions.

D. DISSECTION

Method

In week 14 every hamster was killed by being placed on wire mesh dividing a large gas jar in half. Chloroform was poured in to the jar, the top secured and the animals left in there for one hour. They were then removed and dissected in the usual way for rodents, cutting the ventral skin. In all, 20 golden males, 17 golden females, 23 brown males, 17 brown females, 10 golden piebald males, 16 golden piebald females, 3 piebald males, 21 brown piebald females were dissected after completing experiments. The following investigations were carried out:

1. The stomachs were cut open, food washed out and examined for ulcers. Position and number of ulcers were recorded.
2. The two adrenal glands were taken out, and the glands' surrounding connective tissue removed, put on a small round plastic tray and weighed on a Mettler Type H6 balance, the measurement being made to one tenth of a milligram. This weight was calculated as a percentage of the last recorded body weight.
3. Any abnormalities of the urinogenital tracts were noted.

Results for Stomach Ulcers

One brown male had a small ulcer in the antrum, one brown female had a medium sized one in the rumen, one golden piebald male had a small ulcer in the antrum, two golden piebald females showed ulceration, one with one ulcer in the antrum and the other with two medium sized ulcers and six small ones in the antrum, one brown piebald male had one small ulcer in the rumen, one brown piebald female had a small ulcer in the rumen. As there was a uniformly low incidence of ulceration among the genotypes, these results will not be discussed.

Results for Urinogenital Abnormalities

One brown piebald male showed the right kidney to be missing and the right testis to be vestigial. This was the brown piebald male that showed a small gastric ulcer. One brown piebald female had her left uterus missing, although showed no ulcer incidence.

Only one out of 13 piebald males and one out of 37 piebald females showed any urinogenital anomaly. Foote (1955) found 4.3 percent of his piebald males and 20.8 percent of his piebald females showed anomalies. The incidence in my hamsters was therefore much reduced. It is possible that in the 17 or 18 years since Foote carried out his study, the piebald type has been influenced by selection and urinogenital abnormalities in surviving piebalds are now rare.

Arrangement of Data, Treatment and Results of Adrenal Gland Weights.

First arrangement of data

1. This consisted of:
 - a. 3 genotypes, G, B and GP.
 - b. 2 sexes, male and female.
 - c. 10 subjects per group.

2. Treatment of data: by 2-way analysis of variance.
3. The results were:
 - a. Genotype differences showed an increase in adrenal weight from G to B to GP, with GP having significantly heavier glands than G ($p < 0.01$), and B falling intermediately
 - b. Sex differences showed that males had heavier glands than females ($p < 0.01$).

Second arrangement of data

1. This consisted of:
 - a. 4 genotypes, females only, G, B, GP and BP.
 - b. The subjects were 17 G, 17 B, 14 GP and 20 BP females.
2. Treatment of data: by 1-way analysis of variance.
3. The results were:
 - a. There was an increase from G to B, to GP, to BP in adrenal weight, with B, GP and BP glands being heavier than G's ($p < 0.001$).

Third arrangement of data

1. This consisted of:
 - a. 2 housing conditions, isolated and grouped.
 - b. 3 genotypes, G, B and GP.
 - c. 2 sexes.
 - d. 4 subjects per group.
2. Treatment of data: by 3-way analysis of variance.
3. The results were:
 - a. Genotypic differences showed that adrenal weight increased from G to B, to GP, with GP being significantly heavier than G ($p < 0.001$), and B falling intermediately.
 - b. Sex differences showed males to have heavier glands than females ($p < 0.001$).

Fourth arrangement of data

1. This consisted of:

- a. 2 housing conditions.
 - b. 4 genotypes, females only.
 - c. 5 subjects per group.
2. Treatment of data: by 2-way analysis of variance.
 3. The results were:
 - a. There was an increase in adrenal weight from genotypes G to B, to BP, to GP, with GP being significantly heavier than G ($p < 0.01$).

For summaries of analyses of variance carried out on adrenal weight data, showing housing, genotype and sex differences, see Summary Table VI.

Discussion

1. Genotype differences

In so far as adrenal weight as a proportion of body weight is an indicator of adrenocortical reaction to the environment, the results clearly showed it to be greater in golden piebald and brown piebald than in golden hamsters. The weight of the adrenal glands of the brown animals fell between those of G and GP/BP, and this non-significant trend may implicate an intermediate stress response by brown hamsters.

Foote (1955) in a study of piebald urinogenital abnormalities wrote that the "adrenal glands appeared normal in all cases in two cases the adrenals were enlarged, but in one of these the female was known to be pregnant". It is not clear if Foote was comparing adrenal size of piebalds with that of non-piebalds, when he claimed that they appeared normal, but my results definitely showed that piebalds had enlarged adrenals.

The Maudsley reactive rats have been shown to possess larger adrenal glands than the non-reactive line. These rats also weighed more (Feuer 1963). Piebalds have larger adrenals than non-piebald

Summary Table VI

Analyses of Variance carried out on adrenal weight data, showing housing, genotype and sex differences.

Arrangement of data	Variation	SS	MS	DF	F	Significance level
One	Genotype	16933.30	8466.65	2	7.41	0.01
	Sex	50402.02	50402.02	1	44.13	0.001
Two	Genotype	15354.00	5118.00	3	6.46	0.001
Three	Housing	2.52	2.52	1	0	NS
	Genotype	23674.04	11837.02	2	9.70	0.01
	Sex	34080.02	34080.02	1	27.91	0.001
Four	Housing	211.60	211.60	1	0.17	NS
	Genotype	23401.40	7800.47	3	6.12	0.01

hamsters, but their body weight is less. If adrenal size is a broad indicator of adrenocortical function in both species, interaction with the different networks of hormonal and nervous systems in the two species may lead to different expressions of emotionality physically, for example, in body weight, and behaviourally (as will be seen in Chapters Eleven and Twelve, and is discussed in Chapter Thirteen).

Therefore, the different correlations between adrenal weight and body weight in the two species do not necessarily prove that either or both measures are poor indices of emotionality.

When adrenal weights among genotypes were not calculated as a proportion of body weight they appeared similar. The possibility exists, therefore, that they do not reflect different levels of emotionality (because absolute weights are similar) and that differences in body weight may represent another sort of reaction, unrelated to fear.

2. Sex differences

The findings showed that male hamsters had heavier adrenal glands than females. This agrees with previous findings for hamsters (e.g. Swanson 1967, Zieger, Lux and Kubatsch 1974).

In rats, however, the reverse has been true - adrenals being larger in the female (e.g. Skelton and Hyde 1961, Kitay 1961).

Regarding body weight for rats, males have been found generally to be heavier, but for hamsters a number of investigators have reported that female hamsters were larger, although there have been some cases of inconsistent findings that showed males were heavier than females and contradict some hamster reports.

In gonadectomy studies, Swanson (1967) found that removal of the testes resulted in increased growth in hamsters, which implied that the presence of androgens decreased growth. It was also shown that the large size of the adrenals was due to action by androgens,

since castration caused a decrease, and testosterone treatment an increase, in adrenal weight - a converse result to that obtained in rats.

Swanson (1967) claimed that there was not necessarily a relation between the weight of a gland and its rate of secretion but speculated that as corticosteroids normally depressed growth in hamsters, the larger adrenals in males may result in greater hormone secretion which might depress body growth more than in females.

Although this may be a reasonable speculation from her results, since her females were larger than males, it is not applicable to my results with the opposite trend, males being larger than females. The action of androgens on body weight and adrenal weight are therefore questionably related, with the explanation of my data remaining obscure.

Adrenal weight may reflect adrenocortical function in some cases and the greater adrenal size found in female rats adds to scepticism regarding Gray's suggestion (1971a,b) that male rodents are more emotional than female rodents. Adrenal weight is unlikely to relate, in an orderly fashion, to sex differences in emotionality because these vary with test situation, species, strain and early experience of the animal studied (cf. Chapter Seven).

However, adrenal size may relate more closely to sex differences in aggression which seem more consistent within a species than sex differences in emotionality.

Male rats are considered to be more aggressive than female rats, based on reported responses to pairing (Gray 1971a), yet show smaller adrenal glands. On the other hand, female hamsters are dominant to the males in aggressive encounters and have comparatively lighter adrenals. Therefore there is a correlation in the hamster and rat species between sex differences in adrenal size and amount of aggression shown by each

sex (submission correlates with higher adrenal weight).

Relevant here are studies relating dominance with adrenal weight. For example, Davis and Christian (1957) ranked mice from the most dominant to the most subordinate, in 14 populations. Adrenal weight was least in the dominant animals and most in the subordinate ones, while intermediately ranked mice possessed intermediate weights.

The significance of the relationship between low aggression/subordination and enlarged adrenal glands in terms of fear level is hard to determine. The subordinate mice in the Davis and Christian study may have had difficulty in coping with the hierarchial system, which the authors suggest is reflected in the adrenals, but this is unlikely to be the case for hamsters who probably do not live under the same social conditions as mice.

More plausibly, it would seem that enlarged adrenals are indicators of adrenocortical response in either males or females, to certain kinds of stimuli. Female rats, but male hamsters, react particularly strongly to these stimuli, which cannot be identified beyond the possibility, suggested by the correlation between adrenal weight and aggressive behaviour, that they are associated with conspecific interaction. This would not preclude the likelihood that the opposite sexes in both species, males in rats and females among hamsters, react more fearfully to other types of stimulation, such as novel environments, which is not reflected in adrenal weight.

3. Housing differences

The adrenal results showed no housing effects.

Several studies have shown that isolated housing produced adrenal hypertrophy in rats (e.g. Stern, Winokur, Eisenstein, Taylor and Sly 1960, Geller, Yuwiler and Zolman 1965, Hatch, Wiberg, Zawidzka, Cann, Airth and Grice 1965), although Hatch, Wiberg, Balazs and Grice

(1963) found short-term isolation resulted in smaller adrenals, and Weltman, Sachler, Sparber and Opert (1962) found no difference between isolated and grouped mice. It may be slightly surprising that the short-term differential housing had no effect on adrenal weight, when there were several apparent behavioural effects (Chapters Eleven and Twelve) although the lack of any consistent pattern of emotional behaviour shown by either type of housed hamster is further supported by this finding.

Conclusion

It is concluded that differences in adrenal weights between genotypes reflect differences in adrenocortical response, indicating that piebalds are more emotional than golden hamsters. The intermediate size of the adrenal glands of the brown hamsters may represent intermediate emotionality, which would agree with their tendency, in a few cases, to express fear behaviour between that of golden and piebald genotypes (cf. Chapters Eleven and Twelve).

However, the added variable of sex, involving interaction between the pituitary gland, adrenals and gonads, masks any simple relationship between adrenal size and emotionality, so that sex differences in this crude physiological measure do not permit subtle deductions regarding sex differences in fear.

Use of other measures of adrenocortical activity and their correlation with behaviour, over genotypes and sexes in both hamsters and rats, may clarify the extent to which adrenal weight is an index of emotionality.

E. COMMENTS ON PIEBALD VIABILITY

Introduction

Piebald survival rate was only 60.8 percent compared to that of

non-piebald hamsters which was almost 100 percent. The data showed that death occurred predominantly between hamster arrival in Leicester at four weeks of age and the start of experiments at eight weeks.

Causes of death were searched for by post-mortem examination, but usually the individuals were too autolysed for definite conclusions.

Gastric ulcers were found to occur in a large percent of non-viable hamsters. These agreed with Ader's, Beels' and Tatum's description of the appearance of ulcers in the rat stomach (1960) and diagnosis was confirmed by Doctors R. J. Naftalin and R. O. Law of the physiology department at Leicester University. A random selection of ulcerated stomachs were stained with haemotoxylin and eosin, blocked and sectioned with a Cambridge rocking microtome, to give biological slides and photographs (see photographs 1 and 2).

Piebald mortality and ulceration will be considered in relation to the isolated and grouped housing factors. The high death rate shown by isolated piebalds in conjunction with severe ulceration suggested that, for these hamsters to undergo a train journey and then to be housed solitarily having been accustomed to living with litter mates, was exceptionally stressful. It was thought that if piebalds were group housed with other hamsters they travelled with, from arrival till just before the start of experiments, they might adapt successfully to the new environment and death rate would be alleviated.

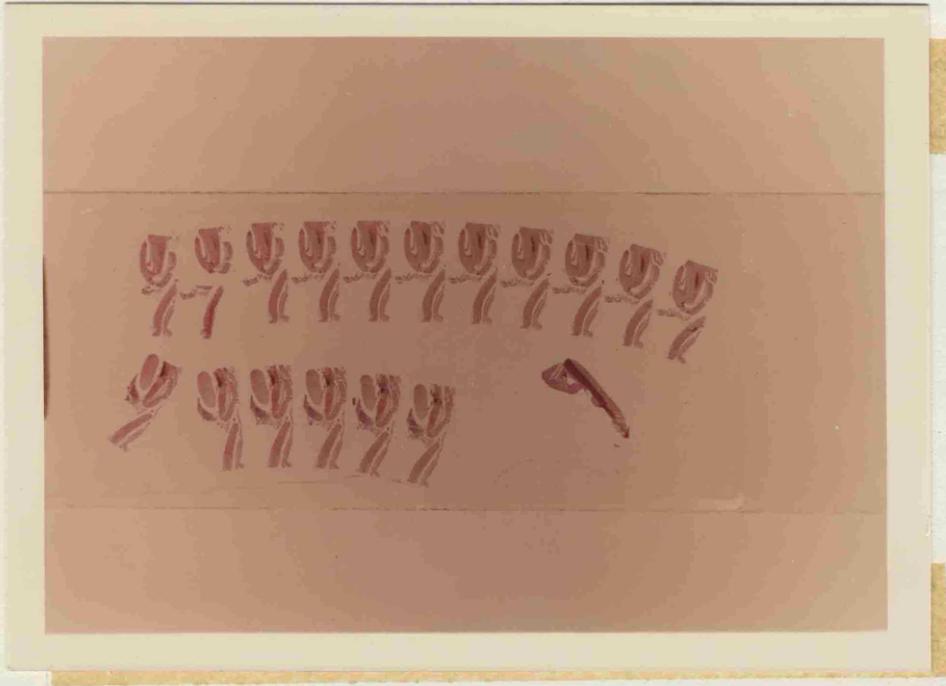
Isolation and Grouping of Piebalds in Relation to Ulceration and Mortality

A number of piebalds of both genotypes and sexes died between four and seven weeks of age, whether isolated or group housed. The death rate among isolated piebalds was not significantly higher than that for group housed piebalds ($p > 0.05$, as shown by a Mann-Whitney U Test, White's modification). My prediction, therefore, that group housing would enhance viability was not confirmed.

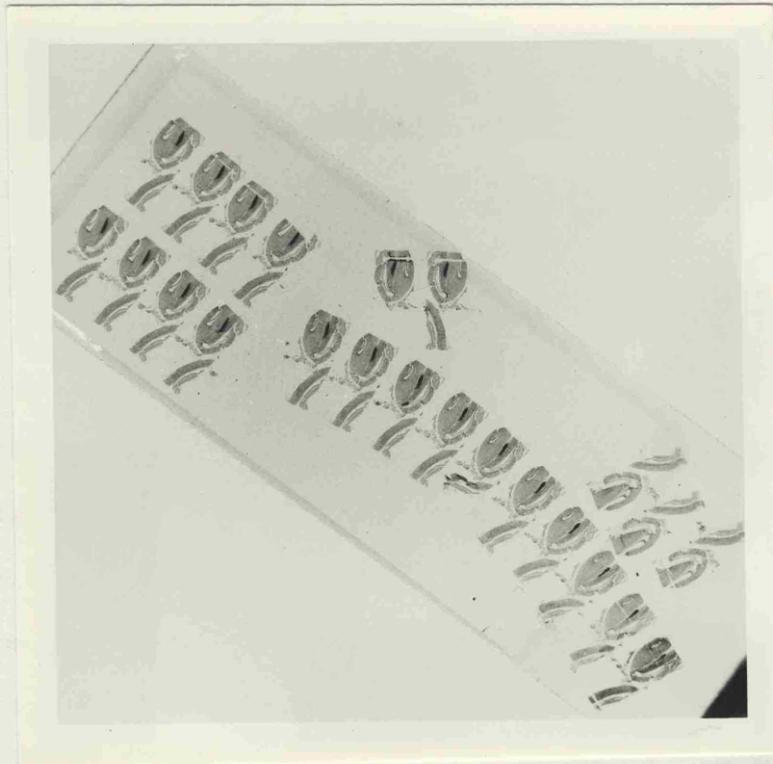
Photographs 1 and 2

Slides of two stained and sectioned piebald hamster stomachs. Dark patches indicate ulceration.

1.



2.



Although four non-piebald hamsters died during isolated housing, not one died during grouped living. To ascertain that significantly more piebald hamsters died than non-piebald genotypes during isolation, a χ^2 one sample test was carried out. A significant difference existed between observed scores in each piebald genotype and sex combination and expected number ($p < .001$). From the raw data, it is clear that piebalds had a higher death rate than non-piebalds (Table III).

Age at Death

When hamsters were isolated, piebalds mostly died in their fourth or fifth week. When they were group housed, mortality did not occur during group living, but during the ten or so days of isolation between the end of grouping and start of the experiments, that is, in the seventh or eighth week. Not a single piebald died while group housed, but they quickly succumbed when isolated, despite $2\frac{1}{2}$ weeks of adaptation to the Leicester environment.

Group housing, therefore, did not prevent death; it merely postponed it.

Isolation seemed to be a critical factor in causing piebald mortality, whether it occurred at four or $6\frac{1}{2}$ - 7 weeks of age, and this underlines the importance of psychological factors in the low piebald viability.

In addition, is the finding that only two hamsters, both piebald, died during the course of experiments. This indicated that the experiments were not, on the whole, severe enough to cause death or that if an animal could survive the train journey, and adapt to the caging conditions, it could endure the experiments. One hamster, a female brown piebald hamster, died on the third electric shock session of the learning experiment. This may well have been a coronary effect,

Table III

Housing conditions, genotype and sex of hamsters that died, with the severity of ulceration and age at death.

1. Isolated Hamsters	Severity of Ulceration	Age at Death
G female	no ulcers	5 weeks
G "	no ulcers	5 "
B male	1 large ulcer, 2 medium, 1 small	7 "
B female	no ulcers	5 "
GP male	2 large, 3 small ulcers	4 "
GP "	1 large, 1 medium, 3 small ulcers	5 "
GP "	1 large, 1 medium, 6 small ulcers	4 "
GP "	2 small ulcers	5 "
GP "	1 large, 1 medium, 4 small ulcers	6 "
GP "	no ulcers	4 "
GP female	several small ulcers	4 "
GP "	no ulcers	5 "
GP "	3 large, 3 small ulcers	4 "
GP "	7 medium ulcers	4 "
GP "	1 large ulcer	6 "
BP male	2 medium ulcers	4 "
BP "	8 small ulcers	6 "
BP "	2 medium and several small ulcers	5 "
BP female	1 large, 1 small ulcer	4 "
BP "	4 medium ulcers	4 "
BP "	4 medium, 2 small ulcers	5 "

Table III continued

2. Group Housed Hamsters	Severity of Ulceration	Age at Death
GP male	3 large, 2 medium ulcers	8 weeks
GP female	several ulcers	8 "
GP "	2 large, 1 medium, 1 small ulcer	8 "
GP "	4 medium ulcers	6 "
GP "	4 large, 2 medium	11 "
GP "	no ulcers	8 "
BP female	3 large, 2 medium ulcers	12 "
BP "	no ulcers	8 "
BP "	7 medium, 14 small ulcers	8 "
BP "	1 large, 2 medium ulcers	6 "
BP "	4 large, 7 medium, 5 small ulcers	7 "
BP "	2 medium, 4 small ulcers	6 "
BP "	2 large, 13 medium ulcers	8 "
BP "	autopsy, unknown results	6 "

but confirmation was not readily available. A golden piebald female was seen to fall into a coma on the third electric shock trial, but she recovered, although the following day was found to have severe wet tail. She was given the retention trial and killed, as wet tail is considered to be highly infectious.

Although this was the only hamster in the main study to have wet tail, the pilot study showed a high incidence, and I tried to gain further information about the disease. A personal communication (1973) from A. Sebesteny (Head of the Animal Health Unit at Imperial Cancer Research Fund Laboratories) on wet tail in hamsters is worth quoting: "The cause of this condition is still not known. There is a suggestion that it may be caused by a virus It may be a classic case of stress-linked condition. Our colony suffered quite a lot from it but a newly established colony appears to be quite free from this condition. This supports the theory that perhaps an agent may be involved".

To return to discussion about the importance of isolation as a psychological factor in causing death among piebalds, this can only be established by a controlled study investigating the effect of group housing for a longer period of time, with, without and during experimentation. Genotypic and sex content and size of the group could be manipulated, with full autopsies searching for the cause of death. At present it can be asked whether piebalds are succumbing to the exhaustion phase of Selye's general adaptation syndrome, due to interaction of psychological stimuli and genetically determined low disease resistance, or whether they die due to onset of diseases and infections, regardless of psychological factors such as living conditions. The limited evidence would suggest that the former is more likely.

Ulceration

A high percent (85-88%) of dying piebalds showed gastric ulceration, with the extent and severity being unassociated with previous

isolated or grouped housing, as shown by a Mann-Whitney U Test (White's modification; $p > 0.05$).

By contrast, an insignificant number of surviving piebalds (five) and non-piebalds (two) developed stomach ulcers, as determined by dissection in the 14th week. Arcari, Gaetani, Glasser and Turolla (1968) found a low incidence of spontaneous ulceration among hamsters and suggested that this has discouraged the use of hamsters in experiments studying ulceration. These authors managed to induce ulcers in the male golden hamster by food deprivation and restraint, but found the incidence in adrenalectomized hamsters and sham-operated controls to be comparable. As a result of this finding, Arcari et al. suggested that secretion of the adrenal hormones was of little importance in restraint induced ulcers.

This may be true for restraint induced ulcers, but my findings for the piebald hamster, showing that this genotype possessed enlarged adrenal glands and a high mortality correlated with a proneness to stomach ulceration, would support the hypothesis that the adrenal system may be relevant to onset of the type of ulcer shown by the piebald hamster.

The cause of ulceration in dying piebald hamsters cannot be established from the present study, but there are various possibilities:

1. They are one reaction to stressful circumstances and the animals die because they can no longer maintain resistance to them.
2. Ulcers may be serious enough to be fatal, hence the correlation between ulceration and death rate.
3. Ulcers may be part of a disease syndrome and death is caused, not by severe ulceration, but by another factor which is part of the syndrome.

Ulcers seem to be linked with mortality in this study, and

are thought to be associated with emotionality (cf. Chapter Six).

The relationship between death among piebalds and solitary living provides support for possibility 1 above, that psychological factors play a role in ulcer formation and subsequent mortality.

Stress-linked Parasitism

Anecdotal evidence also supports the likelihood that psychological influences seriously affect the piebald hamster.

In order to obtain more information on the cause of death in this genotype, two hamsters were sent for autopsy. B.S.H. Potter (B.V.M., M.R.C.V.S.) autopsied one, a golden piebald female, which showed a parasitic infection called coccidiosis in the caecum. Although this parasite is a common laboratory infection, it was unknown in hamsters (Sebesteny, personal communication) and Wantland (1955, 1968) in lengthy accounts of the golden hamster parasitic infections does not mention coccidiosis. However, in Potter's opinion, the coccidiosis in the piebald hamster did not seem severe enough to cause death. No other disease or infection could be found in this hamster.

Therefore, there was an indication that piebalds may get infections which although proving fatal in them, are not normally so in non-piebald hamsters, implying a lowered ability of piebalds to maintain resistance.

As coccidiosis is normally very infectious, it was expected to have affected other members of the colony. Faecal samples from seven other hamsters, piebald and non-piebald, and a dead brown piebald female hamster, were submitted for examination for the presence of coccidial oocytes and autopsy to the Ministry of Agriculture, Fisheries and Food, at Sutton Bonington, Loughborough. The faecal samples proved negative in every case, and the dead hamster was somehow mislaid, so did not receive autopsy.

In view of this finding, the possibility of psychological factors enhancing susceptibility to certain parasitic infections may have validity. The findings of Sheppe and Adams (1957), Robinson (1961), Nelson (1962) and Noble (1961, 1962), all cited in Chapter Six, may be worth following up in the piebald genotype of hamster.

Conclusions

It is clear that separation into individual cages at either four or $6\frac{1}{2}$ - 7 weeks of age has a profound effect on piebald survival. The non-viable piebalds also showed gastric ulcers and one showed a parasitic infection - disorders which by themselves, are unlikely to cause such severe reaction as death.

Therefore there is some evidence that a psychological factor, that is, isolated housing, is influential in causing high piebald mortality, although a more detailed study is needed to give a greater depth of information.

The piebald hamster may offer scope for the study of aspects of disease resistance and mortality, and any possible relationship with psychological agents.

F. RELATIONSHIP BETWEEN PERCENTAGE OF WHITE SPOTTING IN PIEBALD HAMSTERS AND BEHAVIOUR

The amount of white spotting in a piebald hamster varies and Orsini (1952) noted that the heavier animals were usually darker and paler ones were smaller. It can therefore be conjectured that behaviour may relate also to the amount of white spotting. Robinson graded each piebald for spotting before sending them to me, so it was possible to check percentage spotting in relation to behaviour. Spearman's rank correlation coefficient test was carried out to determine whether the weights of 20 randomly selected piebalds (mixed sexes) on arrival in Leicester correlated with spotting grade (the higher the grade, the

more white spotting). A correlation significant at the five percent level was found in the direction of a higher spotting grade accompanying lighter weight, agreeing with Orsini's findings (1952). However, final weights (those taken before dissection) did not correlate with spotting grade, so these do not confirm Orsini's results.

A Mann-Whitney Test (White's Modification) showed that the spotting scores of 30 viable and 30 non-viable piebald hamsters were not significantly different. The spotting grades of 16 piebalds that defecated on one or more trials in the open field and 18 piebalds that did not were also compared by a Mann-Whitney test and were not found to be significantly different.

From this preliminary evidence there would not seem to be a relationship between amount of white spotting (spotting grade) and behaviour, although other aspects of the behavioural tests need to be correlated with the spotting grades before this can be firmly established.

The amount of white spotting shown by piebald hamsters in this study, was due partly to their polygenic background and partly to their uterine environment, involving developmental effects (Robinson, personal communication). Developmental effects occur between fertilization and the stage at which hair growth is complete prior to parturition, and refer to unknown influences which govern the migration of melanocytes from their primary sites of production, and also to differential and/or irregular rates of division of cells capable of expressing or not expressing the piebald gene. As these effects are thought responsible for white spotting variation in the guinea pig (Wright 1920), Robinson attributes some of the variation in piebald hamsters to them (personal communication).

Initial analysis leads to the hypothesis that piebald emotional

behaviour is unrelated to the percentage of white spotting in a consistent way.

G. SUMMARY AND CONCLUSIONS OF NONBEHAVIOURAL EXPERIMENTS

Measurements of body weight showed piebalds weighed less than non-piebalds, females weighed less than males and isolated housed hamsters weighed less than those which had been grouped.

The amount of food taken into the cage was greater in non-piebald than piebald hamsters, although isolates took more in than grouped hamsters.

The significance of the body weight measurement and amount of food taken into the cage are unclear in terms of emotionality.

Adrenal weight was greater in piebald than non-piebald hamsters, and males had heavier glands than females.

Mortality was significantly higher in piebald genotypes than non-piebald genotypes and the relationship of piebald mortality to housing conditions, stomach ulcers and parasitic infection was discussed.

Piebald adrenal weight, their ulcer incidence and mortality may reflect susceptibility to psychologically stressful stimulation, and to this extent support the hypothesis that piebald genotypes are more emotional than non-piebald hamsters.

Sex differences with regard to adrenal weight in the hamster and rat species were discussed, and seemed to relate more consistently to sex differences in aggressive behaviour than to fear.

These nonbehavioural experiments did not provide evidence to support theories concerning sex differences in emotionality.

A principle finding was the importance of housing conditions (whether hamsters were isolated or grouped), in piebald survival. It was suggested that a more detailed study be carried out to determine

the nature of any relation between psychological factors, such as housing, and extreme physiological reaction, such as death.

CHAPTER ELEVEN

BEHAVIOURAL EXPERIMENTS I

A. INTRODUCTION

It was explained earlier in this thesis why the open field and novel situation, two experiments comprising this chapter, were chosen to measure emotionality. The open field has been used by a large selection of workers, who have studied rodent emotionality. It has been used to some extent to study activity in the hamster, although this species has not been examined for emotionality. A detailed investigation of hamster open field behaviour therefore seemed paramount. Furthermore, I wished to replicate the pilot study findings, especially those for defecation.

The novel situation had produced a variety of strain and sex differences in behaviour in the pilot study, so was carried out here to determine whether similar differences could be produced. Data from the open field could then be compared with results from this comparatively less fearful more exploratory situation.

The activity test was designed to gather information on activity in the home cage, which would be a base-line measure, against which activity in the open field and novel situation could be compared.

B. OPEN FIELD

Method

Apparatus: This consisted of an arena marked off into 16 squares, illuminated by bright light and with 80 db. of white noise. Details were given in Chapter Eight, on the pilot studies (see also figure 2 for a floor plan of the arena).

Procedure: Each animal was placed individually in the starting square of the arena for four minutes per day on four consecutive days.

The order for taking part in this test was randomized on every trial (day). The length of time of any bout was recorded only if it lasted five seconds or more. The following were recorded on each trial:

1. Vocalization on placement in the open field.
2. Latency to leave square 13, that is, when the hamster's hind legs had crossed the lines of the square.
3. Total number of lines crossed, that is, ambulation score, measured by recording every square the animal entered. Entrance to a square was recorded when the hamster's hind legs had crossed the lines surrounding that square.
4. Number of times the middle lines were crossed, that is, entrance into squares 6, 7, 10 or 11.
5. Time spent on behaviours lasting more than five seconds in corner squares, that is, squares 1, 4, 13, 16. (Hereafter simply referred to as: 'time spent in corner squares').
- 6.) Number of bouts and length of time spent sniffing.
- 7.) Sniffing was recorded when the hamster had its nose to the ground, its vibrissae twitching.
8. Number of crouching bouts. Crouching took place in one of the four corners and occurred when, with front legs raised, the hamster pressed its ventral surface against the corner, tucked its head under and remained motionless.
9. Number of rearing bouts, that is, the hamster standing on its hind legs only with its forepaws off the ground (or against the side of the arena).
10. Number of scratching bouts. Scratching took place predominantly in the corners and the hamster scratched the base of the wall with its front legs.
11. Number of grooming bouts, that is, the hamster cleaning its body.

12. Number of freezing bouts, that is, the animal standing on four legs, motionless.
13. Time spent on behaviour lasting more than five seconds in squares at the edge (abbr. time spent in squares at the edge).
14. Number of faecal boluses deposited, that is defecation.
15. Vocalization on exit from the field.

At the end of each trial the arena was swabbed down with a mild disinfectant.

Arrangement of Data and Treatment

First arrangement of data

1. This consisted of:
 - a. 3 genotypes, G, B and GP.
 - b. 2 sexes, male and female.
 - c. 4 trials.
 - d. 10 subjects per group.
2. Treatment of data: by 3-way analysis of variance.

Second arrangement of data

1. This consisted of:
 - a. 4 genotypes, females only, G, B, GP and BP.
 - b. 4 trials.
 - c. 14 subjects per group.
2. Treatment of data: by 2-way analysis of variance.

Third arrangement of data

1. This consisted of:
 - a. 2 housing conditions, isolated and grouped.
 - b. 3 genotypes, G, B and GP.
 - c. 2 sexes, male and female.
 - d. 4 trials.
 - e. 4 subjects per group.
2. Treatment of data: by 4-way analysis of variance.

Fourth arrangement of data

1. This consisted of:

- a. 2 housing conditions.
 - b. 4 genotypes, females only.
 - c. 4 trials.
 - d. 5 subjects per group.
2. Treatment of data: by 3-way analysis of variance.

Results

There were 15 measures recorded over four trials and the results are given separately for each measure.

Vocalization on placement in the open field. This was significant for genotype differences ($p < 0.05$). When three genotypes were compared vocalization increased from G to B, to GP, with GP vocalizing more than G ($p < 0.05$), and B falling intermediately. When four genotypes were compared vocalization increased from G to B, to BP, to GP ($p < 0.05$). Housing differences showed that isolates vocalized more than grouped hamsters ($p < 0.05$).

Latency to leave starting square. For three genotypes, G had a longer latency than B or GP ($p < 0.01$). For four genotypes, females only, G had a longer latency than B, GP or BP ($p < 0.01$). Housing differences showed that isolates had shorter latencies than group housed hamsters ($p < 0.01$).

Ambulation. Among genotypes B had a higher ambulation score than G or GP, which showed similar amounts ($p < 0.01$). Sex differences showed that males crossed fewer lines than females ($p < 0.05$).

Rearing bouts. In a sex x trial interaction ($p < 0.05$), females showed more rearing bouts on every trial than males, although the largest difference was on trial one. In a sex x genotype x trial interaction ($p < 0.05$) G males showed the least number of rearing bouts over all trials.

Sniffing bouts. Genotype differences showed that B had a larger number of sniffing bouts than G or GP ($p < 0.05$). Sex differences showed males to have more bouts than females ($p < 0.01$). Housing differences showed grouped

hamsters to sniff for more bouts than isolated ones ($p < 0.01$). A housing x trial interaction showed grouped hamsters to have more bouts on all trials than isolates, although the largest difference appeared on trial one ($p < 0.01$). A graph of this interaction is given in figure 8.

Crouching bouts. Sex differences showed females to have more crouching bouts than males ($p < 0.001$). A sex x trial interaction showed males to vary little over trials in their small number of bouts, but female bouts increased considerably ($p < 0.05$). A graph of this interaction is given in figure 10.

Grooming bouts. Genotype differences showed GP to groom for more bouts than B or G ($p < 0.05$), among three genotypes. With respect to four genotypes, females only, GP scored more highly than G, B or BP. Sex differences showed that males had more bouts than females ($p < 0.001$). In a sex x trial interaction ($p < 0.05$) male bouts increased over trials, whereas female bouts retained a lower level with little variation between trials.

Time spent in corner squares. Genotype differences showed that G spent longer there than B or GP ($p < 0.01$) among three genotypes. For four genotypes, females only, G spent more time in the corner square than B, GP or BP ($p < 0.05$). Housing differences showed that group housed hamsters spent more time in the corner squares than isolated ones. A genotype x trial interaction ($p < 0.05$) showed that G varied little in time spent in the corner squares between trials one to four, and to retain a high level, and that B, GP and BP showed an increase in time over trials to equal that of G by trial four. A graph of this interaction is given in figure 9.

Entrances to middle squares. Genotype differences showed that G entered the middle squares more often than GP ($p < 0.05$), with B falling intermediately. Sex differences showed that males entered the middle squares more than females ($p < 0.001$). Housing differences showed that grouped

Figure 8. Mean open field sniffing bouts:
housing x trial interaction, data
in arrangement three.

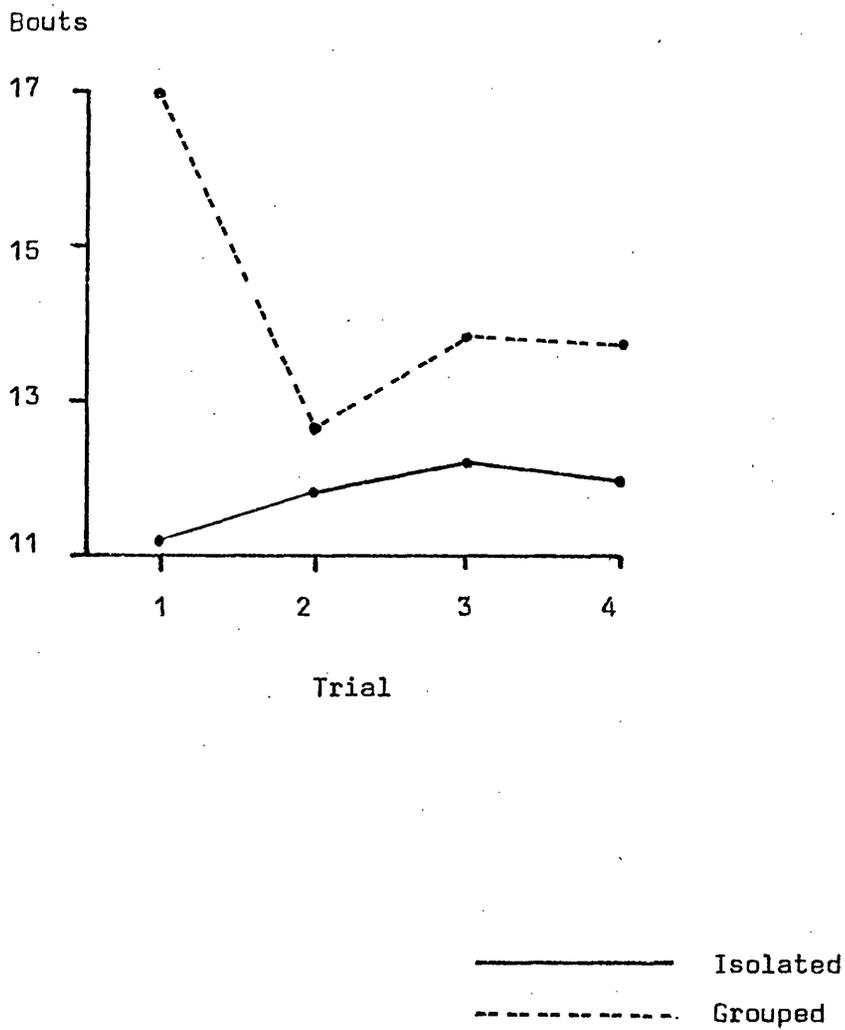
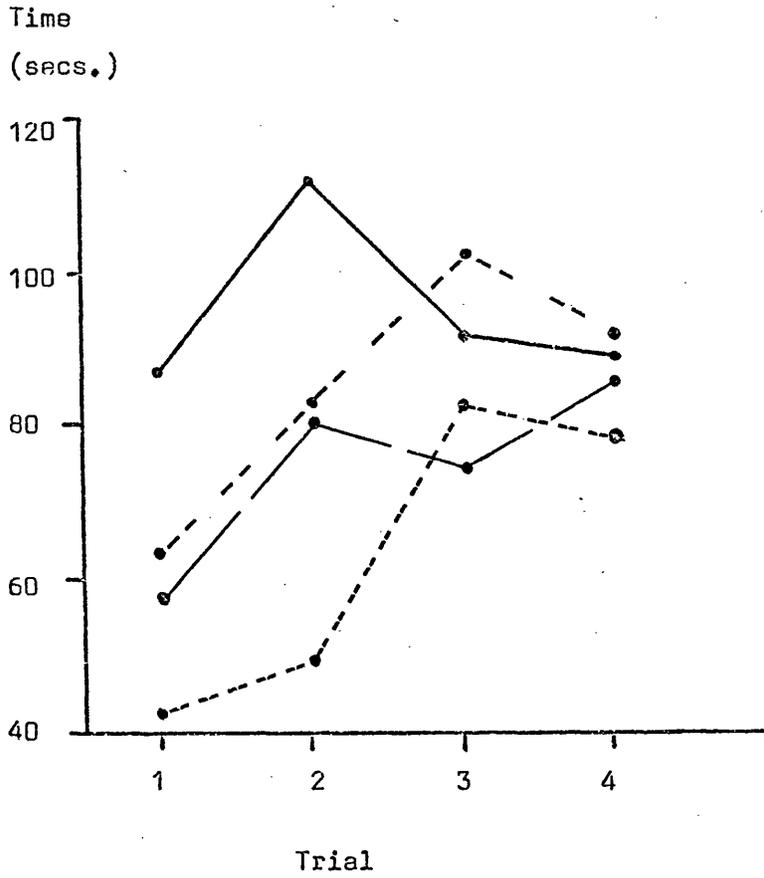


Figure 9. Mean open field time spent on behaviour lasting more than five seconds in the corner squares: genotype x trial interaction, data in arrangement two.



— G
- - - B
· · · GP
- · - BP

animals entered these squares more than isolates ($p < 0.001$). A housing x genotype x sex interaction ($p < 0.05$) showed that grouped G and B males entered the middle squares more often than any other housing x genotype x sex combination of hamster. A graph of this interaction is given in figure 11.

Time spent sniffing. Genotype differences showed a decrease in sniffing time from G to B to GP ($p < 0.01$) with three genotypes, and similar trends among four genotypes, females only, ($p < 0.01$) with decreased time spent sniffing from G to B, to GP to BP. Sex differences showed that males had a greater sniffing time than females ($p < 0.001$). Housing differences showed grouped hamsters to sniff longer than isolated ones ($p < 0.001$). A housing x sex interaction ($p < 0.05$) showed that isolated males and females and grouped females sniffed for a shorter time than grouped males.

Time spent in squares at the edge. Sex differences showed that males spent more time in these squares than females ($p < 0.05$). The genotype x sex interaction ($p < 0.01$) showed that G, B and GP females, and GP males spent little time in the squares at the edge compared to G and B males.

Freezing bouts. These occurred in only a small number of animals and showed no significance.

Defecation. Genotype differences showed an increase in defecation from G and B to GP ($p < 0.05$). Where females only were considered, near-significant trends showed increased defecation from G to B, to BP, to GP.

Vocalization on exit from the field. Genotypic differences showed that vocalization increased from G and B to GP ($p < 0.05$). Where females only were concerned GP vocalized more than G or B ($p < 0.01$), with BP falling intermediately. Sex differences showed that females vocalized more than males ($p < 0.05$).

measures in each data arrangement and level of significance obtained see Summary Table VII and Table IV for a tabular representation of the results.

Discussion

My principle interest was, of course, in the expression of the behavioural trait that could be described as fear or emotionality. In the study a number of open field measures showed significant differences between genotypes, sexes and housing conditions and the implications of these in terms of fear or emotionality are discussed below.

As previous work has validated defecation in rats as being the main open field measure of fear (Broadhurst 1957a, Ivinskis 1970) this is discussed first.

1. Genotype differences in defecation

Defecation increased significantly from golden and brown hamsters to golden piebalds. For females only, trends showed increasing defecation from G to B to GP, with BP defecating slightly less than GP.

Forty percent of the piebald hamsters defecated on one or more trials in the open field while only 7.5 percent of golden and brown genotypes did so. Swanson (1966) found that seven percent of hamsters defecated and considered this a negligible amount, so defecation in hamsters has not been validated as an emotionality response. However the 40 percent shown by piebalds is a significant finding, although lower than the percentage (60%) shown by piebalds in the pilot study.

From the study presented here, it is hard to determine whether or not open field defecation signifies emotionality. There is little literature on this topic for hamsters because open field defecation

Summary Table VIIa

Analyses of variance carried out on open field measures in each data arrangement with levels of significance obtained.

Measure	Data in arrangement one	Data in arrangement two	Data in arrangement three	Data in arrangement four
Genotype differences				
Entrances to middle squares	0.05	NS	0.05	NS
Time spent sniffing	0.01	0.05	0.001	0.01
Sniffing bouts	0.01	NS	0.05	NS
Ambulation	0.05	NS	0.01	NS
Vocalization on entrance	0.05	0.05	0.05	NS
Vocalization on exit	0.05	0.05	0.001	0.01
Latency	0.01	0.05	0.01	0.01
Grooming bouts	NS	NS	0.01	0.05
Defecation	NS	NS	0.05	NS
Time in corner squares	NS	NS	0.01	0.05

Sex differences				
Grooming bouts	0.001		NS	
Time in corner squares	0.001		NS	
Crouching bouts	0.001		NS	
Ambulation	0.05		NS	
Time in edge squares	0.001		0.05	
Time spent sniffing	0.001		0.01	
Entrances to middle squares	NS		0.001	

Summary Table VII_a continued

Measure	Data in arrange- ment one	Data in arrange- ment two	Data in arrange- ment three	Data in arrange- ment four
Sex differences				
Sniffing bouts	NS		0.01	
Vocalization on exit	NS		0.05	
Genotype x sex				
Time in edge squares	0.01		NS	
Genotype x trial				
Time in corner squares	NS	0.01	NS	NS
Sex x trial				
Grooming bouts	0.05		NS	
Crouching bouts	0.05		NS	
Rearing bouts	0.05		NS	
Vocalization on entrance	0.05		NS	
Genotype x sex x trial				
Rearing bouts	0.05		NS	
Housing differences				
Time spent sniffing			0.001	0.001

Summary Table VII, continued

Measure	Data in arrange- ment one	Data in arrange- ment two	Data in arrange- ment three	Data in arrange- ment four
Housing differences				
Entrances to middle squares			0.001	NS
Vocalization on entrance			0.05	0.05
Latency			0.01	0.01
Time in corner squares			0.001	0.001
Sniffing bouts			0.001	0.01
Housing x sex				
Time spent sniffing			0.05	
Entrances to middle squares			0.001	
Housing x genotype x sex				
Entrances to middle squares			0.05	
Latency			0.01	
Housing x trial				
Vocalization on entrance			0.01	NS
Latency			0.05	NS
Sniffing bouts			0.01	0.01
Housing x genotype x trial				
Latency			0.05	NS

Summary Table VIIa continued

Measure	Data in arrange- ment one	Data in arrange- ment two	Data in arrange- ment three	Data in arrange- ment four
Housing x sex x trial				
Vocalization on exit			0.05	
Trial Differences				
Vocalization on entrance	NS	NS	NS	NS
Latency	NS	NS	NS	NS
Ambulation	0.001	0.001	0.001	0.001
Rearing bouts	0.05	0.001	NS	NS
Sniffing bouts	NS	NS	NS	NS
Crouching bouts	0.001	0.001	NS	NS
Grooming bouts	0.001	0.05	0.001	NS
Time in corner squares	0.01	0.01	0.05	0.001
Entrances to middle squares	NS	NS	NS	NS
Time sniffing	NS	NS	NS	0.05
Time in edge squares	NS	NS	NS	NS
Freezing bouts	NS	NS	NS	NS
Defecation	NS	NS	NS	NS
Vocalization on exit	NS	NS	NS	NS

Summary Table VII b.

Four-way analysis of variance carried out on entrances to the middle squares, data in third arrangement.

Variation	SS	MS	DF	F	Significance level
Housing	155.88	155.88	1	12.81	0.001
Genotype	80.17	40.08	2	3.29	0.05
Housing x Genotype	41.54	20.77	2	1.71	NS
Sex	174.42	174.42	1	14.34	0.001
Housing x Sex	322.92	322.92	1	26.55	0.001
Genotype x Sex	39.50	19.75	2	1.62	NS
Housing x Genotype x Sex	84.13	42.06	2	3.46	0.05
Trial	12.77	4.26	3	0.38	NS
Housing x Trial	61.56	20.52	3	1.84	NS
Genotype x Trial	97.75	16.29	6	1.46	NS
Sex x Trial	32.18	10.73	3	0.96	NS
Housing x Genotype x Trial	31.46	5.24	6	0.47	NS
Genotype x Sex x Trial	44.33	7.39	6	0.66	NS
Housing x Sex x Trial	54.43	18.14	3	1.62	NS
Housing x Genotype x Sex x Trial	51.96	8.66	6	0.77	NS

Table IV

Tabular representation of significant open field results.

Genotype differences (brown piebalds are not included)

Measure	Golden hamsters	Brown hamsters	Golden piebald hamsters
Latency	longer	shorter	intermediate sig. only from G
Ambulation	less	more	less
Sniffing bouts	less	more	less
Sniffing time	most	intermediate NS to G but sig. to GP	least
Grooming bouts	less	less	more
Time in corner squares	more	less	less
Entrances to middle squares	more	intermediate NS	less
Defecation	less	intermediate NS to G sig. to GP	more
Vocalization on entrance	least	intermediate NS	most
Vocalization on exit	less	less	more

Table IV continued

Sex differences

Measure	Males	Females
Ambulation	less	more
Sniffing bouts	more	less
Sniffing time	more	less
Crouching bouts	less	more
Grooming bouts	more	less
Entrances to middle squares	more	less
Time in squares at the edge	more	less
Vocalization on exit	less	more

Housing differences

Measure	Grouped hamsters	Isolated hamsters
Latency	longer	shorter
Sniffing bouts	more	less
Sniffing time	more	less
Time in corner squares	more	less
Entrances to middle squares	more	less
Vocalization on entrance	less	more

Table IV continued

Measures which change over trials

Ambulation	decrease to trial 2
Rearing bouts	decrease to trial 3
Crouching bouts	increase to trial 4
Grooming bouts	increase to trial 4
Time in corner squares	increase to trial 2
Sniffing time (females only)	increase to trial 2, then some decrease to trial 4

Interactions

Measure	Interaction
Rearing bouts	sex x trial females scored more on every trial
Crouching bouts	sex x trial males varied little over trials, but females increased
Grooming bouts	sex x trial females varied little over trial, but males increased
Time in corner squares	genotype x trial G retain high amount over trials 1 - 4 B, GP, BP show increase 1 - 4
Entrances to middle squares	housing x genotype x sex grouped G and B males entered the middle squares more than all other housing, genotype sex combinations
Sniffing time	housing x sex grouped males sniffed more than isolated males and females and grouped males

is not a common response. However it could be envisaged that hamsters, like mice, defecate on some occasions to display territorial behaviour and this reaction is stronger in piebalds or that piebalds have weak alimentary tracts that have difficulty in retaining food, which is unrelated to fearfulness. Investigation of home cage defecation should help to clarify this latter point.

It could also be hypothesized that defecation is an emotionality response in hamsters, but that it is not normally displayed because the open field is not frightening enough for hamsters and is unsuitable for the study of this kind of behaviour. The piebald defecation rate would therefore represent extreme hamster emotionality, elicited by situations relatively non-fearful to most of the species.

Although open field defecation can be interpreted in a number of ways and auxiliary studies are needed, in view of the findings for rats it is tentatively proposed that defecation in the open field by hamsters is also an emotionality response.

The two non-piebald genotypes, brown and golden, could not be discriminated on their defecation scores, but it does not follow that they are necessarily equal in emotionality. Non-significant trends showed that brown hamsters defecated more than golden ones, although the numbers involved may be too small to justify the drawing of any firm conclusions. Defecation is an all-or-nothing response so cannot differentiate small genotypic differences. Thus, although a score of zero would seem, at first sight, to indicate that an animal is not emotional, if defecation occurred only at high levels of emotionality (as is possible with regard to the piebald hamster) a score of zero might conceal variations in emotionality below the threshold needed to elicit defecation, for example in the brown and golden hamsters. Therefore, zero defecation does not necessarily signify non-emotionality in the two

non-piebald genotypes of hamster.

2. Genotype differences in ambulation

The validity of ambulation as a measure of fear was discussed in Chapter Seven. Over trials in rats it has been found to decrease (e.g. Ivinskis 1970, Zimbardo and Montgomery 1957), to show an initial decrease then to level out (Broadhurst 1958), or to increase on days one to two and to decrease thereafter (Stretch 1960). My findings for ambulation agree with Broadhurst's.

The relationship between ambulation and fear has not been validated for hamsters. I tried to show that activity differences in experimental situations were not merely representative of basal activity differences, by measuring home cage activity over 20 hours (see section D of this chapter). The results showed no genotypic, sex or housing differences in home cage activity and although this may indicate that activity differences in experimental situations are real, there were methodological problems in the measurement of home cage activity, so it cannot be definitely assumed that there are not basal activity differences.

The meaning of open field ambulation and its relationship to other open field measures have been extensively questioned by a number of researchers as reported in Chapter Seven. The meaning of open field activity, in hamsters especially, must remain uncertain.

My findings cannot support the existence of a negative correlation between open field defecation and ambulation that has generally been found for rats and mice. Archer (1973), however, emphasized that this relationship can be easily upset by strain, sex and early experience differences, so my findings involving the use of another species are not surprising.

When Swanson (1966) considered hamster open field ambulation, she found a non-significant number defecated and concluded that hamsters

resembled the Maudsley non-reactive rats. However by this argument the fact that a high proportion of my piebalds defecated in the open field accompanied by low ambulation, suggests that they resemble the Maudsley reactive line. In addition, the low defecating, high ambulating brown hamsters would seem to resemble the similarly behaving non-reactive rats but the low defecating, low ambulating golden genotype did not behave like either rat line. A negative correlation between defecation and ambulation cannot be said to hold consistently for these genotypes of hamster.

In view of this rather complex finding, it would seem that ambulation may have different meanings for different genotypes, three of which (brown, brown piebald and golden piebald) have not been observed in the open field in previous studies. In Chapter Seven it was shown that high or low ambulation could represent different sorts of behaviour. For example, Archer and Blackman (1971) suggested that the ambulation measure was of limited value because of the difficulty of interpreting reasons for such ambulatory movements as investigation of the ground with the nose and vibrissae with walking, just walking or faster, more jerky movements. The first type of behaviour is exploratory, the second is transport and the third is rapid movement from an aversive situation (Archer and Blackman 1971).

In my open field test, the hamsters had three choices on entrance to the starting square:

1. To explore immediately the rest of the field
2. To remain in the square some time (allowing dissipation of fear?) and then explore.
3. To remain in the square carrying out non-locomotive behaviour for much of the trial.

The hamster behaviour will now be discussed.

Golden hamsters had a long latency and a low ambulation score and they followed procedure 2. Sniffing bouts were significantly fewer

than for browns, but sniffing time was longer than that of browns (non-significant trend) and golden piebalds. This implied that each sniffing bout lasted a long time. They also spent longer in the corner squares than B or GP, which in view of the way it was scored, indicated that G tended to follow a behaviour through to last more than five seconds. G also showed a larger number of entrances to the middle squares and this is considered a priori to be a non-emotional reaction. However it has received inadequate validation and in my open field experiments it did not show an increase over trials, as would be expected if it was a negative index of fear, so its meaning remains obscure.

It would seem that the ambulation score of G hamsters was low partly because of the short length of time left for ambulation after a comparatively long latency and partly because they did not seem to move extensively around the field. Their behaviour seemed similar to that described by Archer and Blackman (1971), as investigation of the ground with their noses and vibrissae, and it could be added that this investigation occurred only over a limited area.

Brown hamsters had a short latency and high ambulation score; it appears that they followed choice 1 on entrance to the starting square, that is, they moved around the rest of the field immediately. Walker (1957) suggested that when emotional animals were placed in a novel situation, they were at first seeking an avenue of escape displayed by high initial activity, and brown hamsters could be doing this hence their short latency. This gave more time for ambulation, so the hamsters became familiar with the environment, their fear level was lowered, and they showed a high ambulation score. Brown hamsters showed many sniffing bouts, lasting a medium length of time, which would be expected if they were exploring the whole environment. They spent a shorter time in the corner squares than G. Again, it would seem that this was because

they were exploring the whole field and did not spend long in any one place. They entered the middle squares an intermediate amount between that of G and GP (non-significant trend).

It seems likely that B hamsters fell into Archer's and Blackman's second category of ambulation, that is, walking or transport, although it is likely that for B this also involved general exploration, but not the close investigation shown by G.

On the other hand, golden piebald hamsters and brown piebald females showed a short latency and low ambulation score because they may have been initially seeking a passage of escape, and quickly left the starting square for this purpose. They entered the middle squares significantly less than G. Fear did not dissipate (hence vocalization in response to handling on exit from the field) and activity may have decreased, because their attempts to escape had been unsuccessful.

With reference to piebalds, I would agree with previous findings that low ambulation could represent high emotionality in their case. Piebalds showed few sniffing bouts and each one lasted, on average, a comparatively short time. They showed little time in the corner squares on behaviour lasting more than five seconds and crossed few middle lines. Piebalds did not therefore seem to be engaging in much behaviour that could be defined as exploratory and it is suggested that their behaviour fell into Archer's and Blackman's third category, defined as (rapid) movement from an aversive situation. Initially piebald movement could have been rapid, fitting closely with the definition, in view of the short latency, but closer analysis of the order of open field behaviour would be needed before any assured conclusions about this can be made. However, it appeared that they were responding to an aversive situation.

Although G and GP showed similar ambulation scores, when the rest of their open field behaviour and that of B is considered, it seems

that ambulation could have different significance for the three genotypes. Low ambulation may, in some cases, indicate emotionality, but not in others. Similarly, high ambulation may not always represent non-emotionality.

The overall impression is that both G and B were engaging in extensive exploratory behaviour, but with different levels of ambulation. By contrast, piebalds showed little exploration. Further evidence was provided by time spent in the corner squares when the method of recording was taken into account. The total time was the sum of time spent by any one genotype on behaviours in these squares, and although all behaviour was recorded in the form of a bout, it received a time score also, only if it lasted more than five seconds. An interesting speculation is that the different times in the corner squares probably represent differences in persistence of any one behaviour pattern. Golden hamsters showed a high score because once having started a behaviour they tended to continue it for five seconds or more. Brown and piebald hamsters, on the other hand, showed lower scores because of a tendency to behave in short bouts. This is also true of piebald sniffing and from an ethological common-sense viewpoint it would seem that the rapidly changing, non-persisting behaviour of the GP genotype, in conjunction with high defecation, is characteristic of reactive animals.

There is also some indication, based on their defecation score and behaviours comprising exploration, that B, although less emotional than GP were somewhat more emotional than G hamsters. This could be due to the fact that B hamsters have red eyes and are therefore more sensitive to bright light than either G or GP animals. However, brown piebald hamsters also have red eyes, but there is no evidence here that BP females are more fearful in the open field than GP hamsters. Therefore, the suggestion that brown hamsters may be intermediate in emotionality between golden and piebald animals in this situation remains inconclusive.

3. Genotype differences in grooming

Another measure showing genotypic differences was grooming bouts. Repeated testing has shown grooming to decrease (e.g. Streng 1971, for mice) and to increase (e.g. Bolles 1960 for rats), although it has commonly been assumed that grooming is a positive index of fear.

Over all trials, GP showed more grooming bouts than G or B, which, according to the common assumption of the meaning of grooming and Gray's observation that MR rats groomed more than MNR rats, implies a higher fear level in piebalds. However the increase in grooming bouts over trials in this study indicates that it has a negative relationship with fear (as measures of fear should decrease over trials).

Attempts to validate grooming, by considering its correlation with defecation, appear to have been unsuccessful; for example Satinder (1968) found a negative correlation between them while Ivinskis (1966) revealed no significant correlation. The meaning of grooming in relation to emotionality is therefore uncertain.

4. Genotype differences in vocalization

Vocalization on entrance to and exit from the open field showed the same pattern for genotypic differences. Golden piebalds vocalized the most and G the least, with B and BP falling somewhere between, although B was likely to be nearer G, and BP nearer to GP.

It must be emphasized that vocalization was only measured in response to placement into and out of the open field by handling. Vocalization in the field could not be recorded as any that occurred was drowned by the white noise. It is therefore only a reaction to handling and not necessarily representative of a fear reaction to the open field. Vocalization as a fear response is discussed in the next chapter (Chapter Twelve). Certainly, on this measure, in this situation, piebalds were more vocal than non-piebalds, but it cannot definitely

be said on the sole basis of this measure that they were also more fearful in the open field, although they may have been.

5. Sex differences

There were sex differences on a number of open field measures, but they formed no clear cut pattern. There were no sex differences in defecation, the most validated open field measure of fear available, among the GP genotype and it is more difficult to interpret the differences on other measures in terms of fear.

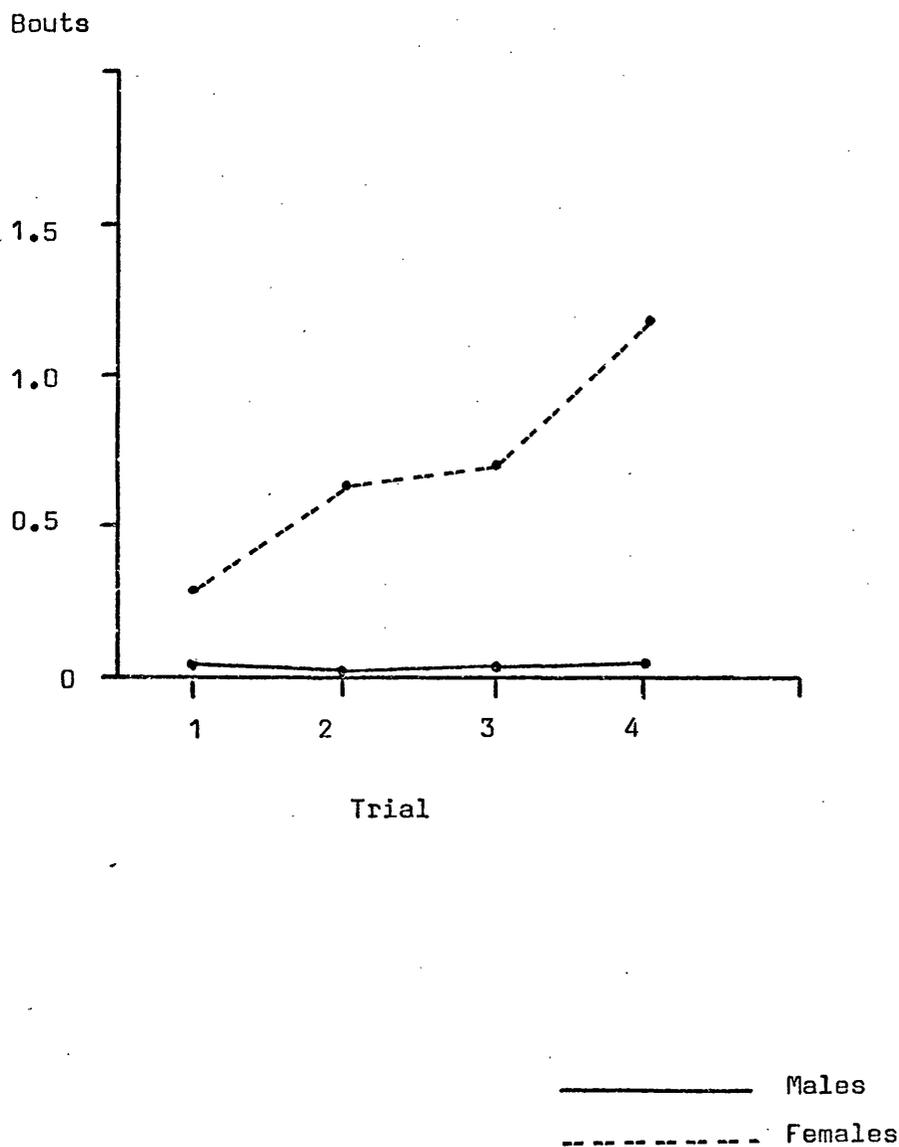
Compared to males, females ambulated more, had fewer and shorter sniffing bouts, more crouching bouts, fewer grooming bouts, entered the middle squares less, spent less time on behaviours lasting more than five seconds and vocalized more on handling on exit from the field.

These results could be interpreted in several ways:

1. Males are more emotional than females. They ambulated less and many findings have shown ambulation to be a negative index of fear, so that lower male ambulation could indicate greater emotionality. Higher female ambulation agrees with Swanson's findings for the hamster species in the open field (Swanson 1966).
Males had more grooming bouts than females but the conflicting literature on the validity of grooming enables either more or less grooming to be interpreted as indicative of emotionality.
2. Females are more emotional than males. Females had fewer sniffing bouts and shorter sniffing time, and although sniffing has not been validated, on ethological grounds, it would seem that lack of sniffing represents lack of investigation and possibly emotionality.
Females showed a greater number of crouching bouts. Crouching behaviour was very like freezing, but an insignificant number of hamsters froze. Crouching could, therefore, be interpreted as an emotionality response, in as much as freezing, being one of the operational definitions of emotionality (immobility/escape) is a direct index of

fear in the open field. On the other hand, crouching increased over trials, which is not expected in a positive index of fear, and a significant sex x trial interaction (figure 10) showed the increased bouts to be primarily among the females. Possibly, crouching should not be interpreted in terms of female emotionality level but regarded as representing a learnt coping response with the open field. By trial four the hamsters should have learnt that the open field was a temporary situation and females, in particular, may have discovered that an effective coping procedure was to remain still in a corner (sometimes with head tucked under to minimize light and noise intensity), having learnt on previous trials that there were no escape paths (hence high ambulation). If females adopted this mode of response in the open field (that is crouching) and males adopted another (not explicit in the present results) it would be contrary to the 'sex -typical' behaviour patterns for emotionality tentatively proposed by Archer (¹⁹⁷⁵ ~~in press~~). A significant sex x trial interaction for rearing bouts showed that females had more rearing bouts on every trial than males. However observation of rearing behaviour indicated that an excessively rearing hamster tended to move quickly around the arena, rearing against the walls and participating little in other behaviour; this rearing activity resembled a kind of scrabbling against, rather than exploration of, the walls. Females entered the middle squares less than males. As mentioned previously, this measure has not been validated but on a priori grounds it would seem that emotional hamsters would enter the more exposed central area less than non-emotional animals. Females also spent less time on behaviours lasting more than five seconds in the squares at the edge. The fact that they had fewer sniffing bouts and a shorter sniffing time indicates that they spent less time than males on these behaviours, but if they did exceed five seconds, the behaviour was likely to be carried out in the corner squares. A more

Figure 10. Mean open field crouching bouts: sex x trial interaction, data in arrangement one.



emotional hamster would seem less likely to carry out extensive behaviour patterns in the more exposed squares at the edge.

Finally, females vocalized more than males when handled on exit from the open field. This is primarily a reaction to handling but it could be significant that they did not vocalize more than males on entrance to the field. This could be because generally they were not more reactive to stimuli on entrance, or that handling did not discriminate high from low fear at this stage. Alternatively, exposure to the fearful open field may have lowered the threshold to fearful stimuli sufficiently in emotional animals so that on exit they responded by vocalizing. This, in fact, suggests that either the female basal fear level is higher than that of males, or can be raised more easily.

3. Males and females are equal in emotionality. Males and females showed different open field behaviours on a number of measures, but as none of these has been validated as a strong indicant of emotionality, the possibility remains that fear levels are not different, but that the two sexes express fear in response to stimuli differently. It could be hypothesized that females, as demonstrated by their high ambulation, rearing behaviour, few entrances to the middle squares and little sniffing, would escape from the open field, given the opportunity, and so fear is displayed in search of an escape route around the edge of the field.

Males, by contrast, with their low ambulation, much grooming, extensive sniffing and persistent behaviour, are not active in the open field, and this comparative immobility may reflect a different form of fear reaction to that of females.

This interpretation does not necessitate the conclusion that one sex behaves more emotionally than the other, but that the two sexes respond differently to this fear provoking situation. It agrees with an idea put forward by Archer (¹⁹⁷⁵in press), discussed in Chapter Seven, and needs to be tested more convincingly than is demonstrated

here. Closely linked to this is a fourth possibility that, if emotionality is a complex state, males may be more emotional than females with regard to certain behavioural aspects and females more so than males in other ways. For example, females may show heightened initial responding to the open field, in terms of fear, but may adapt more quickly to the situation, so that thereafter greater emotionality is shown by males. Record of the order of behaviour in the open field needs to be examined in relation to this.

In conclusion, there is evidence in support of all proposals mentioned above. None of the relevant measures have been conclusively validated, by their association with direct fear behaviour, immobility and escape, for either rats or mice and certainly not for hamsters. Any one measure may be valid for males but not for females. Until the meaning of these measures in relation to fear has been established, clear sex differences in emotionality in the open field for hamsters cannot be claimed.

In this study, the difficulty with interpreting the significance of the different behaviours of the sexes shown in the open field in terms of fear points to the inadequacy of this situation, as it stands, for measuring emotionality in hamsters. The measures are not pure indices of fear and their meaning can become distorted when variables such as the sex of the animals are involved. This may also apply to the rat studies, which although differentiating the sexes on defecation, are conflicting with regard to the pattern shown over all other open field measures and a closer examination of these behaviours may reveal inconsistencies in emotionality or non-emotionality, by males and females.

Therefore, studies (for example Gray 1971a, b) which claim that male rodents are more emotional than female rodents, cannot be supported

by the open field hamster findings presented above and would seem to be an oversimplification of rodent behaviour.

6. Housing differences

Once again, many measures varied significantly with housing conditions. Compared to group housed hamsters, isolated animals had a shorter latency, showed fewer sniffing bouts and less sniffing time, spent less time on behaviours in the corner squares, entered the middle squares less and vocalized more on entrance to the open field.

Lack of defecation differences and the earlier point that almost none of these measures has been validated as indices of fear over different strains in different species, and that available evidence is conflicting, apply here, so that four proposals about emotionality in differently housed hamsters can be postulated:

1. Group housed hamsters are more emotional than isolated ones. Group housed hamsters had a longer latency. Ivinskis (1970) found that extreme stimulus conditions of light and noise increased latency indicating, therefore, that a long latency was a sign of emotionality.
2. Isolated hamsters are more emotional than group housed ones. They showed fewer sniffing bouts and a shorter sniffing time, spent less time on behaviours lasting more than five seconds in the corner squares and entered the middle squares less than group housed ones. As explained earlier, these behaviours indicate less exploratory behaviour and less persistent behaviour, that is, when a behaviour pattern occurs it is likely to be a short bout. These together could indicate emotionality.

Finally, isolates vocalized more on entrance to the field, but this was only a reaction to handling. The fact that grouped individuals vocalized less indicates that isolates were more susceptible to handling in terms of fear, if vocalization is a valid index of fear, but this does not necessarily mean that they were also more emotional in the open field, although they may have been.

3. Grouped and isolated hamsters are equal in emotionality.

The two types of hamster may be equal in level of emotionality, but due to differential postweaning housing conditions, develop different patterns of emotional reaction to the open field. As none of the measures showing housing differences was a strong indicant of emotionality, and as neither grouped nor isolated hamsters displayed much escape or immobile behaviour, implicating emotionality, the possibility remains that they are not different in emotionality, but express any fear in different ways.

4. A final possibility is that isolated hamsters are more emotional in response to certain configurations of the open field and less so in response to others, than group housed individuals and vice versa.

Earlier rat and mouse studies, on the whole, indicated that isolated animals were more emotional than group housed ones. My results did not show a significant ambulation difference, agreeing with Archer (1969), who found that short term differential housing for two weeks was insufficient to produce activity differences in the open field for rats, whereas 24 weeks were. Longer isolation or group rearing may have produced different results in the hamster species.

Clearly, the present findings do not allow claims to be made with regard to emotionality differences arising from short postweaning housing factors.

An interesting finding was that when three genotypes, two sexes were subjected to analysis of variance, seven measures showed significance on genotype differences. When each group was divided into the two different housing conditions, so that each group consisted only of four animals, there were ten significant genotype differences. Initially, as hamsters were chosen randomly, the chances were that the majority in each group had been group housed, as more hamsters were housed in this way than were isolated. Allowing for the housing variable, in data in

arrangements three and four, half of each group experienced each type of housing. In view of the increase in genotype significance on this occasion, despite the decrease in number of subjects per group, it appears that housing interacts with genotype, so that isolation housing enhances genotype differences.

Entrances to the middle squares was the only measure to show a significant housing x genotype x sex interaction (figure 11). Even if fewer entrances to the middle squares is a priori a fear response, the only clear finding represented by the graph is that grouped G and B males are therefore less emotional than hamsters from every other genotype x sex x housing combination.

This illustrates the difficulty of measuring emotionality when several factors are involved (genotype, sex and housing) and distorting influence of any one, when indirect measures of fear behaviour, rather than immobility or escape, are used to estimate emotionality.

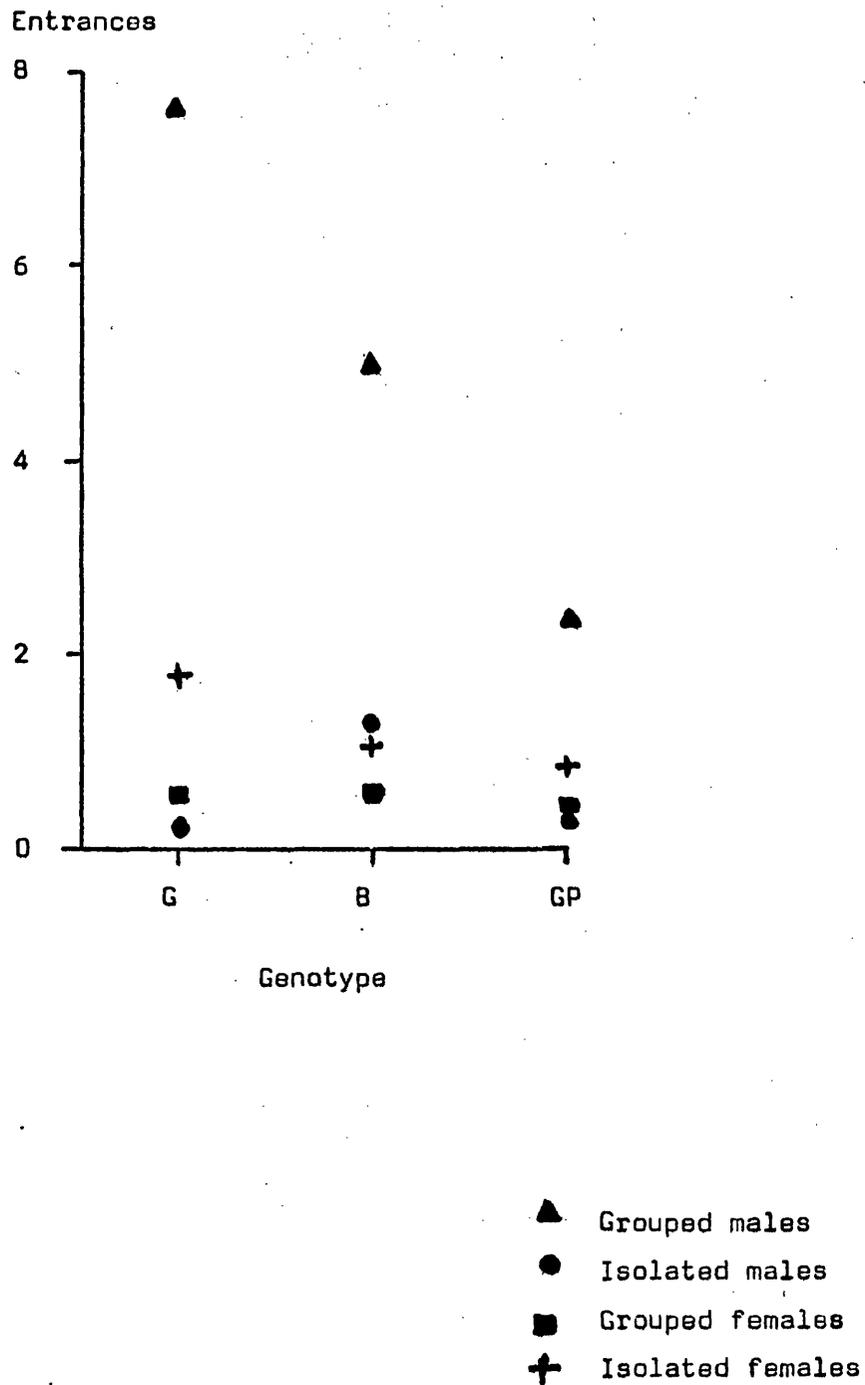
Conclusions

The most clear differences in emotionality were between genotypes, with golden piebalds, males and females, and brown piebald females, showing a pattern of open field behaviour that could be described as more fearful than that of brown and golden hamsters.

No conclusions about emotionality differences between sexes and hamsters housed in two ways can be made, partly because there were no differences in defecation, the principle open field index of fear, and partly because other open field behaviour showed no consistent pattern, so could be interpreted, with regard to emotionality, in a number of conflicting ways.

Initial findings only were presented, and the data could have been arranged and treated in a variety of ways. For example, other

Figure 11. Mean open field entrances to the middle squares: housing x genotype x sex interaction, data in arrangement threea.



measures could have been correlated with defecation, at least in the piebald genotype, or the order of behaviour within any trial could have been considered. However, a larger sample of animals is needed to confirm the genotype findings and to enlarge on other tentative interpretations.

C. NOVEL SITUATION

Method

Apparatus. The apparatus involved a modified open field, consisting of an arena marked off into squares with a water trough, an activity wheel and a box placed along different walls. Details were given in Chapter **Eight**; see also figure 3.

Procedure. Animals were placed individually in the arena for six minutes per day for four consecutive days (trials) and their behaviour recorded. Details were given in Chapter **Eight**. These measures were recorded on each trial:

1. Latency to investigate, that is, sniff with nose and vibrissae the first object, either trough, box or wheel.
2. Number of lines crossed, that is, ambulation, recorded by a digital counter. Hamsters were considered to have crossed a line when their fore and hind limbs had passed over it.
- 3.)
- 4.) Number of bouts spent sniffing trough, box or wheel
- 5.)
- 6.)
- 7.) Time spent sniffing trough, box or wheel
- 8.)
9. Time actually in the box.
10. Time actually on the wheel.
11. Number of food bouts, that is, sniffing, picking up or eating food pellets.
12. Number of startle bouts, that is, when the hamster gives a sudden jerked movement to an indefinite stimulus.
13. Number of rearing bouts.

- 14.) Number of sniffing bouts and length of time of
- 15.) each
- 16.) Number of grooming bouts and length of time of
- 17.) each
- 18.) Number of scratching bouts and length of time
- 19.) of each.

Arrangement of Data and Treatment

First arrangement of data

1. This consisted of:
 - a. 3 genotypes G, B and GP.
 - b. 2 sexes, male and female.
 - c. 4 trials.
 - d. 10 subjects per group.
2. Treatment of data: by 3-way analysis of variance.

Second arrangement of data

1. This consisted of:
 - a. 4 genotypes, females only, G, B, GP and BP.
 - b. 4 trials.
 - c. 14 subjects per group.
2. Treatment of data: by 2-way analysis of variance.

Third arrangement of data

1. This consisted of:
 - a. 2 housing conditions, isolated and grouped.
 - b. 3 genotypes.
 - c. 2 sexes.
 - d. 4 trials.
 - e. 4 subjects per group.
2. Treatment of data: by 4-way analysis of variance

Fourth arrangement of data

1. This consisted of:
 - a. 2 housing conditions.
 - b. 4 genotypes, females only.
 - c. 4 trials.
 - d. 5 subjects per group.
2. Treatment of data: by 3-way analysis of variance.

Results

There were 19 measures recorded over four trials and the results are given separately for each measure.

Ambulation. There were sex differences with females ambulating more than males ($p < 0.01$). A genotype x trial interaction ($p < 0.001$) showed that ambulation decreased over trials in all genotypes, although GP showed the greatest ambulation on trial one.

Latency to investigate first object (box, wheel or trough).

Genotype differences showed that G and B had a longer latency than GP ($p < 0.001$). The same trend was apparent among females only ($p < 0.05$) although BP latency was slightly longer than GP. Sex differences showed males to have a longer latency than females ($p < 0.05$). A genotype x trial interaction ($p < 0.01$) showed that latency decreased over trials for all genotypes, although G had the largest latency on trial one. In a housing x trial interaction ($p < 0.001$) it was shown that the grouped hamsters' score decreased slightly over trials, but that isolates' score, while initially greater, had a larger decrease and equalled that of grouped hamsters by trial four.

Box and wheel bouts. It was decided to combine scores for box bouts and wheel bouts after data in arrangements one and two had been analysed, and to leave out trough bouts and time, which showed little significance. (Box and wheel scores combined would seem to give a general exploratory measure which may contribute to information on the nature of the reaction to this type of novel environment). Genotype differences showed that box and wheel bouts were fewer for G than either B or GP ($p < 0.05$). Sex differences showed that males had fewer bouts than females ($p < 0.05$). Trial differences showed that bout number decreased over trials ($p < 0.001$).

Box and wheel time. Box time and wheel time were also combined. Genotype differences showed that G had a shorter time than B or GP ($p < 0.05$). A genotype x trial interaction

($p < 0.05$) showed that all genotypes increased their time over trials. A graph of this interaction is given in figure 13. A genotype x sex x trial interaction ($p < 0.05$) showed that G males, G females, B males and GP females varied little between trials, whereas B females and GP males had a marked increase between trials one and four, so by trial four scored the highest on this measure. Similarly, a housing x trial interaction ($p < 0.05$) showed that isolates increased their score over trials to exceed that of grouped hamsters by trial four.

Rearing bouts. Sex differences showed that females reared more than males ($p < 0.01$). A genotype x trial interaction ($p < 0.05$) showed all genotypes to decrease number of bouts over trials, although this was greatest in GP among three genotypes. Group housed hamsters had more bouts than isolated animals ($p < 0.001$).

Startle bouts. For three genotypes, startle bouts increased from G and B to GP ($p < 0.001$), and among four genotypes, GP startled more than G or B ($p < 0.05$) and BP fell intermediately. A genotype x trial interaction ($p < 0.01$) showed that the greatest discrepancy between G/B and GP occurred on trial one. G and B showed little variation in number of startle bouts over trials whereas GP decreased to trial four, but did not score as lowly as B or G.

Grooming bouts. Group housed hamsters displayed more bouts than isolated ones ($p < 0.01$).

Grooming time. Males spent more time grooming than females ($p < 0.05$). A genotype x sex x trial interaction ($p < 0.05$) showed that G males, B males, B females and GP females had little variation over trials, compared to GP males and G females, which increased to groom much more by trial four. Grooming time for females only, showed housing differences with grouped animals having a longer time than isolates ($p < 0.01$).

Sniffing time. Sex differences showed that males sniffed longer than females ($p < 0.01$). A genotype x trial interaction ($p < 0.05$) showed a sharp decrease in sniffing time for G, B and GP between trials one and two. Housing differences showed that isolates sniffed less than grouped hamsters ($p < 0.001$).

Summaries of analyses of variance carried out on novel situation measures in each data arrangement and levels of significance obtained are given in Summary Table VIII, and the results are shown in tabular form in Table V.

Discussion

The only strong indicator of fear in this experiment was the startle response. Although startle cannot be qualified as part of either immobility or escape, it is by definition a response to frightening or surprising stimuli and requires little validation.

Its decrease over trials implies that it is a positive index of fear. Ideally, it should have been validated by considering its association with flight and freezing in the novel situation, but the fact it has not been is less serious than for other measures, which are not direct indices of fear and are consequently much harder to interpret in terms of emotionality.

1. Genotype differences

Golden piebalds showed significantly more startle bouts than G and B, and where females only were concerned, BP showed an intermediate amount. As startle is considered to be a good measure of fear, it is the principle evidence that in the novel situation GP were the most emotional hamsters, followed by BP females.

Box and wheel bouts would seem a priori to be investigatory activities and their decrease over trial may suggest satiation of this type of exploratory behaviour.

Summary Table VIIIa

Analyses of variance carried out on novel situation measures in each data arrangement with levels of significance obtained.

Measure	Data in arrange- ment one	Data in arrange- ment two	Data in arrange- ment three	Data in arrange- ment four
Genotype differences				
Latency to investigate	0.01	NS	0.001	0.05
Box and wheel bouts			0.05	NS
Box and wheel time			0.05	NS
Startle bouts	NS	NS	0.001	0.05
Sex differences				
Sniffing time	0.01		0.01	
Rearing bouts	0.01		0.001	
Grooming time	0.05		0.001	
Latency	0.05		NS	
Box and wheel bouts			0.05	
Ambulation	NS		0.01	
Genotype x sex				
Rearing bouts	0.05		NS	
Grooming bouts	0.05		NS	

Summary Table VIII, continued

Measure	Data in arrange- ment one	Data in arrange- ment two	Data in arrange- ment three	Data in arrange- ment four
Genotype x trial				
Startle bouts	0.01	NS	0.01	NS
Sniffing time	0.05	NS	NS	NS
Latency	0.01	NS	NS	NS
Ambulation	0.05	NS	0.05	NS
Rearing bouts	NS	NS	0.05	NS
Box and wheel time	NS	NS	NS	0.05
Genotype x sex x trial				
Box and wheel time	NS		0.05	
Grooming time	NS		0.05	
Housing differences				
Rearing bouts			0.001	0.05
Sniffing time			0.001	0.001
Grooming bouts			0.01	0.001
Grooming time			NS	0.01
Housing x genotype				
Latency			0.05	NS
Grooming bouts			NS	0.05
Grooming time			NS	0.05

Summary Table VIII, continued

Measure	Data in arrange- ment one	Data in arrange- ment two	Data in arrange- ment three	Data in arrange- ment four
Housing x trial				
Latency			0.001	0.001
Box and wheel time			0.05	0.01
Trial differences				
Ambulation	0.001	0.001	0.001	0.001
Latency to investigate	0.001	0.001	0.001	0.001
Box and wheel bouts			0.001	0.001
Box and wheel time			0.001	0.001
Rearing bouts	NS	0.001	0.001	0.001
Startle bouts	0.05	NS	0.05	NS
Grooming bouts	NS	0.01	0.05	0.01
Grooming time	0.01	0.001	0.01	0.001
Sniffing bouts	0.001	0.001	NS	NS
Sniffing time	0.001	0.001	0.001	0.001

Summary Table VIII b.

Four way analysis of variance carried out on box and wheel bouts,
data in arrangement three.

Variation	SS	MS	DF	F	Significance level
Housing	37.60	37.60	1	3.01	NS
Genotype	107.31	53.65	2	4.29	0.05
Genotype x Housing	47.66	23.83	2	1.90	NS
Sex	82.84	82.84	1	6.62	0.05
Housing x Sex	23.44	23.44	1	1.87	NS
Genotype x Sex	7.73	3.86	2	0.31	NS
Housing x Genotype x Sex	15.07	7.54	2	0.60	NS
Trial	172.95	57.65	3	10.86	0.001
Housing x Trial	13.41	4.47	3	0.84	NS
Genotype x Trial	33.59	5.60	6	1.05	NS
Sex x Trial	25.58	8.53	3	1.61	NS
Housing x Genotype x Trial	36.57	6.10	6	1.15	NS
Genotype x Sex x Trial	65.11	10.85	6	2.04	NS
Housing x Sex x Trial	41.05	13.68	3	2.58	NS
Housing x Genotype x Sex x Trial	53.89	8.98	6	1.69	NS

Table V.

Tabular representation of significant novel situation results.

Genotype differences (brown piebalds are not included)			
Measure	Golden hamsters	Brown hamsters	Golden Piebald hamsters
Latency	longer	longer	shorter
Box and wheel bouts	fewer	more	more
Box and wheel time	shorter	longer	longer
Startle bouts	less	less	more

Sex differences		
Measure	Males	Females
Ambulation	less	more
Latency	longer	shorter
Box and wheel bouts	fewer	more
Rearing bouts	less	more
Grooming time	more	less
Sniffing time	longer	shorter

Housing differences		
Measure	Grouped hamsters	Isolated hamsters
Rearing bouts	more	less
Grooming bouts	more	less
Grooming time females only	longer	shorter
Sniffing time	more	less

Table V. continued

Measures which change over trials

Ambulation	decrease to trial 3
Latency	decrease to trial 4
Box and wheel bouts	decrease to trial 3
Box and wheel time	increase to trial 3
Rearing bouts	decrease to trial 3
Startle bouts	decrease to trial 3
Grooming bouts	increase to trials 2 - 4
Grooming time	increase to trial 4
Sniffing bouts	decrease to trial 2
Sniffing time	decrease to trial 2

Interactions

Measure	Interaction
Ambulation	genotype x trial
Latency	genotype x trial housing x trial
Box and wheel time	genotype x trial genotype x sex x trial B females and GP males showed marked increases over trials housing x trial
Rearing bouts	genotype x trial
Startle bouts	genotype x trial
Grooming time	genotype x sex x trial GP males and B females increased groom- ing time over trials
Sniffing time	genotype x trial

If the non-significant genotype x trial interaction for box and wheel bouts is considered (figure 12), trends indicate that although all genotypes decrease their bout number between trials one and four, GP and B retain a higher level of exploration on all trials.

Similarly, if the significant genotype x trial interaction for box and wheel time is considered, B and GP spend more time exploring these objects (figure 13).

Latency to investigate first object decreased over trials which could suggest a reluctance to investigate the novel objects on trial one, due to increased emotionality. A short latency leaves more time for bouts on the box and wheel, than a longer one; GP had a shorter latency than either G or B, although B showed as many bouts and as much time on the box and wheel as GP. G showed a long latency with little investigation of the box and wheel.

No other measures showed significance between genotypes in this situation. The pattern of behaviour shown by the three genotypes (golden, brown and golden piebald hamsters) can be subjected to various interpretations.

Piebalds showed heightened fear, at least to certain aspects of the novel situation, as exhibited by their incidence of startle. However, with brown hamsters, they also showed a shorter latency, more box and wheel bouts and a longer time on these objects than golden hamsters. The difference on these three measures would seem to indicate greater exploration by B and GP, compared to G. The findings for piebalds, based on the increased number of startle responses, can be expounded in three ways:

1. The behaviour of piebalds may be an example of the Halliday-Lester theory which proposes that mild fear motivates exploration. At any rate, fear induced by the novel situation is, a priori less intense than that

Figure 12. Mean novel situation box and wheel bouts: genotype x trial interaction, data in arrangement three.

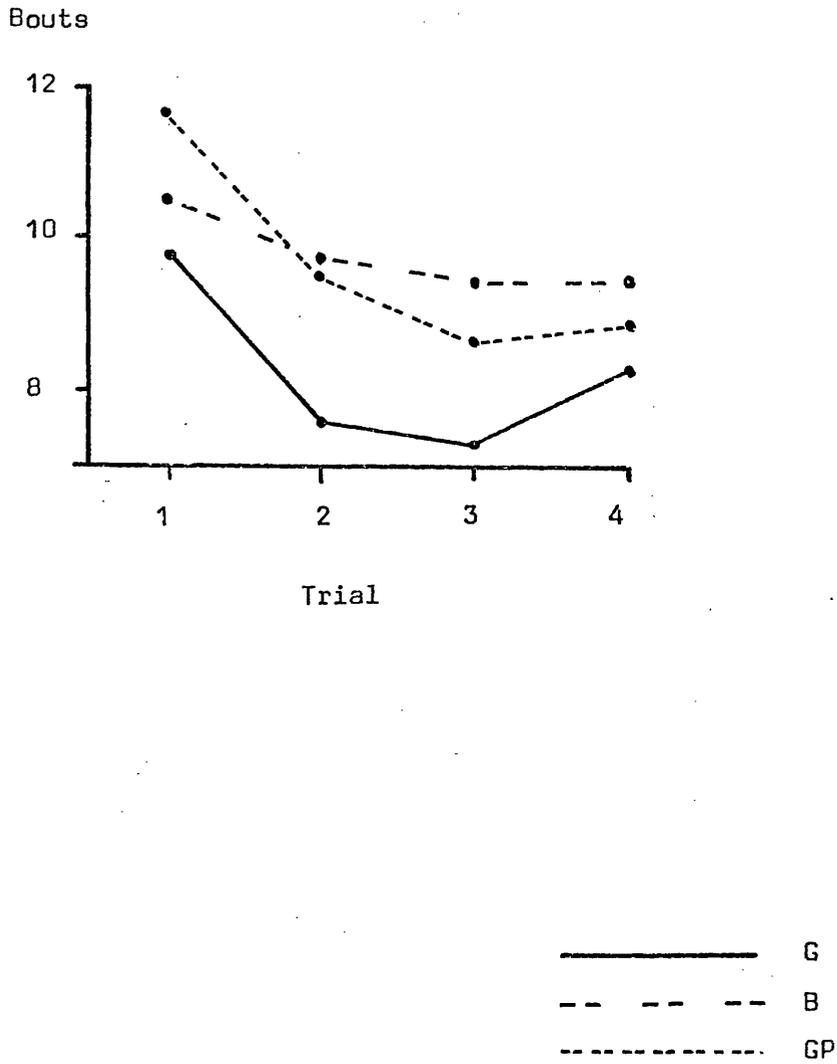
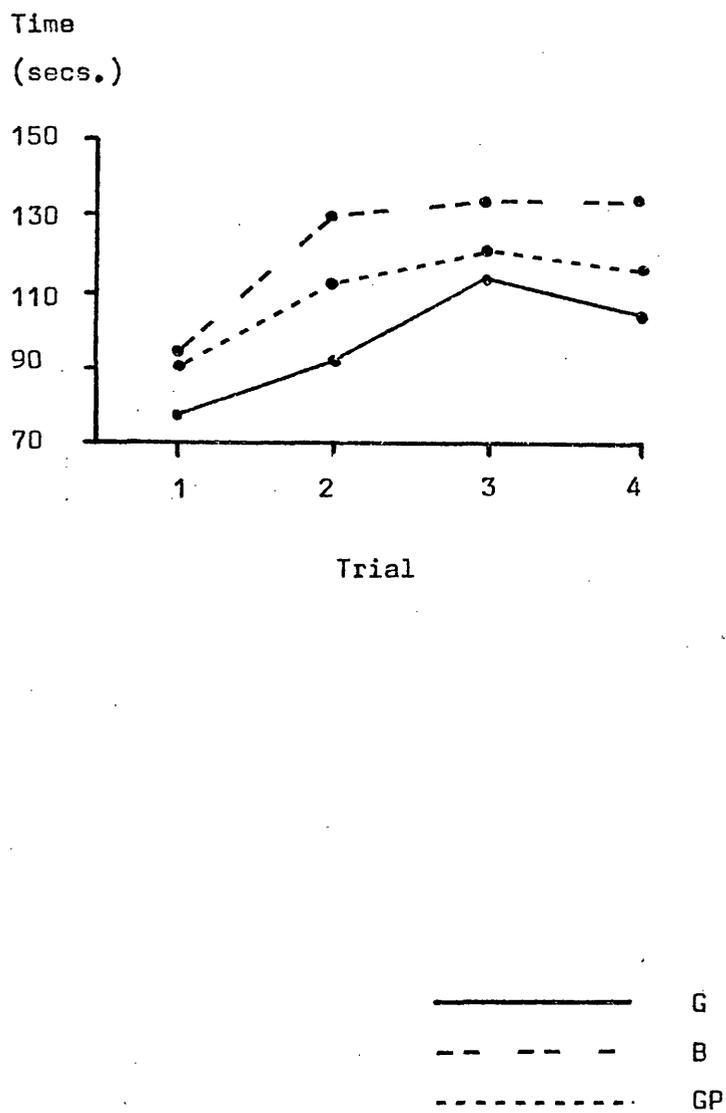


Figure 13. Mean novel situation box and wheel time: genotype x trial interaction, data in arrangement three.



evoked by the open field and may therefore initiate investigation.

However, the behaviour of B hamsters cannot be subsumed under the Halliday-Lester theory because although B showed the same amount of exploration as GP, they cannot be described as fearful in the novel situation. An alternative explanation would be necessary for their behaviour.

2. Golden piebalds are more fearful than either G or B in the novel situation, according to a measure of startle and the piebalds' shorter latency may represent initial rapid movement in order to find an escape route; hence these hamsters come across an investigatory object sooner than the others. Their increased number of bouts and time spent on the objects, compared to G, may be due to repeated returning to 'safe havens'.

The order of behaviour within a trial would be relevant information to this type of interpretation.

3. Similarly, the shorter latency and high ambulation of GP could signify a search for escape, but with unsuccessful attempts, they quickly adapt to the situation and explore.

Even if there are various ways of interpreting the piebald behaviour relative to G and B as they seemed to be more fearful (as shown by startle responses), it is difficult to explain the behavioural differences between G and B hamsters without further experiments.

The results suggest that fear and exploration are not consistently related (as illustrated also in the open field genotype findings). Although B and GP differ in fear, as measured by heightened startle reaction by GP, this does not affect exploration, which is equal in the two genotypes in this relatively non-fearful situation. In addition, G, which cannot be differentiated from B on startle response, explore less.

In this case, therefore, low exploration is unlikely to be associated with increased emotionality, and the two seem to be differently related in the three genotypes.

2. Sex differences

There were no sex differences in startle bouts and the absence of this only good measure of fear in the novel situation lends the behavioural patterns of each sex to various interpretations in connection with emotionality.

1. Males are more emotional than females. Males ambulated and reared less than females. Low incidences of these behaviours in the open field were generally thought to represent inhibition of exploration and possibly fearfulness. However, in the novel situation, both ambulation and rearing decreased to trial 3, then stabilized, which agrees with a variety of open field workers (for example, Zimbardo and Montgomery 1957, Broadhurst 1958) who suggest this happens because exploration has satiated. The longer male latency and fewer box and wheel bouts could also represent lack of exploration due to fear. Grooming time was shown to be higher in males, but the meaning of open field grooming in relation to fear has been debated. Gray, Levine and Broadhurst (1965) considered grooming to be a positive measure of fear, as MR rats groomed more than MNR rats. However, grooming was shown to increase with trial in my study on hamsters and by Bolles for rats (1960), which conflicts with the idea that it is a positive indicator of fear.

Fentress (1968a, b) has yet another theory, which is that an optimal level of arousal is needed to elicit grooming activity. This is rather unsatisfactory because an optimal 'arousal' level would be difficult to determine and could easily involve circular reasoning on fear levels and their relationship to the instigation of grooming.

Males also showed a longer sniffing time, which in conjunction with less ambulation could imply that males do not explore the novel situation as much as females, but sniff extensively in one place. This lower exploration could be associated with higher emotionality.

2. Females are more emotional than males. The female behaviour pattern could be interpreted as one that is more emotional than the male pattern if the shorter latency, high ambulation and greater number of rearing bouts are indicative of searching for escape. This could then explain the female greater number of box and wheel bouts, shorter sniffing time, and little indulgence in irrelevant activities, like grooming, which would impede the finding of an escape route.
3. Females and males are equal in emotionality, but express their reactions to the comparatively non-fearful novel situation differently, hence the conflict in interpretation of the measures. The greater female participation in exploration as suggested by the measures, may in fact represent search for escape while the inactive males may respond with relative immobility. Both patterns are emotional reactions.

The comparatively non-fearful novel situations may not evoke strong enough fear responses to allow differentiation between the sexes in either form or intensity of emotionality.

These hamster findings once again point to the error involved when endeavouring to make generalizations about sex differences in fear in rodents. Three interpretations about emotionality can be made from my findings, and although one, that males are more emotional than females, would agree with Gray's hypothesis (1971a), the other interpretations, that the two sexes are equal but show different patterns of emotionality or that females are more emotional than males, are equally justified.

3. Housing differences

The housing differences provided similar complex patterns of behaviour as did the sexes, and are amenable to three interpretations.

1. Group housed hamsters are more emotional than isolated ones. Their greater number of grooming bouts, longer grooming time and longer sniffing time could all indicate heightened emotionality, if grooming is a positive index of fear and if a long sniffing time represents lack of exploration, which may in turn represent fear.
2. Isolates are more emotional than grouped hamsters. If their fewer rearing bouts signifies lack of exploration, which implies fear, then isolates could be more fearful than group raised hamsters in the novel situation, and other behaviour, such as their grooming bouts, and shorter grooming and sniffing times can all be interpreted in a way that indicates increased emotionality among isolates.
3. Isolated and group reared hamsters are equal in emotionality, but express their reaction to the novel situation differently. As it is hard to determine which of the two groups of hamsters are more emotional and either an increase or decrease in some measures can be said to indicate fear this possibility remains.

It is true that differentially housed hamsters, to some extent, behave differently in the novel situation. The lack of knowledge on the meaning and validity of the relevant measures makes an interpretation about differential emotionality impossible.

Priestnall (1970) utilized a similar test situation and found mice isolated postweaning until ten weeks of age showed less emotionality, in terms of a negative relationship between defecation and ambulation, than mice housed in groups of eight to ten. This conflicts with previous reports on rats that isolated animals are more emotional

than group raised ones, and Priestnall pointed out that this could be a species difference.

If postweaning housing conditions affect rats and mice differently, in terms of the relationship between defecation and ambulation, and until hamster exploratory behaviour is studied in the wild, no assumptions about the effects of isolation or group rearing on this kind of behaviour can be made.

Conclusions

Genotype differences in emotionality were most clear on the number of startle bouts which showed that hamsters carrying the piebald gene were more fearful than those without it. In view of this, other behavioural measures shown by the three genotypes in this novel but not very frightening situation seemed to represent an entanglement of fear and exploration, which were probably differently related in the three genotypes.

As neither sex nor housing conditions showed differences in the number of startle reactions, a simple pattern of greater emotionality in one sex or one hamster housing condition could not be established. Sex and housing differences in the open field and novel situation were less clear than genotype differences, and consequently open to misinterpretation.

The novel situation gave less information on hamster emotionality than the open field, presumably because, being less intense, it could not provoke fear behaviour to the same extent.

D. ACTIVITY

Introduction

There were two types of activity test, one involving four trials each of two minutes and one other extending over 20 hours.

Method

Apparatus. This consisted of an Animex Activity Meter, Type SE, supplied by LKB Instruments Ltd. The home cage was placed on the top of the Animex and hamster movement across the floor of the cage was digitally counted. It was kept in the animal room and used there.

Procedure. The procedures were:

1. Each cage, containing one hamster was taken from the rack and placed on the Animex. Reactivity to this situation was recorded for two minutes for four trials, one trial per day. Every animal took part in this experiment.
2. Random samples of animals were tested for home cage activity over a longer period of time, by being placed in their own cages on top of the Animex for one trial of 20 hours. The animals used were eight golden male, eight golden female, seven brown male, eight brown female, five golden piebald male, eight golden piebald female, three brown piebald male and eight brown piebald female hamsters. They were placed on the Animex at 14.00 or 15.00 hours and moved at 10.00 or 11.00 hours respectively the following day. This period included 14 hours of light and six hours of darkness. On removal their activity score was noted.

Arrangement of Data, Treatment and Results of Two Minute Activity

First arrangement of data

1. This consisted of:
 - a. 3 genotypes, G, B and GP.
 - b. 2 sexes, male and female.
 - c. 4 trials.
 - d. 10 subjects per group.
2. Treatment of data: by 3-way analysis of variance.
3. The results showed no significant differences.

Second arrangement of data

1. This consisted of:
 - a. 4 genotypes, females only, G, B, GP and BP.

- b. 4 trials.
 - c. 14 subjects per group.
2. Treatment of data: by 2-way analysis of variance.
3. The results were:
- a. Genotype differences showed that G and B had more activity than GP or BP ($p < 0.01$).

Third arrangement of data

1. This consisted of:
- a. 2 housing conditions, isolated and grouped.
 - b. 3 genotypes.
 - c. 2 sexes.
 - d. 4 trials.
 - e. 4 subjects per group.
2. Treatment of data: by 4-way analysis of variance.
3. The results were:
- a. Housing differences showed that isolates were more active than grouped hamsters ($p < 0.001$).

Fourth arrangement of data

1. This consisted of:
- a. 2 housing conditions.
 - b. 4 genotypes, females only.
 - c. 4 trials.
 - d. 5 subjects per group.
2. Treatment of data: by 3-way analysis of variance.
3. The results were:
- a. Housing differences showed that isolates were more active than group housed hamsters ($p < 0.01$).
 - b. Genotypic differences showed that G and B females were more active than GP and BP females ($p < 0.05$).

For a summary of the analysis of variance carried out on data in arrangement three see Summary Table IX.1.

Arrangement of Data, Treatment and Results of 20 Hour Activity

First arrangement of data

1. This consisted of:
 - a. 3 genotypes, G, B and GP.
 - b. 2 sexes, male and female.
 - c. 1 trial.
 - d. 5 subjects per group.
2. Treatment of data: by 2-way analysis of variance.
3. The results showed no significant differences.

Second arrangement of data

1. This consisted of:
 - a. 4 genotypes, females only.
 - b. 1 trial.
 - c. 8 subjects per group.
2. Treatment of data: by 1-way analysis of variance.
3. The results showed no significant differences.

For a summary of the analysis of variance carried out on data in arrangement one, see Summary Table X.

Discussion of Activity Results from Two Minute Test

There were few significant effects in these results. For two minute activity, females only, genotypic differences showed G and B to have more activity than GP or BP. Piebald females tended to show less activity in the open field and novel situation, than B or G females, and this may be a reaction to novelty, as happened in this situation, when the home cage was placed in novel conditions.

When males were added and three genotypes, both sexes, were compared, the genotype differences disappeared, which implied that either there were no differences between the males thus masking overall genotypic differences or that they operated in the opposite direction to those of the females.

Sex differences were not significant in two minute activity,

Summary Table IX

Four-way analysis of variance carried out on two minute activity,
data in arrangement three.

Variation	SS	MS	DF	F	Significance level
Housing	6912.00	6192.00	1	13.44	0.001
Genotype	2406.51	1203.26	2	2.34	NS
Housing x Genotype	1174.03	587.02	2	1.14	NS
Sex	85.33	85.33	1	0.17	NS
Housing x Sex	229.69	229.69	1	0.45	NS
Genotype x Sex	508.95	254.47	2	0.49	NS
Housing x Genotype x Sex	406.22	203.11	2	0.39	NS
Trials	2371.02	790.34	3	3.87	0.01
Housing x Trial	1611.29	537.10	3	2.63	0.05
Genotype x Trial	1726.45	287.74	6	1.14	NS
Sex x Trial	706.04	235.35	3	1.15	NS
Housing x Genotype x Trial	1872.43	312.07	6	1.53	NS
Genotype x Sex x Trial	1324.68	220.78	6	1.08	NS
Housing x Sex x Trial	624.60	208.20	3	1.02	NS
Housing x Genotype x Sex x Trial	937.24	156.21	6	0.76	NS

Summary Table IX

Two-way analysis of variance carried out on 20 hour activity, data in arrangement one.

Variation	SS	MS	DF	F	Significance level
Genotype	26735361.06	13367680.53	2	1.19	NS
Sex	8226803.33	8226803.33	1	0.74	NS
Genotype x Sex	22864379.48	11432189.74	2	1.02	NS

although open field and novel situation both showed females ambulated more than males. The activity experiment was designed to be less intense than the novel situation or open field and this characteristic may account for the fact that no sex differences became apparent.

Housing differences showed isolates to be more active than grouped hamsters, but neither open field nor novel situation showed housing differences in ambulation, so the meaning of this finding is unclear.

In addition, the validity of this test is open to scepticism. It seemed desirable to place the animal in its home cage on the Animex for a base-line measure of activity because if the hamster was placed in a different container and then placed on the Animex, reaction to a novel environment would then be tested, varying little from the novel situation.

The Animex recorded activity across the floor of the cage only so that climbing activity which seemed common in these hamsters would not be recorded. Thus, a low score could mean that the hamster remained in its nest for the two minute period or that it climbed on to the bars at the top of the cage, where it could be still or active. Although the female only data showed that G and B were more active than GP and BP hamsters, which agrees with previous data for activity response to a new situation, genotype differences were not significant when males were involved, nor were there any significant genotype interactions, so the meaning of this result is not clear.

Discussion of Activity Results from the 20 Hour Test

It was decided to record activity over 20 hours in the hope that climbing activity would randomize out over all animals. The 20 hour period involved 14 hours of light and six of darkness. A longer period of darkness (that is, maximum activity time) would have been preferable,

but this period was chosen as it was the time with least experimenter interruption, such as entrances to and exits from the room and the carrying out of experiments. Experiments of similar length but started at other times of the day may have resulted in different results.

The results showed no significance for genotype differences, sex differences or any interaction effect. Although this experiment aimed to give a basal measure of home cage activity over 20 hours, it cannot be concluded definitely that no significant genotype or sex differences in this test imply no differences in home cage activity, because the same flaw in the experiment as mentioned above applies. At the same time, although some hamsters may have a greater tendency to climb than others, there is no reason to expect systematic group effects and to this extent the results are valid.

Conclusion

The only conclusion that can be derived from these results is that there are no differences between genotypes, sexes or housing conditions in movement across the floor of the cage over 20 hours. If the lack of significant differences also meant basal home cage activity was similar for all the hamsters, then activity differences shown during other experiments could be said to result from genotype or sex differences in response to a new situation.

E. SUMMARY AND CONCLUSIONS OF BEHAVIOURAL EXPERIMENTS I.

Three behavioural experiments, the open field, novel situation and activity were presented and discussed.

The most clear indicator that piebald hamsters were more emotional than non-piebalds was the defecation response in the open field.

Forty percent of piebalds defecated against only seven percent of non-piebalds. Ambulation and scores on other measures in this situation were open to a number of interpretations, but in combination with the defecation scores tended to indicate golden piebalds were more emotional than either golden or brown hamsters.

The startle response in the novel situation similarly showed piebalds to startle significantly more than non-piebalds and this was considered to be evidence of a fear reaction.

In neither test situation could firm conclusions be drawn about the emotionality levels of males in relation to females or isolates in relation to group housed hamsters.

The two minute activity showed genotype and housing differences although the significance of this finding was unclear. Twenty hour activity showed no significant results, which however must be regarded as inconclusive due to possible flaws in the methodology. Nevertheless, this experiment may have yielded a basal level of activity in the individual hamsters, which would indicate that genotype and sex differences in open field and novel situation ambulation, reflect different reactions to fearful environments.

CHAPTER TWELVE
BEHAVIOURAL EXPERIMENTS II
A. REACTION TO HANDLING

Introduction

On arrival, hamsters received the routine handling necessary for identification and caging. Handling then only occurred at weekly weighing (from arrival to the end of experiments) and when hamsters were placed in or were removed from test situations.

At the age of eight weeks and when animals that had been living in groups were isolated they were then given scored handling tests weekly for five consecutive weeks. This was followed by weighing.

Riding gloves were worn during the handling experiment and other tests because hamsters, especially piebalds, were found to bite frequently during the pilot studies, although they did not do so to any significant extent in the study to be reported.

Method

A hamster's cage was placed on the bench to the left of the scales. The metal top of the cage was removed. The experimenter's hands approached the hamster, enveloped it, raised it in cup-shaped hands and placed it in the small metal cage on the balance (for weighing). The following measures were taken:

1. Withdrawal, that is, when the hamster withdrew as the hands approached.
2. Fight and Escape: that is, when the hamster had been picked up but struggled and/or escaped from the hands.
3. Vocalization: that is, when the hamster squealed as it was being picked up.

4. Latency: that is the time taken from start of hands approaching the hamster, to the animal resting securely in the experimenter's hands, ready for placing in the balance cage.

Arrangement of Data and Treatment

First arrangement of data

1. This consisted of:
 - a. 2 housing conditions, isolated and grouped.
 - b. 3 genotypes, G, B and GP.
 - c. 2 sexes, male and female.
 - d. 5 trials (from eight weeks of age).
 - e. 4 subjects per group.
2. Treatment of data: by 4-way analysis of variance.

Second arrangement of data

1. This consisted of:
 - a. 2 housing conditions.
 - b. 4 genotypes, females only, G, B, GP and BP.
 - c. 5 trials (from eight weeks of age).
 - d. 5 subjects per group.
2. Treatment of data: by 3-way analysis of variance.

Results

These are given separately for each measure.

Withdrawal. Group housed hamsters showed fewer withdrawals in response to handling than isolates ($p < 0.01$). Genotype differences showed that where females only were concerned, GP had more withdrawals than G, B or BP. ($p < 0.01$). Sex differences showed that females had more withdrawals than males ($p < 0.01$).

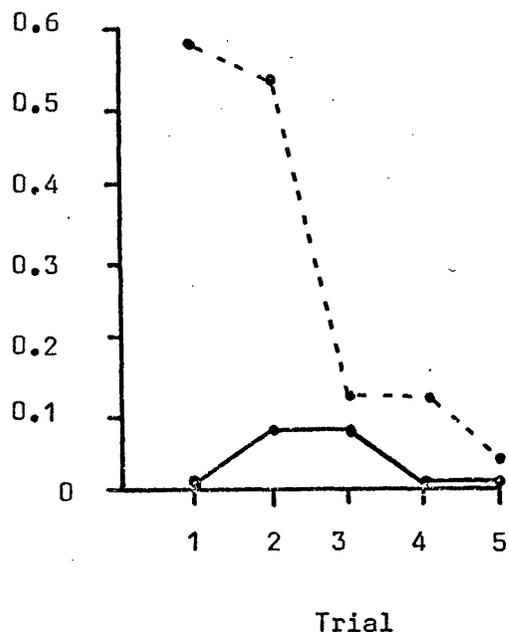
Fight and escape. Housing differences showed that isolates made fewer responses than grouped hamsters, among females only ($p < 0.01$). Genotype differences showed that GP gave more fights and escapes than G or B ($p < 0.001$), when three genotypes were compared, and among four genotypes the same pattern occurred ($p < 0.001$) with BP also showing more responses than G or B but not significantly so.

Vocalization. Housing differences showed that isolates vocalized more than grouped hamsters ($p < 0.01$). GP vocalized more than G ($p < 0.05$) and B fell intermediately, although not significantly different from either G or GP. Vocalization decreased over trials ($p < 0.001$). A housing \times trial interaction ($p < 0.001$) showed that grouped hamsters gave a small vocalization with little variance over trials. Isolates showed a large amount of vocalization on trial one, but decreased over trials to equal the grouped animals by trial five. A graph of this interaction is given in figure 14. In a genotype \times trial interaction ($p < 0.01$) all genotypes decreased vocalization over trials, although GP did not reach the low levels shown by G and B. A graph of this interaction is given in figure 15. A genotype \times sex \times trial interaction ($p < 0.05$) showed that GP females, GP males and G females had the highest amount of vocalization on trial one, followed by B females, B males and G males. By trial five, both sexes of each genotype had adapted to a zero vocalization level, except GP females, which still vocalized although at a lower level than on trial one. A housing \times genotype \times trial interaction ($p < 0.05$) showed that grouped hamsters retained a low level of vocalization over trials. Isolated G and B hamsters adapted to a low level by trial five, although GP isolates, with the greatest vocalization on trial one did not adapt as well as the other isolates over trials.

Latency. The latency for being handled was longer for isolates than grouped hamsters ($p < 0.05$). Genotype differences for females only showed that GP had a longer latency than G or B ($p < 0.001$) and that BP fell between GP and B/G, but was not significantly different from them. Sex differences showed that females had a longer latency than males ($p < 0.01$). Latency for being handled decreased over trials ($p < 0.001$). A housing \times trial interaction ($p < 0.05$) showed that grouped hamsters had a small latency on all trials with little variation over trials, whereas isolates showed a large latency on trial one, but decreased over trials to equal that of grouped animals by trial five.

Figure 14. Mean vocalization during handling:
housing x trial interaction, data
in arrangement one.

Vocalization
response



———— Grouped
----- Isolated

Summaries of the analyses of variance carried out on the handling data are given in Summary Tables XI and XII, and the results are shown in tabular form in Table VI.

Discussion

The view that resistance to handling may be an indication of emotional arousal was suggested from comments like these "...inherently timid strains are harder to tame by handling procedures than more docile strains" (Fox, 1968^{p.69})._λ Robinson (1958, 1968) observed that piebalds "require more considerate handling" than other hamster types. It was therefore hypothesized in the handling experiment that piebalds would show greater resistance to handling than brown or golden hamsters, and that resistance would indicate fear.

This experiment allowed the display of direct fear responses, namely, escape and immobility. Vocalization, also measured, is on the other hand only an indirect measure and in the past has received little validation as a measure of emotionality (Berryman 1974).

Other workers have used vocalization as indicative of fear (cf. Chapter Seven) and this, along with my own incidental observations, have led me to consider it in the same way. For example, experimenter approach to a piebald cage resulted in vocalization in some cases, but seldom as a result of approach to a G or B cage, indicating that vocalization may occur in response to strange stimuli, which may also be fear provoking.

Vocalization decreased over trials, which weakly validates it as a positive measure of fear, in that the emotionality responses could be expected to decrease as the handling procedure became more familiar. A far better validation would involve correlation of vocalization with escape and freezing behaviour occurring in the handling test - in fact a relationship is detectable from the present results.

Summary Table XI

Four-way analyses of variance carried out on data in arrangement one and levels of significance obtained.

Measure	Variation	SS	MS	DF	F	Significance level
Withdraw	Housing	8.82	8.82	1	8.31	0.01
	Sex	8.82	8.82	1	8.31	0.01
Fight and Escape	Genotype	12.66	6.33	2	9.02	0.001
	Housing x Sex	4.54	4.54	1	6.47	0.05
	Housing x Genotype	5.58	2.79	2	3.97	0.05
	x Sex					
Vocalization	Housing	3.75	3.75	1	22.50	0.001
	Genotype	1.41	0.70	2	4.22	0.05
	Trial	3.48	0.87	4	14.75	0.001
	Housing x Trial	3.08	0.77	4	13.06	0.001
	Genotype x Trial	1.22	0.15	8	2.58	0.01
	Housing x Genotype	1.02	0.13	8	2.15	0.05
	x Trial					
	Genotype x Sex x Trial	1.07	0.13	8	2.26	0.05
	Trial					
Latency	Housing	158.44	158.44	1	10.56	0.01
	Sex	121.84	121.84	1	8.12	0.01
	Trial	223.18	55.80	4	6.23	0.001
	Housing x Trial	109.67	27.42	4	3.06	0.05

Summary Table XII

Three-way analyses of variance carried out on data in arrangement two and levels of significance obtained.

Measure	Variation	SS	MS	DF	F	Significance level
Withdraw	Genotype	14.48	4.83	3	4.70	0.01
Fight and Escape	Housing	4.50	4.50	1	11.18	0.01
	Genotype	13.70	4.57	3	11.35	0.001
	Housing x Genotype	3.94	1.31	3	3.26	0.05
Vocalization	Housing	2.64	2.64	1	7.61	0.01
	Trial	3.68	0.92	4	12.69	0.001
	Housing x Trial	1.68	0.42	4	5.79	0.001
	Housing x Genotype x Trial	1.84	0.15	12	2.11	0.05
Latency	Housing	42.32	42.32	1	4.80	0.05
	Genotype	192.16	64.05	3	7.26	0.001
	Trial	90.15	22.54	4	2.61	0.05

Table VIII

Tabular representation of significant handling results.

Genotype differences (brown piebalds are not included)			
Measure	Golden hamsters	Brown hamsters	Golden Piebald hamsters
Withdraw (females only)	less	less	more
Fight and Escape	less	less	more
Vocalization	less	intermediate NS	more
Latency (females only)	shorter	shorter	longer
Sex differences			
Measure	Males	Females	
Withdraw	less	more	
Latency	shorter	longer	
Housing differences			
Measure	Grouped hamsters	Isolated hamsters	
Withdraw	less	more	
Fight and Escape (females only)	more	less	
Vocalization	less	more	
Latency	shorter	longer	
Measures which change over trials			
Vocalization		decrease over trials	
Latency		decrease over trials	

It could be argued that this test, by its very nature, that of handling the hamster and recording reactions, is subjective, so the results should be viewed within this limitation.

1. Genotype differences

These revealed GP to withdraw more (among females only), to fight and escape more, to vocalize more and to have a longer latency (among females only) than G or B hamsters. BP females showed more fight and escape and a tendency towards a longer latency (not significant) than G or B hamsters.

In a significant genotype x trial interaction for vocalization (figure 15) GP needed five trials to bring them near the low levels of B and G, although even on trial five, GP retained more resistance to handling in terms of vocalization.

It seems quite clear that GP were more resistant to handling, as shown by their greater escape behaviour on three measures and increased vocalization than either G or B hamsters, and in this experiment can therefore be said to be more emotional.

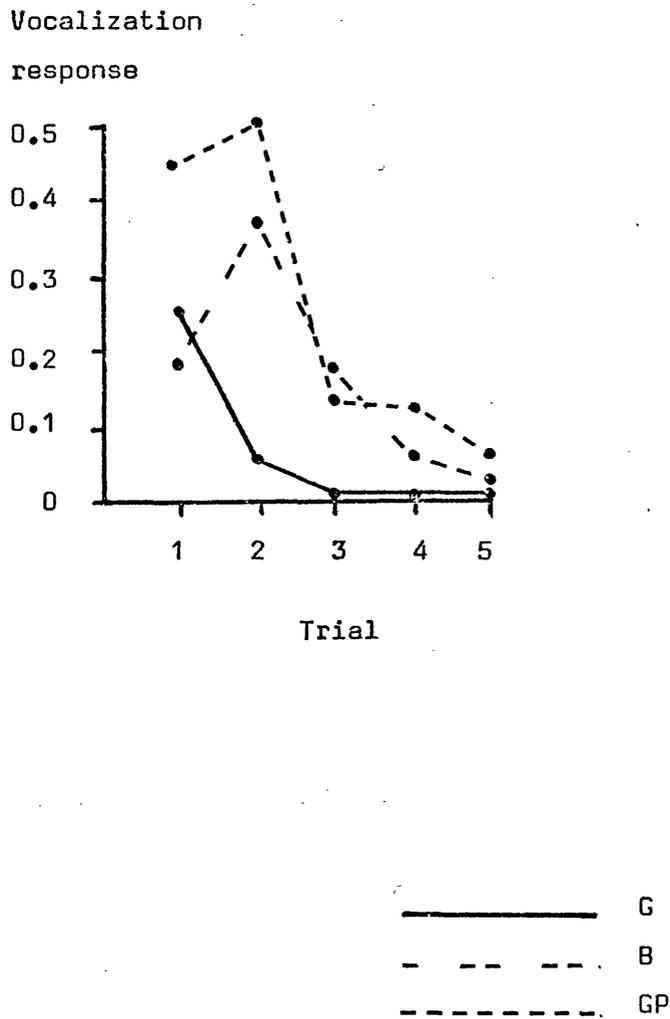
2. Sex differences

Females withdrew more and had a longer latency than males, so on two measures, involving escape, they showed greater resistance to handling. Therefore, on an escape-type reaction to handling, females showed greater emotionality than males. There was no indication that males tended to display immobile behaviour (or other type of fear response, such as biting) and it seems likely that in this kind of situation females are more reactive than males.

3. Housing differences

These showed that isolated hamsters vocalized more, withdrew more and had a longer latency than group raised animals. These results indicate that greater resistance to handling is exhibited by the isolates.

Figure 15. Mean vocalization during handling: genotype x trial interaction, data in arrangement one.



However, one result, at first sight, does not seem to conform to this pattern, as isolates among females only, scored less on the fight and escape measure than group reared hamsters. The relationship of this measure to fear may be more complex than the others, thus rendering interpretation difficult. Fight and escape could only take place when the experimenter's hands were around the hamster ready to transfer it to the weighing cage. Lack of struggling could indicate a casual response to the situation or it could signify immobile behaviour. The former indicates non-emotionality and the latter, emotionality, so that lack of fight and escape as a solitary measure does not necessarily imply non-emotionality.

Here therefore, is an example of a measure that potentially allows the expression of fear in two ways. The uncertain patterns shown by isolated and grouped females prevents a firm conclusion about emotionality in one type, although trends are towards it being higher in isolates.

This conclusion generally agrees with the rat work. Stern, Winokur, Eisenstein, Taylor and Sly (1960) compared reaction to handling in adult rats subjected to postweaning individual or group housing. They found that individually housed rats "showed more resistance to handling". They retreated from a hand when it was put into a cage and vocalized more when removed from the cage. Moyer and Korn (1965) rated rats on a six point scale of emotionality when picked up. Some subjects were isolated from weaning and others group housed. They used the following ratings:

0. S made no attempt to escape from E and did not vocalize or jump.
1. Startle response but no vocalization or rigorous escape attempt.
2. Startle and vocalization.

3. Startle, greater vocalization and escape attempt.
4. Extreme vocalization, struggling and defecation.
5. Same as 4, plus biting E's glove.

The workers found that ten out of 13 isolated rats scored rating 2 or higher, while only two out of 12 group housed rats scored this highly. They may have had difficulty differentiating between ratings 2, 3 and 4, but my results mostly agree with theirs for withdrawal, vocalization and latency. They found isolated animals made more fight and escape responses, which conflict with the present findings (for females only data).

Conclusions

It is concluded that the pattern shown by piebald hamsters justifies a description of their behaviour as more fearful than that of golden or brown hamsters in this experimental situation. This is displayed by greater escape behaviour, a criterion of emotionality.

The incomplete pattern shown by the sexes indicated that females tended to escape more than males. However, greater female resistance to handling was only exhibited on two measures and it is therefore a more tentative conclusion that females react with greater emotionality than males to handling.

The conflicting patterns of reaction shown by isolated and grouped hamsters render interpretation of housing differences in terms of emotionality difficult. On the majority of measures, though, isolates may be said to be more resistant to handling than group reared hamsters. Repetition of the experiment and more detailed analysis of the results may clarify the significance of the controversial measure (fight and escape), which was only significant for females from four genotypes.

B. PASSIVE AVOIDANCE LEARNING

Introduction

In this experiment avoidance behaviour (considered to be fear motivated) was provoked by the administration of electric shock, which is thought to be painful and therefore fearful. Gray (1971a) suggested that the learning of avoidance may contribute information about the organization of fearful behaviour.

Carran (1967) interpreted Mowrer's theory of fear motivated behaviour in this way: when an act is later performed, initial response correlated stimuli may elicit fear, a complex intervening emotion. If the fear generated is powerful enough, it should inhibit further responding and motivate passive avoidance. Carran predicted that strain differences in fearfulness would cause differences in passive avoidance, the more fearful strain performing better. As mentioned in Chapter Seven, Carran's experiment partly supported Mowrer's theory.

However, it was proposed in Chapter Seven that although immobility or inhibition of responding were types of reaction to a fearful situation, they were not the only ones and in some cases they may be an alternative response to preferred escape behaviour.

Initially, passive avoidance learning, as opposed to other sorts of learning, was studied in the hamster genotypes predominantly because of the time factor. Only two days and four trials were needed for the particular experiment chosen. Information was sought on whether hamsters judged as more emotional in other experimental situations were also better at passive avoidance learning or whether the pattern of learning more closely followed the common-sense hypothesis and findings for some human reactions (Lazarus 1966) that intermediate emotionality is associated with the best learning. This experiment

was therefore carried out to give some information on how fear may relate to passive avoidance learning.

It seemed appropriate to allow two five minute exploration trials before the start of the experiment, so that by trial one the hamster should have become familiar with the environment, and consequently would be expected to explore less. Lubow (1973) has reviewed the literature on latent inhibition, that is, the decrement in learning performance resulting from non-reinforced pre-exposure of the to-be-conditioned stimulus. The number of pre-exposures involved in my study should not have been sufficient to alter learning. For example, Grant and Young (1971) demonstrated that pre-exposure to test apparatus facilitated subsequent avoidance learning, when there were 7-19 pre-exposure sessions lasting 15 minutes each.

Kumar (1970) was one worker who, measuring passive avoidance of a white arm of a Y-maze, demonstrated that fear incubated with time. Rats received two shocks of ten seconds duration each in a white box. They were then tested in the Y-maze for passive avoidance of the white arm at intervals ranging from half an hour to 120 hours after receiving the shock. Passive avoidance was most complete after six hours. Rats tested after only half an hour behaved like unshocked controls and Kumar concluded that fear incubated after conditioning. The 20 hour interval chosen for my experiment was therefore expected to result in reasonable avoidance behaviour, through incubation.

An experiment by Riccio, Rohrbaugh and Hodges (1968) considered developmental aspects of passive and active avoidance in rats. Their apparatus was similar to mine, although the procedure varied. Rats were given only a one second shock. They found that passive avoidance improved markedly with age, although retention over 24 hours was complete for all ages. This result emphasizes the effectiveness of this type of passive avoidance procedure for rats.

A pilot study for my experiment was not carried out as rats have been found to learn passive avoidance effectively after shock administration and it was thought hamsters would also. Observations were carried out to determine suitable shock intensity.

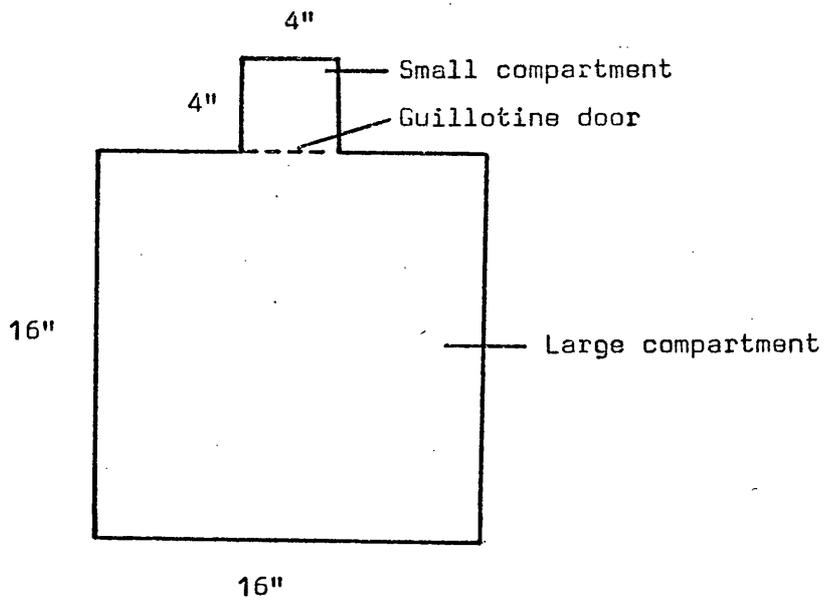
Method

Apparatus. This was similar to that used by Bures, Buresova and Fifkova (1964). It consisted of two compartments with metal walls and a grid floor, with bars half an inch apart. The large compartment was 16 inches square with white walls, and joined to a small compartment four inches square, with black walls, by a perspex guillotine door. (A floor plan of this apparatus is given in figure 16). The grid floor of the small compartment was attached to a shock device Type TV-3B 0.3KVA and set to 40 volts a.c. The grid floor of the large compartment was not electrified. This experiment took place in the animal room which was lit by the normal red light. A white light was added to illuminate the large compartment.

Procedure. It was hypothesized that the hamster, being a nocturnal and burrowing animal, would prefer the small compartment to the large, as shown for rats. The light above the large compartment was added to make it more frightening and to aid discrimination. However, as adding light meant another variable in the experiment, it was only used for half the subjects. In this way, the importance of lighting effects could be determined.

The experiment lasted two days. On the first day subjects were given two five minute exploratory trials of the apparatus, half an hour apart. This was so that when they were placed in the experiment the environment was not entirely novel. Three hours later, they were given three trials of three minutes each to explore the apparatus. Each hamster was placed in the centre of the large

Figure 16. Floor plan of apparatus for passive avoidance learning. Area covered by shock grid, bars half an inch apart.



compartment, facing the small compartment. The number of bouts and the lengths of time the animals spent in the large and small compartments on each trial were recorded. An animal was considered to be in the small compartment when its hind legs had crossed the bar between the large and small compartments. Also, the bouts and length of time a hamster sniffed the perimeter of the small compartment, while resting in the large were recorded. The three trials were separated by 30 minutes. At the end of each trial, the hamster was returned to its cage for one minute. The guillotine door was inserted and the subject placed in the small compartment, from which it could not escape. It was then given one minute of intermittent electric shock pulses (every two seconds) of 40 volts a.c. During this time the intensity of vocalization was recorded. No vocalization received a score of 0. Infrequent and quiet vocalization scored 1, infrequent but loud vocalization scored 2, and continuous loud vocalization scored 3. The animal was then removed from the small compartment and returned to its cage. Each trial was therefore followed by shock. On the following day, 20 hours later, the subjects were given one retention trial lasting three minutes (referred to as R). Bouts and time in the small compartment, large compartment and sniffing the small compartment were recorded.

From the raw data, sniffing time on trials 2, 3 and R as a percentage of sniffing time on trial 1 (= sniffing time), and time spent in the small compartment on trials 2, 3 and R as percentage of that on trial 1 (= learning measure) were calculated. A low percentage indicated good learning i.e. the animal learned from shock administration that the small compartment was fearful, so spent little time there on the retention trial compared to trial 1 before shock had been given. A percentage of 100 or above indicated no learning had taken place i.e.

the hamster spent as much time or more in the small compartment on the retention trial as on trial 1, despite the intervening electric shock. Sniffing bouts and bouts in the small compartment on trials 1, 2, 3 and R were also recorded.

Arrangement of Data for Sniffing Time and Treatment

First arrangement of data

1. This consisted of:
 - a. 2 lighting conditions, light and dark.
 - b. 3 genotypes, G, B and GP.
 - c. 2 sexes, male and female
 - d. 3 trials, 2, 3 and R.
 - e. 5 subjects per group.
2. Treatment of data: by 4-way analysis of variance.

Second arrangement of data

1. This consisted of:
 - a. 2 lighting conditions.
 - b. 4 genotypes, females only, G, B, GP and BP.
 - c. 3 trials, 2, 3 and R.
 - d. 5 subjects per group.
2. Treatment of data: by 3-way analysis of variance.

Arrangement of Data for Sniffing Bouts and Bouts in the Small Compartment and Treatment

First arrangement of data

1. This consisted of:
 - a. 2 lighting conditions, light and dark.
 - b. 3 genotypes, G, B and GP.
 - c. 2 sexes.
 - d. 4 trials, 1, 2, 3 and R.
 - e. 5 subjects per group.
2. Treatment of data: by 4-way analysis of variance.

Second arrangement of data

1. This consisted of:
 - a. 2 lighting conditions.

- b. 4 genotypes, females only.
- c. 4 trials, 1, 2, 3 and R.
- d. 5 subjects per group.

2. Treatment of data; by 3-way analysis of variance.

Arrangement of Data for Vocalization and Treatment

First arrangement of data

1. This consisted of:

- a. 2 lighting conditions.
- b. 3 genotypes, G, B and GP.
- c. 2 sexes.
- d. 3 trials, 1, 2 and 3.
- e. 5 subjects per group.

2. Treatment of data; by 4-way analysis of variance.

Arrangement of Data for Learning Measure and Treatment

First arrangement of data

1. This consisted of:

- a. 2 lighting conditions.
- b. 3 genotypes, G, B and BP.
- c. 2 sexes.
- d. 3 trials, 2, 3 and R.
- e. 5 subjects per group.

2. Treatment of data: by 4-way analysis of variance.

Second arrangement of data

1. This consisted of:

- a. 2 lighting conditions.
- b. 4 genotypes, females only, G, B, GP and BP.
- c. 3 trials, 2, 3 and R.
- d. 5 subjects per group.

2. Treatment of data: by 3-way analysis of variance.

Third arrangement of data

1. This consisted of:

- a. housing conditions, isolated and grouped.

- b. 3 genotypes.
- c. 2 sexes.
- d. 3 trials 2, 3 and R.
- e. 4 subjects per group.

2. Treatment of data: by 4-way analysis of variance.

Fourth arrangement of data

1. This consisted of:

- a. 2 housing conditions.
- b. 4 genotypes, females only.
- c. 3 trials, 2, 3 and R.
- d. 5 subjects per group.

2. Treatment of data: by 3-way analysis of variance.

Results

Genotype differences. Golden piebalds had fewer sniffing bouts than G or B ($p < 0.01$), and GP and BP had a shorter sniffing time than G or B ($p < 0.05$). Vocalization was greater in GP than G or B ($p < 0.01$).

Trial differences. Sniffing time ($p < 0.05$) showed a sharp decrease between trials 2 and 3, and an increase on the retention trial which equalled that on trial 2.

Sniffing bouts ($p < 0.05$) showed a decrease between trials 1 and 3 and an increase on R to equal that on trial 2. Bouts in the small compartment ($p < 0.001$) decreased to trial 3 and increased on R almost to equal those on trial 1, before shock was received. The learning measure ($p < 0.001$) decreased to trial 3 and a large increase on R showed a higher percentage than on trial 2. Vocalization decreased over trials ($p < 0.01$).

Interactions. Bouts in the small compartment and sniffing time showed complicated lighting x genotype interactions. As lighting differences showed no significance, the interactions will not be examined. A housing x genotype x trial interaction for the learning measure ($p < 0.01$) showed that isolated B and grouped GP learned better than hamsters from all other housing x genotype combinations.

A graph of this interaction is given in figure 18.

A summary of the analysis of variance carried out on the learning measure in data arrangement three is given in Summary Table XIII and the results for this experiment are shown in tabular form in Table VII.

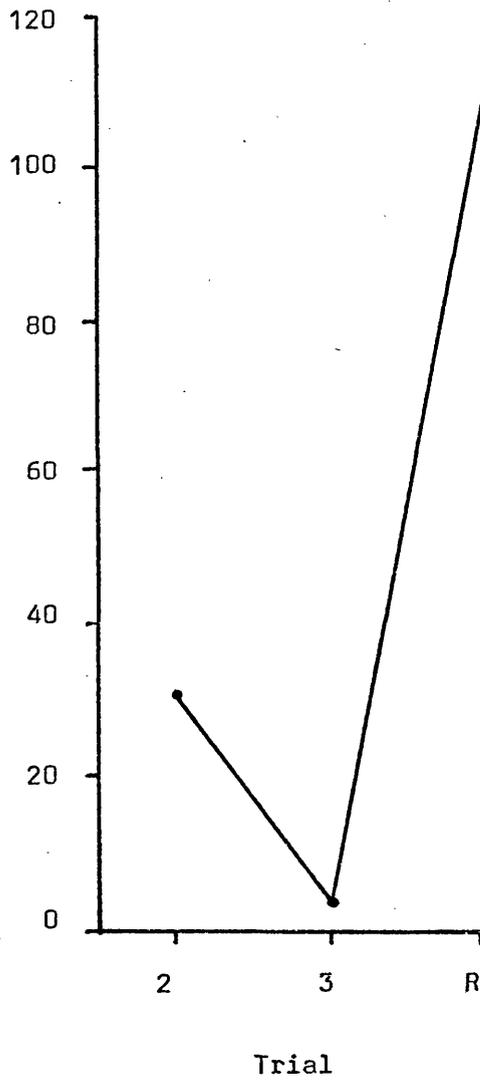
Discussion

It can be seen that the results give little information on learning differences between genotypes, sexes or housing conditions.

Trends over trials should show the extent to which learning had taken place. If electric shock acted as a punishing stimulus inducing fear of the small compartment, it would be expected that time spent there on trial one (before electric shock was administered) should decrease to trial three and retention 20 hours later would indicate the extent to which learning had taken place. Similarly, the number of bouts in the small compartment and sniffing of the small compartment should decrease over trials. Trial differences show the predicted decrease between trials one to three, but the learning measure on retention indicates that no learning took place, with time spent in the small compartment being 112 percent of that on trial one (for data in first arrangement), that is, the hamsters spent more time in this compartment on retention than they did on trial one (figure 17). This implies no learning took place. However, where housing conditions were also considered (i.e. learning measure, data in third arrangement), time spent in the small compartment was 88 percent of that on trial one, indicating that some learning had taken place. In this data arrangement where half the hamsters were isolated, instead of mostly being grouped (cf. open field discussion, pg. 201), the results which showed some learning, could have been biased by the isolates.

Figure 17. Passive avoidance learning:
mean learning measure over
trials 2,3 and R, data in
arrangement one.

Time in small
compartment as a
percentage of time
spent there on
trial 1.



Summary Table XIII

Four-way analysis of variance carried out on learning measure,
data in arrangement three, with levels of significance obtained.

Variation	SS	MS	DF	F	Significance level
Housing	1813.34	1813.34	1	0.52	NS
Genotype	10573.85	5286.92	2	1.53	NS
Housing x Genotype	5953.35	2976.67	2	0.86	NS
Sex	1757.01	1757.01	1	0.51	NS
Housing x Sex	540.56	540.56	1	0.16	NS
Genotype x Sex	7923.01	3961.51	2	1.14	NS
Housing x Genotype x Sex	4857.13	2428.56	2	0.70	NS
Trials	185534.06	92767.03	2	41.36	0.001
Housing x Trial	1284.22	642.11	2	0.29	NS
Genotype x Trial	3885.53	971.38	4	0.43	NS
Sex x Trial	998.22	499.11	2	0.22	NS
Housing x Genotype x Trial	34002.78	8500.69	4	3.79	0.01
Genotype x Sex x Trial	3326.19	831.55	4	0.37	NS
Housing x Sex x Trial	2650.50	1325.25	2	0.59	NS
Housing x Genotype x Sex x Trial	21735.50	5431.37	4	2.42	NS

Table VII.

Tabular representation of significant learning results.

Genotype differences (brown piebalds are not included)			
Measure	Golden hamsters	Brown hamsters	Golden Piebald hamsters
Sniffing bouts	more	more	less
Sniffing time (females only)	more	more	less
Vocalization	less	less	more

Sex differences		
Measure	Males	Females
Vocalization	less	more

Measures which change over trials	
Sniffing time	less time on trial 1, than 2, 3, R, but of these, less time on trial 3.
Sniffing bouts	decrease to trial 3 but an increase on R.
Bouts in the small compartment	decrease to trial 3 and in increase on R.
Learning measure	decrease to trial 3, but an increase on R.
Vocalization	decrease to trial 3.

Sniffing showed the same pattern as the learning measure.

Sniffing time and bouts in the small compartment decreased to trial three. Sniffing time showed an increase on retention to equal that of trial two and the bouts increased to equal the number on trial one.

There is one clear conclusion: electric shock is remembered very well over short (half hour) intervals, as evidenced by increasing avoidance of the small compartment in trials two and three. But, with a 20 hour interval there is little evidence of learning.

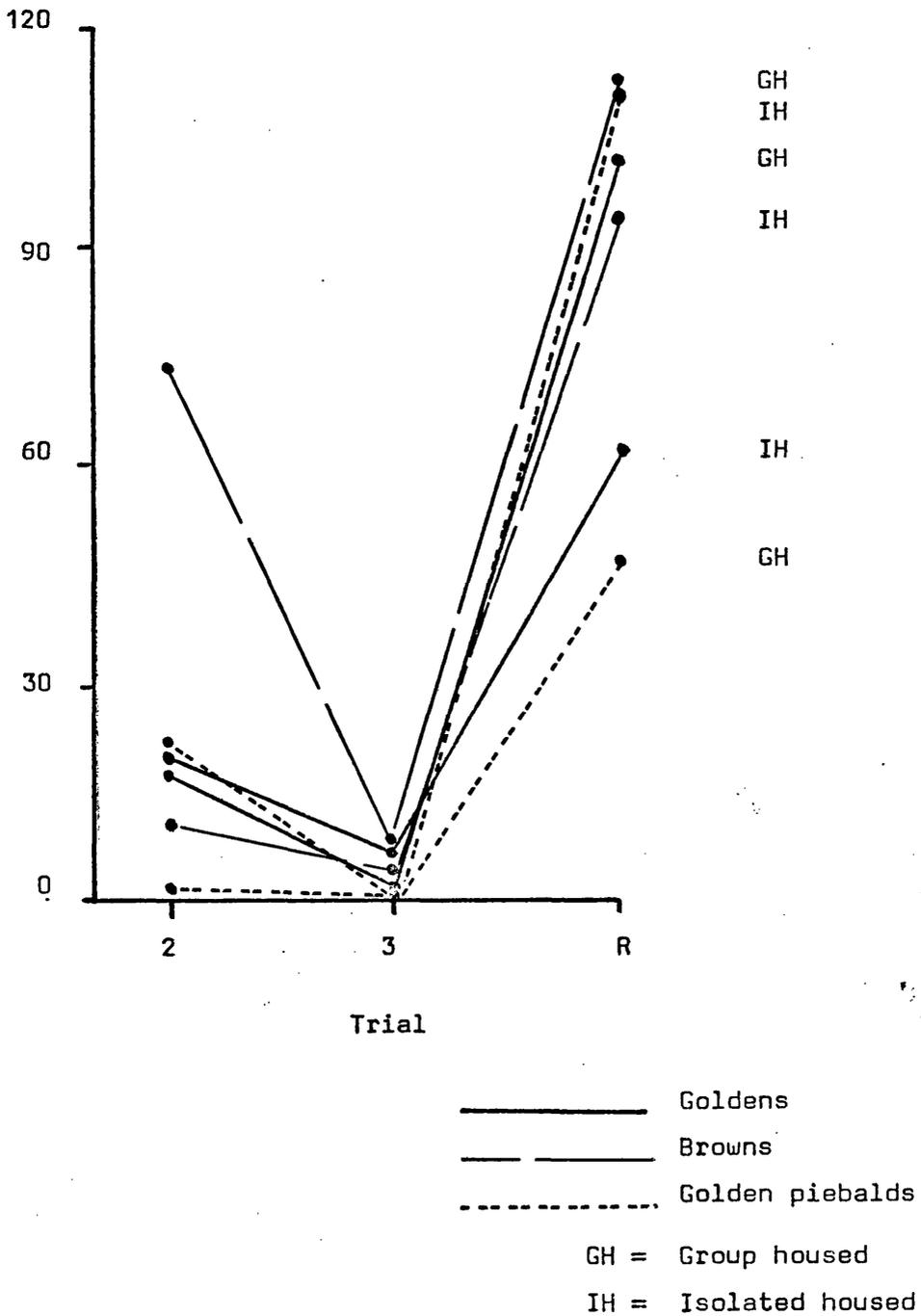
If, on the retention trial, fear of the small compartment elicited by shock is remembered, a hamster, on being placed in the large compartment may approach the otherwise more desirable small compartment and sniff its perimeters, while still in the 'safe' large compartment. On discovering the small compartment to be safe also, the hamster may enter. This could distort any learning effect and account for the high proportion of time spent in the small compartment on the retention trial. Sniffing time showed a big increase on the retention trial over that of trial one. Only very fearful hamsters would not approach the small compartment, test its safety or enter, thereby showing good learning.

If the housing x genotype x trial interaction for the learning measure (figure 18) is considered, the genotype pattern over over trials is apparent. After two shock trials, that is, on trial three, all genotypes have learned that the small compartment is fear provoking, and they spent only a small amount of time there. On the retention trial the findings comprise two groups of hamsters, those that learnt well, isolated G and grouped GP, and those that show no learning at all, grouped and isolated B, isolated GP and grouped G.

Therefore genotype interacts with housing to produce differences in learning but they do not form an interpretable pattern. For example

Figure 18. Passive avoidance learning, mean learning measure: housing x genotype x trial interaction, data in arrangement three.

Time in small compartment as a percentage of time spent there on trial 1.



if fear enhanced passive avoidance learning and emotionality was characteristic of the piebald genotype, then isolated piebalds should have shown as good learning as grouped piebalds. If isolated goldens showed good learning, why did isolated browns not show it also? If intermediately emotional animals perform best in learning tasks on the basis that non-emotional animals are not motivated enough by shock to learn and very emotional ones are too disturbed by shock to learn (Denenberg 1962), then animals which on other tests had shown trends toward intermediate emotionality, that is, the brown hamsters, should have shown the best learning. This was not the case.

Sex differences were not significant on any measure except vocalization, which was more frequent in females than males, and there were no significant interactions with sex. These findings do not support other work which showed males performed better on passive avoidance than females (e.g. Denti and Epstein 1972). The importance of vocalization as a measure of fear in response to electric shock will be discussed in Section C of this chapter.

Reasons for Inconclusive Results

Either male and female hamsters of the genotypes studied do not show differences in passive avoidance learning which can be reliably demonstrated or other explanations, besides the one previously mentioned (that approach to the small compartment on the retention trial and sniffing of it may reveal it to be safe, so the hamsters enter) may account for the inconclusive results.

Firstly, shock may not have been intense enough. My experiment was based on that of Bures et al. (1964) who used 100 volts for rats. However, in my preliminary observations use of this voltage seemed excessively painful for hamsters (one piebald fell into a coma and

subsequently died). Since Denenberg and Karas (1960) used only 60 volts with rats and as it seemed likely that because they are smaller a lesser shock would suffice for hamsters, the voltage was reduced to 40. The reactions of the hamsters to this shock level, in terms of vocalization and jumping, indicated that it would be adequate for the experiment. However, this level may have been too low for good learning, even in hamsters with higher basal fear levels. Different findings may arise from administration of a more powerful shock.

Secondly, it is possible that the hamsters could not discriminate easily between the two compartments despite the obvious size differences. Those completing the experiment under red light may not have been able to detect differences in the wall paint and those performing with a light shining above the large compartment may have found this section nearly as fearful as the shock compartment. A difference in the floors would probably have aided discrimination but if the large compartment had had a solid floor and the small one a grid floor, the hamster may have been fearful about exploring this part on trial one and any preference for compartment would have been distorted.

Thirdly, another confounding factor could be olfactory cues. Cheal and Spratt (1971) and Schultz and Tapp (1973) have reviewed the importance of pheromones in rodent behaviour. One of the earliest and most complete studies on 'alarm' pheromones was carried out by Muller-Velten (1966) who showed that wild mice would avoid the alley of a previously frightened mouse and run down the other alley.

Olfactory cues left in a situation have been shown to be influential in open field behaviour (Whittier and McReynolds 1965), runway alternation behaviour (Ludvigson and Sytsma 1967), retention

of acquired fear (King, M.G. 1969), attraction by other animals (Carr, Mortorano and Krames 1970, Carr, Roth and Amore 1971). Pheromones as possible confounding factors, especially in learning experiments have been stressed (Sprott 1969, Davis and Ludvigson 1969, Gleason and Reynierse 1969) yet no one has suggested an appropriate control for them. Clear water as a washing material has been shown to be ineffective (Whittier and McReynolds 1965, Davis and Ludvigson 1969). A detergent or disinfectant may themselves be fearful odors and consequently modify behaviour. The same applies to a spray, which presumably gets rid of odors in the air as well as wall and floor surfaces. The only advantage of these procedures is that the situation should be more or less equal in terms of resident odors, for all subjects. Alternatively, a new apparatus for each subject would have the same effect, but often this would not be practical. One compromise would be to place half the subjects in disinfected apparatus and compare their results with similar animals placed in unwashed apparatus. This experiment would, of course, involve twice as many subjects.

Much recent evidence has shown olfactory cues to be an integral part of rodent social behaviour. Most learning experiments have not controlled for odor effects and the extent to which they could mask the results is not known. In my experiment a hamster receiving electric shock in the small compartment is followed by another hamster, being placed in the large compartment, beginning a three minute exploration trial. 'Alarm' odor cues from the small compartment may have encouraged or prevented the exploring hamster's entrance to this compartment. Any odor may differ in its degree of alarm arousal for different hamsters. Odor emission may vary. Hamsters that find the receipt of shock a very emotional experience may emit more odor than those finding it less so. Order for taking part in the experiment within any one group of

hamsters was random, but it is conceivable that the behaviour of the hamster receiving shock enclosed in the small compartment affected the exploratory behaviour of the subsequent hamster, and this may have resulted in overall confusion in the results.

A final reason for the lack of clear findings is that hamsters may not be suitable for learning experiments of this type. Few, if any, learning experiments of this kind have been carried out using hamsters and more investigations are needed before any comments about their suitability for learning experiments can be made.

Conclusions

Unfortunately, no conclusions about which hamsters performed best on passive avoidance and how this relates to fear can be drawn. Future researchers using a similar experimental design for hamsters, could use better methodology improved along the lines already suggested.

Furthermore, as mentioned in Chapter Seven, either type of fear response, immobility or escape, can occur in learning situations involving shock. Immobility is demanded in passive avoidance, but escape behaviour under active avoidance conditions is desirable. An animal that learns passive avoidance poorly may be frantically searching for an escape path, so that its poor learning, in this case, would not reflect a low fear level. Also, studies of piebald performance on passive avoidance in conjunction with active avoidance learning and CER would perhaps give broader information on the association between fear and learning in hamsters.

C. COMMENT ON VOCALIZATION BY THE HAMSTER IN RESPONSE TO EXPERIMENTAL SITUATIONS

Vocalization occurred in three experimental situations in this study. It happened during placement into and removal from the open

field, as a reaction to handling, and in response to electric shock in passive avoidance learning.

As mentioned previously, the validity of hamster vocalization as a measure of fear has not been established.

Considering the occasions where vocalization occurred in this study, it would appear to be a response to pain. Previous research has suggested that squeals are a reflex reaction to pain in mice (e.g. Scott 1946) and are a "natural response to shock" in rats (e.g. Cowles and Pennington 1943). King (1958) considered vocalization during testing of a conditioned avoidance response in rats to be a measure of emotionality. Therefore, it seems likely that electric shock was painful where continuous sounds were emitted. It was also noticed that some piebalds vocalized when placed in the large compartment of the passive avoidance apparatus for exploration on trials two and three. This may have been a response in anticipation of pain, which was associated with this environment. Similarly vocalization in response to handling may have occurred either because the handling procedure itself was painful or because it warned of pain.

Incidental observations have led me to believe that only one or two 'squeals' would be given in response to handling, whereas electric shock could elicit almost continuous vocalization. This could be because pain caused by intermittent electric shock over one minute is more intense than that arising from handling.

Vocalization was further recorded during aggressive encounter (experiment D of this chapter) and observations suggested that it occurred mostly during attack behaviour.

Morgret and Dengerink (1972) correlated mouse 'squeals' with their agonistic behaviour and found a strong positive relationship between squeals and other measures of fighting, such as number of attacks.

As in the case of my experiment, they could not separate vocalizations emitted by each mouse in the encounter, but on the whole felt that squealing was a response given by the attacked mouse, so that vocalization was not a measure of agonistic behaviour itself, but of the effects of this type of behaviour on the other mouse. If the attacked hamster, and therefore the bitten hamster is the one that vocalized in the aggression experiment, then pain as partially responsible for the emission of acoustic behaviour is implicated.

The occurrence of vocalization could thus be viewed as correlating with pain, the anticipation of pain or of further pain. This possibility, coupled with the finding that hamsters did not commonly vocalize during procedures designed to be less fearful (when in their home cages on the Animex, while food pellets were counted or in the novel situation) suggests that vocalization may also represent increased emotionality, in this species.

Specifically, in the reported study, GP vocalized more than G or B hamsters in response to electric shock, and females more so than males. Vocalization also showed a decrease over trials, which adds to evidence that it is a fear response.

In response to handling, it was found that GP vocalized more than G or B over trials.

The open field data showed that GP gave more acoustic responses than either G or B when handled on entrance to and exit from the field, and that females vocalized more than males on exit.

When genotype and sex differences in vocalization can be discriminated by its occurrence or non-occurrence (an all-or-nothing response), the experimental procedure is simple, as in handling and the open field. However, in the learning experiment, recording the amount of vocalization of each hamster was open to experimenter bias.

Hamsters scored 1, 2 or 3, for vocalization in response to electric shock (a subjective assessment of the calls' frequency of occurrence and intensity by the experimenter). Improvements in the procedure would involve the use of other judges who did not know the identity of the animals receiving shock, so unbiased scores and correlations could be produced, or better still, use of a sound level meter could give information on the number of pulses and intensity of vocalization within any time period.

Despite misgivings about the subjectivity of recording vocalizations in response to electric shock, the three experiments displayed similar results in terms of genotypic and sex differences in vocal response, with piebalds vocalizing more than non-piebalds and females responding in this way, more than males. The heightened female vocalization response to electric shock agrees with other studies on rats (for example, Beatty and Beatty 1970, Wilcock 1968) which showed females had lowered thresholds to electric shock in terms of flinching, jumping and running.

Conclusions

The data obtained from the experiments presented in this thesis do, on the whole, indicate that piebalds vocalized more than non-piebalds and it is hypothesized that this is related to pain, probably coupled with fear responding.

Females may have vocalized more than males in some conditions, but the problem of finding a consistent pattern of fear reaction by one sex, reiterated throughout the experimental discussions, prevents too much emphasis being placed on the interpretation of heightened female vocalization. It could imply that female hamsters have a lower pain threshold than males, respond with more vocalization and may also be more emotional in these types of situation (but not others),

or that the female emotional reaction to the particular situation is in terms of greater vocalization, and the male response could be of equal intensity, although of a different nature.

There is scope for future research on the relationship between vocalization, pain and fear.

D. AGGRESSIVE ENCOUNTER

Introduction

Arnold (1944) described emotionality as characterized in rats by various traits, including lack of aggression. His paper does not elucidate this idea, so it must remain an incidental observation. Lester (1967a) reported early findings which implied that more timid rats were less aggressive, more emotional and more active than less timid ones. Activity, in the form of ambulation, is usually considered to be a negative index of fear in the open field, so the conflicting early findings emphasize the likelihood that activity constitutes different forms of behaviour. Excessive activity in one situation may be an emotional reaction whereas lack of activity in another may indicate emotionality.

"The golden hamster differs from the more common laboratory rodents as both sexes are highly aggressive" (Payne and Swanson 1970). In mice, males have been found to be more aggressive but studies including females are rare. For example, Davis and Christian (1957), Lagerspetz and Wuorinen (1965) and Southwick (1972) only considered male mouse aggressiveness.

There seems to be little literature dealing with conspecific aggressiveness and fear or emotionality. Even Moyer, who tried to classify aggression (1968), and referred to fear induced aggression (fighting preceded by escape attempts) did not cite any evidence on

how emotionality may affect aggression.

Therefore, the validity of my measures in relation to emotionality, which showed significance in this experiment, has not been established, although some of the behaviour shown by the different hamsters in an aggressive encounter would seem to relate to fear level.

Method

Apparatus. A clean unfamiliar laboratory cage, identical to those the hamsters inhabited, was used and the test carried out in the animal room. Females were not tested when in oestrus, measured by response elicited when paired with a male.

Procedure. Hamsters were matched in pairs for genotype, age and weight (but not sex). Each member of a pair was marked for easy identification. Each pair was introduced into the novel cage and their social interaction for one trial lasting ten minutes observed. These measures were recorded - nos. 2 to 10 being recorded for each hamster individually and nos. 11 to 15 for the pair:

1. The latency of the first hamster to sniff any part of the other.
- 2.) Number of sniffing bouts and length of time of
- 3.) each one, that is, when one hamster sniffs with its nose, another hamster.
4. Number of approach bouts, that is, when one hamster orientates and walks towards the other.
- 5.) Number of grooming bouts and the length of time
- 6.) of each.
- 7.) Number of ventral bouts and the length of time
- 8.) of each, that is, one hamster lying on its dorsal side with its opponent sniffing its ventral side, which is uppermost.
9. Number of vocalizations emitted. Each pulse (squeal) scored one.

10. Number of attacks, that is, when one hamster lunged forward and bit the other.
- 11.) Mutual nosing bouts and length of time of each,
- 12.) occurring when the hamsters' noses came together but did not actually touch.
- 13.) Mutual avoidance, that is, number of bouts and
- 14.) time spent apart by the hamsters, when they were not in physical contact and were usually carrying out activities in different parts of the cage.
15. Number of faecal pellets deposited. These were counted at the end of the test when both hamsters had been returned to their own cages.

Arrangement of Data, Treatment and Results.

One hundred and four hamsters took part in this experiment. They were matched in pairs of two males, two females or one male and one female, for age, weight and genotype. This resulted in the following taking part in the experiment: six male pairs, four female pairs and two male-female pairs of the golden genotype; nine male pairs, six female pairs and three male-female pairs of the brown genotype; four male pairs, five female pairs and three male-female pairs of the golden piebald genotype; and zero male pairs, eight female pairs and two male-female pairs of the brown piebald genotype. In view of the small numbers in each genotype/sex group, it was decided to combine scores of hamsters of any one genotype, regardless of sex, to find genotypic differences and to combine scores of all hamsters of any one sex pair, regardless of genotype, to find sex differences. Encounter pairs were compared, rather than individuals within a pair, so that although some scores were recorded for individuals, scores within a pair for any one measure were combined in this analysis. In this way, genotype and sex differences in behaviour in an aggressive encounter could be displayed.

First arrangement of data

1. This consisted of:
 - a. 4 genotypes, both sexes, G, B, GP and BP.
 - b. 1 trial.
 - c. The subjects were 12 G, 18 B, 12 GP and 10 BP.
2. Treatment of data: by 1-way analysis of variance.
3. The results were:
 - a. Approach bouts showed that GP approached more than G ($p < 0.05$), with B and BP falling intermediately.
 - b. The mutual avoidance measure showed that GP and BP abstained from physical contact more than either G or B ($p < 0.01$).
 - c. Attack was carried out more by G than GP or BP ($p < 0.05$), and B fell intermediately.

Second arrangement of data

1. This consisted of:
 - a. 3 sex pairs, male-male, female-female and male-female.
 - b. 1 trial.
 - c. The subjects were 19 male-male pairs, 15 female-female pairs and 8 male-female pairs.
2. Treatment of data: by 1-way analysis of variance.
3. The results were:
 - a. Mutual avoidance was higher in female pairs than male-female pairs ($p < 0.01$) and male pairs fell intermediately.
 - b. Attack occurred more often in female pairs than in either male or male-female pairs ($p < 0.05$).
 - c. Females showed a longer grooming time than male or male-female pairs ($p < 0.001$).

Summaries of the analyses of variance carried out data in the first and second arrangements with significance levels obtained are given in

Summary Tables XIV and XV and Table VII show the results in a tabular form.

Discussion

1. Genotype differences

Genotype differences were significant for approach bouts and showed that golden piebalds orientated towards their opponents more than goldens, and browns and brown piebalds fell intermediately. Mutual avoidance, scored when the animals were neither in physical contact nor approaching, but carrying out some other behaviour in the cage, a priori, could be thought to indicate fear. This could be easily validated by considering its relationship to escape from the novel cage or freezing in it, but at present, this has to remain a reasonable deduction only. Both piebald genotypes showed more mutual avoidance than the two non-piebald genotypes. This seems unlikely to mean that piebalds were more interested in the rest of the environment and less so in their opponents, because they approached each other more and engaged in as much investigatory activity as non-piebalds, shown by the lack of significant differences on number of sniffing bouts, sniffing time, number of ventral bouts, ventral time and bouts, and time of mutual nosing.

Attacks occurred mostly between golden hamsters. Piebalds attacked less and the brown hamsters scored intermediately. Although different behavioural components from those of Payne and Swanson (1970) were recorded, measurement of attack must have been similar and 50 percent of their tests resulted in no attacks at all, whereas only 23 percent of my encounters resulted in no attack. When piebalds were compared to non-piebalds, 36 percent of the piebald interactions ended with no fighting, but only 13 percent of the non-piebald interactions ended this way.

Summary Table XIV

One-way analysis of variance carried out on the aggressive encounter data in arrangement one, with significance levels obtained.

Source of variation	SS	DF	MS	F	Significance level
Approach bouts					
Treatments	988.42	3	329.47	3.85	0.05
Experimental error	4103.87	48	85.49		
Mutual Avoidance					
Treatments	119297.00	3	39765.00	4.98	0.01
Experimental error	382699.00	48	7972.00		
Attacks					
Treatments	515.47	3	171.82	3.08	0.05
Experimental error	2675.52	48	55.74		

Summary Table XV

One-way analysis of variance carried out on the aggressive encounter data in arrangement two with significance levels obtained.

Source of variation	SS	DF	MS	F	Significance level
Mutual Avoidance					
Treatments	78999.00	2	39499.50	5.85	0.01
Experimental error	256191.00	38	6741.86		
Attacks					
Treatments	339.37	2	169.68	3.55	0.05
Experimental error	1812.54	38	47.69		
Grooming Time					
Treatments	23896.77	2	11948.38	15.59	0.001
Experimental error	29117.93	38	766.26		

Table VIII

Tabular representation of significant aggression results.

Genotype differences				
Measure	Golden hamsters	Brown hamsters	Golden Piebald hamsters	Brown Piebald hamsters
Approach bouts	least	intermediate NS	most	intermediate NS
Mutual avoidance	less	less	more	more
Attack	most	intermediate NS	least	least

Sex differences			
Measure	Two males	Two Females	Male-Female
Mutual avoidance	intermediate NS	most	least
Attack	less	more	less
Grooming time	less	more	less

More detailed study is needed to determine whether, when comparing piebalds with non-piebalds, attack occurred after failed escape attempts. Measure of latency to attack may have given some indication of this.

A further investigation of aggressive behaviour in these hamster genotypes should include analysis of the two measures considered to be important in relation to fear behaviour, as displayed by search for escape or immobility.

At this stage, it is hypothetical that the increased mutual avoidance and low attack rate of the piebald genotypes, compared to non-piebald hamsters, represent emotionality. If early suggestions (e.g. Arnold 1944) that more frightened animals show less tendency to fight are correct, then the findings from my study could be interpreted as showing that piebalds are more emotional than non-piebalds in aggressive encounters.

It is also noticeable that vocalization and defecation, although not necessarily indicators of emotionality in this situation, were not significantly different between genotypes. Vocalization seemed to occur predominantly with attacks (that is, biting), so that despite the low attack rate shown by piebalds, they vocalized as much as non-piebalds which were attacking more. This implies that either piebalds were more sensitive to pain in cases where attack occurred and/or they were more frightened. A similar interpretation could apply to the occurrence of defecation, although it is not known when defecation occurred during the encounter. It is possible the subordinate hamster was the principle defecator, so it is surprising that piebalds defecated as much as non-piebalds, when their encounters seldom reached the dominance or subordination of one, or the other.

If vocalization and defecation can be validated as measures of

fear in an aggressive encounter, these non-significant findings could contribute important information about the emotionality of the fighting animals.

Summarizing, it would seem that despite high mutual avoidance, indicating fear, piebalds were as curious about their opponents as non-piebalds and investigated each other as much, but failed to carry investigation through to attack as frequently as G and B hamsters. Order of behaviour in the aggressive encounter may be a significant variable here. An investigation into whether mutual avoidance tends to occur before or after investigation or randomly throughout the encounter and whether it involves search for escape would add information about the meaning of this measure.

The low piebald attack rate, when considered in conjunction with other piebald behaviour in this situation, is tentatively proposed as being associated with increased emotionality in this hamster.

2. Sex differences

Payne and Swanson (1970) reported that the female hamster is larger and dominant over the male. They have emphasized the importance of matching for body weight, so in my experiment animals were matched within a genotype, as it would have been difficult to find piebalds equal in weight to non-piebalds. This would also show up genotypic differences in interaction which could not have arisen had the encounters involved mixed genotypes.

My results cannot support Swanson's finding (1967) that female hamsters are larger (cf. body weight data), but are compatible with the suggestion that females are more aggressive (Payne and Swanson 1970). Payne and Swanson (1972) considered the relationship of growth rate to agonistic success. Dark patches on the hamster ventral surface were

exposed during conflict and Grant, Mackintosh and Lerwill (1970) who enlarged these patches by dyeing them, found exposure of them elicited intense flight behaviour in other hamsters. In Payne and Swanson's study (1972) there was a decreased growth rate in hamsters exposed to the artificially exaggerated threat stimulus. They suggested that the lower growth rate resulted from physiological changes associated with 'stress'. Piebald hamsters showed a lower growth rate than non-piebald hamsters. If it is hypothesized that this was the result of 'stress', it is coincident that piebalds also show less agonistic behaviour than non-piebalds, which have a higher growth rate.

There were possible combinations of antagonizing pairs, which were male-male, female-female or male-female. Females showed more mutual avoidance than male-female pairs and males fell intermediately. The high female mutual avoidance rate may have indicated heightened emotionality, as it was suggested, it did for piebalds. Females also attacked more than male or male-female pairs, which does not, at first sight, agree with the higher fear level associated with mutual avoidance. Females also showed more grooming time than male or male-female pairs. If grooming is a positive index of fear and if, as classical ethological theory holds, displacement activities like grooming occur in conflict situations, then this and the mutual avoidance rate of the female pairs both indicate that they are more emotional than the other sex combinations in aggressive encounters. On the other hand, increased attack bouts would not be expected to indicate heightened emotionality - unless the position that fear induces aggression is upheld.

Once again the importance of studying attack and mutual avoidance in aggressive situations in relation to occurrence of the fear responses, escape and immobility, is emphasized. If the heightened female

aggressive behaviour is preceded by considerable escape attempts, thus falling in the category of fear induced aggression, explanation of sex differences in this type of situation may be altered.

Another interpretation could be that males and females are equally fearful in an aggressive encounter, but whereas females display this by increased attack following escape attempts, males show decreased mutual avoidance, in association with comparatively immobile behaviour. Further experiments are needed to test this mode of interpretation.

Payne and Swanson (1970) showed that female hamsters tended to be dominant over male hamsters, but that the sexes interacted similarly. As they found no sex differences in measures such as number of encounters per test or number of tests without fights, they suggested that "females are not naturally more aggressive than males, nor do they use different measures to establish dominance". Dominance was considered established when one animal chased another, following a measure of fight - comparable to my measure, attack. Chasing was not recorded as it seldom occurred, and Payne and Swanson's finding of female dominance was probably similar to my results which showed that females had more attack bouts.

Male-female pairs had the fewest attack bouts, least time apart and lowest grooming time. Payne and Swanson (1970) investigated the behaviour of opposite sex hamsters in a neutral observation area. Each pair was observed for four consecutive days, which is the length of the oestrous cycle. On all four days the male attempted copulation by sniffing the female's anogenital region and following her when she moved away. When in oestrus the female responded with lordosis. They found that when the female was unreceptive, she won significantly more encounters and was therefore dominant to the male. Possibly my ten minute observation was not long enough to elicit female dominance over

the male. As females were not tested when in oestrus, male-female pairs, which showed a large amount of interaction (low mutual avoidance), could predominantly have involved the male sniffing the female. Investigatory behaviour carried out by the male-female pair may have been of a different kind from that participated in by male-male or female-female pairs.

Conclusions

The main findings from this experiment are:

1. Non-piebalds attacked more than piebalds.
2. Non-piebalds had a lower rate of mutual avoidance than piebalds.
3. Female pairs showed a higher number of attack bouts than male or male-female pairs.
4. Female pairs showed a greater amount of mutual avoidance than male or male-female pairs.

The high mutual avoidance and lack of antagonistic behaviour shown by piebalds largely indicate that the piebald genotype is more emotional than the non-piebald ones, if the hypothesis that fear inhibits aggression is accepted. The piebald defecation and vocalization rate in a low attack situation could be additional evidence that piebalds are more emotional than either golden or brown hamsters.

Sex differences are harder to understand. If there is a definite relationship between fear and aggression, it may be dissociated by sex differences. Different genotypes may not have different neurophysiological systems controlling aggressive responding, but the two sexes may, especially as sex hormones have been shown to play an important role in aggressive interaction. There are various interpretations about fear in relation to sex differences in aggressive responding:

1. Male pairs are more emotional than female pairs, shown by fewer attack bouts, so that despite more interaction (lower mutual avoidance) they did not carry it through to attack as much.
2. Female pairs are more emotional than male pairs. This was shown by the higher rate of mutual avoidance and longer grooming time and their greater attack behaviour may represent fear induced aggression.
3. Male and female pairs seem to express reaction to conspecifics differently, but the modes of fear responding may not give information with regard to intensity of emotionality which may be the same in both sexes.
4. A fourth possibility is that the behaviour patterns shown by each sex are unrelated to emotionality.

Therefore, conclusions cannot be drawn on how sex differences in aggressive responding relate to sex differences in the expression of emotionality.

E. SUMMARY AND CONCLUSIONS OF BEHAVIOURAL EXPERIMENTS II

Three more behavioural experiments were presented in this chapter.

The reaction to handling experiment, despite limitations regarding methodology, allowed the emission of freezing, and escape behaviour, considered to be direct measures of fear, more completely than any other experiment in this thesis. Results were therefore more conclusive. Golden piebalds withdrew more, fought and escaped more, vocalized more and showed a longer latency than brown or golden hamsters, and it seems fair to suggest that on these measures in this situation, the golden piebald hamster is more emotional than the others (excluding brown piebalds).

Sex and housing differences indicated that females were more emotional than males and isolates more so than grouped hamsters, respectively, but the pattern for each of these was less complete than for the genotypes, so other interpretations are plausible.

There was little evidence of passive avoidance learning in the hamsters tested. Possible reasons for this were given. The most meaningful measure from this experiment in relation to fear, seemed to be vocalization. The vocal response of the four hamster genotypes to a variety of experimental situations was discussed with the overall conclusion that vocalization (greatest in piebald genotype) was given in response to pain, (or expectation thereof) and therefore may be a fear response.

The aggressive encounter clearly discriminated genotypes and sexes on two measures, mutual avoidance and attack behaviour. The piebald behaviour in the situation implicated little antagonism compared to that of the golden and brown genotypes. In genotype comparisons, the piebald behaviour may be associated with increased fearfulness/emotionality. As regards sex comparisons, no clear cut relationship between fear and aggression was evident and it is possible that any relationship may hold for genotype differences but becomes dissociated when factors such as sex and early experience are involved.

CHAPTER THIRTEEN

GENERAL DISCUSSION

A. INTRODUCTION

Section B of this chapter recapitulates conclusions drawn from Chapters Two to Seven, which dealt with literature on the topic of this thesis. It is then demonstrated that the genotype, sex and housing differences cannot agree with views that emotionality is a unitary concept. The significance of the nonbehavioural findings is outlined and the relationship of the hamster genotype findings to strain differences in emotionality in rats given. Whether or not hamster behaviour under laboratory conditions can give information about adaptability and survival in the wild is discussed.

Indication of the extent to which the aims of the thesis were fulfilled is given and finally comment made on the future potential of the piebald hamster as an experimental animal.

B. CONCLUSIONS FROM CHAPTERS TWO TO SEVEN

Chapter Two discussed the contribution that major gene studies could make to psychology. Specifically these would seem to be:

1. that they provide a starting point for discovering the actual biochemical and neurophysiological mechanisms underlying the behaviour, that is, pathways of gene expression or gene action, because major genes can be mapped precisely on chromosomes;
2. that, if suitable gene changes, experimental controls and procedures are chosen, study of the behavioural phenotype may lead to a greater understanding of psychological concepts invoked to explain or describe the behaviour.

In Chapter Three, problems surrounding the concepts of 'stress', 'fear' and 'emotionality' were discussed and it was concluded that stress was a term associated with the physiological response, called the general adaptation syndrome (GAS) by Selye (1946, 1956), and that fear and emotionality were synonymous and would be used as descriptive intervening variables alluding to the state of an animal having perceived certain stimuli and

about to elicit particular responses.

The terms, fear and emotionality, as unitary concepts, suggest that the attribute they are describing is a general characteristic and a result of the same underlying mechanism in every animal. Unless, therefore, a class of animal can be shown to be more fearful/emotional than other classes in a variety of behavioural situations, description of them as more fearful/emotional is inappropriate and could be misleading.

The validity of various tests used to measure emotionality was discussed in Chapter Seven. Unfortunately it appeared that most experimental procedures did not include observation of behaviours which could be defined as fear responses, that is, escape and immobility. Consequently, most measures used have been indirectly validated only and this may partially account for the conflicting reports throughout the emotionality literature.

A second reason for these contradictory reports would seem to rest with the way the concept of emotionality has largely been viewed. If fear/emotionality is considered to be a unitary state (a view which seems to be held by a number of researchers) it is difficult to explain the results when a category of animal, such as the Maudsley reactive rat or male rat, does not behave in a manner predicted as more fearful in any experiment.

If, on the other hand, fear was viewed as complex, so that at any time certain aspects of emotional behaviour are affected more than others depending on a variety of factors, the results would be less surprising. If all the behaviour occurring in any given situation could be categorized, it may become clear that fear can be expressed in various ways and may well be more intense for some classes of animal in some situations, but less so for the same classes in other circumstances. Different forms of fear responding could be searched for, which may give information about the intensity of emotionality experienced but not necessarily. This limits

the applicability of the terms fear/emotionality as general constitutional traits.

Chapter Four indicated that animal studies added to knowledge about the development and organization of emotional behaviour. In Chapters Two and Five, the importance of controlling for genetic, maternal, sibling and housing factors in a study of rodent emotional behaviour was emphasized. Genetic, maternal and sibling effects were controlled in this project by choice of particular hamsters and a suitable breeding programme. Housing was controlled for as part of the experimental procedure.

A number of behavioural and nonbehavioural measures were taken. Certain aspects of behaviour were considered to be representative of emotionality, based on previous work in the field and a priori reasoning, although, as mentioned in Chapter Seven, a more complete validation of measures of fear would have been preferable.

In this study, when looked at collectively, the findings for genotype, sex and housing differences do not comprise a discernible pattern, in terms of a unitary emotionality state, as shown in the following sections.

C. GENOTYPE DIFFERENCES

Genotype differences were the most easily interpretable results as far as intensity of emotionality in one category of hamster was concerned (compared to sex and housing differences).

It was shown that on the whole, hamsters possessing the piebald gene were more emotional on the tests carried out than those without it (cf. Chapters Ten to Twelve). Some tests were better indicators than others. For example, when handled, piebalds showed greater resistance on all four measures recorded, which were in turn thought to be symbolic of fear, whereas in the novel situation, the only strong evidence that

piebalds were more emotional than non-piebalds was their increased number of startle bouts.

However, the results over tests provided evidence (to a greater or lesser extent) which suggested that the description of golden piebald hamsters and brown piebald females as more emotional than golden or brown hamsters was appropriate. Therefore, increased emotionality, hypothesized as a characteristic of the piebald genotype, is predicted as being demonstrable in these hamsters in a wider variety of test situations than were used here.

How does the Piebald Gene Produce its Effects?

The reported study was designed to reach a fairly definite conclusion about whether certain behavioural characteristics were related to the piebald gene, by comparing it in two otherwise different genotypes with hamsters not carrying it. Unfortunately, due to lack of brown piebald males the conclusions are incomplete, although the general picture appears to be an increase in emotionality from golden and browns to golden piebalds, with brown piebald females usually falling close to golden piebald females.

In spite of the maternal and sibling control and the fact that every animal possessed at least one brown gene and one piebald gene, genotypic differences were still evident. (It could still be possible that the brown and piebald genes have partial penetrance as regards behaviour). As linkage effects are not forthcoming (Robinson, personal communication), it is likely that the differences are due to the piebald gene.

It was mentioned in Chapters Nine and Eleven that brown and brown piebald hamsters had red eyes, which affected sensitivity to light, although to what extent is apparently unknown at present (Robinson, personal

communication). Heightened sensitivity to light may help explain the behaviour of brown animals in the open field, (where they seemed in some ways intermediate in emotionality between golden and golden piebald hamsters) but no other experiment was carried out under bright light. In this experiment there was no evidence that brown and piebald interacted in brown piebald females to produce a hamster more emotional than golden piebald females.

Although a peripheral effect may yet prove responsible for the behavioural effects of the piebald gene, it would seem, at this stage, that the gene is causing its effects predominantly in one of two ways:

1. The piebald gene may influence those parts of the brain and central nervous system responsible for emotional behaviour thus heightening their sensitivity to punishing stimuli, whether they are physical, physiological or psychological. If parts of those neural systems only, are affected, this could result in greater fearfulness under some conditions, but not others.
2. The piebald gene may affect a metabolic pathway indirectly associated with the emotionality system. For example, in this case, the immunity system may be altered, so that piebalds have decreased resistance to disease and this chronic susceptibility may also make them more emotional. Closely related to this, is the possibility that the piebald gene induces the stress response (the GAS) and the resulting highly tuned autonomic nervous system enhances emotionality.

However the piebald gene causes its effects, closer analysis of the mechanism could give information on one kind of physiological system that results in emotionality. If the first method is correct, Wilcock's requirement (1969) that "interesting psychological functions" are investigated by major gene studies would seem to be fulfilled. If increased emotionality is caused by the second method, although possibly of less significance for psychology, it could have useful implications for medical studies. The fact that it is possible to suggest at least two mediators of emotionality causation would agree with Ginsburg's findings (1954, 1958, 1967) that there can be a variety of genetic pathways producing any one phenotype.

D. SEX DIFFERENCES

Sex differences were apparent on several measures in the tests, but were much harder to understand in terms of a single emotionality trait, than were genotype differences.

Sometimes females seemed more emotional than males, for example, in reaction to handling; in other situations males were more fearful than females, for example, in showing little attack in an aggressive encounter; or there was no discernible difference between the sexes, for example, as displayed by no significant differences in open field defecation (among the piebald genotype), or in startle in the novel situation.

Although it has been proposed that male rats and rodents generally are more emotional than females (for example, Gray 1971a, b) a closer consideration of the literature and my own findings for the hamster species do not wholly support such an unequivocal position.

Bolles (1970) suggested that speed of active avoidance learning may be related to the appropriateness of an animal's most readily emitted escape response. Archer (1971) suggested that the greater female tendency to escape, compared to males, may account for the sex difference in active avoidance learning. Archer (¹⁹⁷⁵~~in press~~) elaborated this idea to refer to 'sex-typical fear responses', whereby males and females reacted differently in the form of emotional behaviour, although intensity experienced may be similar.

Among rats, it seemed that, on various occasions, females responded more readily with escape behaviour and males with immobility (cf., Chapter Seven). Such a definite explanation of sex differences in emotionality is not fully transferable to the hamster findings at this stage, where type of test situation and measures recorded were limited. However, there were indications in the open field and novel situation that female hamsters ambulated around the whole arena, whereas males remained relatively stationary in a smaller area, which may go some way towards supporting the kind of interpretation for rat sex differences in emotionality presented by Archer (¹⁹⁷⁵~~in press~~).

The hamster findings showed that males and females reacted differently from one another in various experimental situations. These differences do not provide a consistent model of emotional behaviour in one sex. Archer's proposal (¹⁹⁷⁵~~in press~~) may have validity for the hamster species and could be tested. On the other hand, the type of response elicited by either sex may relate more closely to the nature of the experimental situation than a 'sex-typical fear response'. For

example, female hamsters may be more emotional than males in social circumstances involving a conspecific or member of another species, but not in others, irrespective of any tendency to escape or become immobile. Among the results, female hamsters showed greater resistance to handling on two measures and more mutual avoidance in the aggressive encounter than males - behaviours thought to be associated with fear. Observation of a greater variety of social experiments could clarify this point.

In conclusion, among the hamsters studied, one sex cannot be described generally as more fearful than the other.

Why Do the Sexes Behave Differently with Respect to Emotionality?

Although there is now some understanding of the form of fear responding in each sex, the question as to why they are different remains.

1. Hormonal differences. Males and females typically secrete different sex steroids. Archer (1975) reviewed studies which suggested that oestrogen affected activity and presented his own work, which showed that testosterone-injected male chicks displayed more immobility in response to a bell in the open field than oil-injected controls, as some evidence that testosterone aided freezing-like behaviour.

If it can be proved that sex hormones are linked with the differentiation of behavioural patterns, they may be of utmost importance in explaining sex differences in emotionality expression.

2. Odor differences. As mentioned in Chapter Twelve, odors emitted by one animal have been found to affect behaviour of subsequently tested animals. Perception of odors and consequent reactions may vary among rodents.

An indication that there may be a sex difference in odor discrimination was provided by Pietras and Moulton (1974). They developed a two-tunnel odor

discrimination apparatus, and noticed that female rat performance altered with the stage of the oestrous cycle, although male odor detection was unchanged over a similar period and was at all times superior. Even ovariectomized females did not respond as efficiently as the male rats. Administration of testosterone raised the performance level of the ovariectomized females to that of males and increased testosterone enhanced it even further.

Implicit in this work is the possibility that males (at least in rats) detect some odors more easily than females. It remains to be discovered whether they can more readily detect the kind of odor emitted by conspecifics in fearful situations, but it can be hypothesized that heightened male sensitivity leads to different behavioural reactions in these situations.

These two factors (sex hormones and odor discriminability) are likely to be causally associated with sex differences in fear and emphasize the point that emotionality cannot refer to a unitary state. In some cases, elicitation of a fear response may relate specifically to odor discriminability (possibly superior in males) and in others it may depend more markedly on an oestrogen activity effect (as seen in females).

E. HOUSING DIFFERENCES

Housing differences although occurring regularly, showed, like sex differences, no consistent pattern of emotionality over tests. For example, with regard to reaction to handling, isolates showed more resistance on three measures, but on the fourth, trends were reversed, so that grouped hamsters were more resistant.

It is perhaps surprising that the differential housing results showed any significance at all, when not only was it short (2 - 2½ weeks) but the samples analysed were small (4 - 5 hamsters per group).

Therefore, in some unaccountable way housing factors affected later behaviour. At this stage, however, the nature of the behaviour affected cannot be determined.

Generally, animals raised in isolation have been found to be more emotional (for example, Ader, Kreutner and Jacobs 1963, Korn and Moyer 1968, Moyer and Korn 1965), although the evidence is equivocal and there are contradictory findings (Priestnall 1970).

The many differences shown by differentially housed hamsters in the variety of experiments cannot be logically interpreted within an emotionality framework and unfortunately as hamsters have not been studied in their natural surroundings in Syria (Murphy 1971), it is not known how the differences relate to their social organization. Eibl-Eibesfeldt (1953) in an account of the ethology of the European hamster, suggested that the Syrian hamster behaved in much the same way and similarly lived solitarily, but study of the Syrian (golden) hamster in natural surroundings is needed to confirm this.

However, it is likely that rearing hamsters in Britain as pets and for laboratory conditions has acted as a domestication process by selecting those animals which prefer group living.

It should also be mentioned that one difference between isolated and grouped hamsters is that isolated hamsters have had the opportunity of adapting to this kind of housing for four weeks before the onset of experiments. By contrast, group raised individuals have been solitarily housed for only one week or ten days, and it could be argued that this factor could differentiate the groups at the start of experiments. The interaction of this kind of variable with the type of preferred housing could have helped give rise to the intangible results.

Therefore, neither isolated nor group housed hamsters can be described as more fearful than the other.

Finally, the dramatic finding that piebald hamsters died only when isolated needs emphasizing. The study of longer-term group and isolated housing in relation to piebald viability is demanded, but the present work has yielded the hypothesis that psychological/social factors may be critical in the onset of disease, the GAS and mortality among piebald hamsters.

F. SIGNIFICANCE OF THE NONBEHAVIOURAL FINDINGS

A main implication in these results is that piebald hamsters succumb to the GAS. For example, piebalds had heavier adrenal glands, and gastric ulcers were found among those that died. Although no data ^{were} ~~was~~ recorded on the thymus, spleen and lymph nodes or counts of white blood cells, piebalds were shown to have a low viability in this and earlier studies, and there is anecdotal evidence that piebalds are susceptible to stress-linked parasitic infections. Both of these effects could be associated with a low white blood cell count and disturbance of the thymus, spleen and lymph nodes, all symptomatic of the GAS. Inability to maintain resistance could result in the stage of exhaustion, described as part of the GAS, and death, thus accounting for the low piebald viability.

Depressed secretion of the growth hormone and lowered sexual and reproductive behaviours were also mentioned as part of the GAS (Selye 1956). It was shown here that piebalds had a lower body weight than non-piebalds, which may have been due to somatotrophic deficiencies, and the difficulties shown by piebalds with regard to mating, parturition, litter size and pup survival, evident in the pilot investigation and earlier studies, implies disturbance of the reproductive system.

Selye described a physiological stress reaction called the GAS which occurred in response to certain punishing stimuli. Gray (1971a)

indicated that physical, physiological and psychological stimuli could set off the GAS and in addition claimed that heightened emotionality could accompany it.

Therefore, any animal could show:

1. Heightened susceptibility to punishing stimuli in terms of physiological reaction (GAS).
2. Heightened susceptibility to punishing stimuli in terms of behaviour.
3. Heightened susceptibility to punishing stimuli both physiologically and psychologically (behaviourally).

In view of the results of the behavioural experiments and the indications that piebalds succumb to the GAS, it would appear that piebald hamsters are examples of number 3.

G. THE RELATIONSHIP OF THE HAMSTER FINDINGS TO STRAIN DIFFERENCES IN EMOTIONALITY SHOWN BY RATS

This section primarily investigates the relationship of emotionality in hamsters to that in the Maudsley reactive and non-reactive rats. If MR rats are more emotional than the MNR rats and piebalds more so than non-piebald hamsters, it would be instructive about rodent emotionality to examine similarities and differences between the MR rats and piebald hamsters, and MNR rats and non-piebald hamsters, especially as the rats were selected for their high open field defecation and the piebalds show high defecation in this situation, although not selected for this characteristic.

Joffe (1969) reported that MNR females produced larger litters than MR rats but that their infant mortality rate was higher. Foote and Foote (1950) found golden hamsters similarly produced larger litters than piebalds, but a higher proportion of their young survived than of the fewer number born to piebald mothers. The pilot study findings

(not presented here) tended to agree with Foote and Foote. The hamster and rat results, although agreeing with regard to litter size, are at variance in relation to infant mortality.

MR rats were significantly heavier than MNR rats (Watson 1960, Blizard 1968). This is contrary to my hamster results and earlier findings which showed that the more emotional piebald hamster weighed significantly less than the comparatively non-emotional brown and golden types.

The reactives had larger adrenal glands than the MNR rats, according to Feuer (1963), which is concordant with my findings that piebalds have larger adrenals than the two non-piebald genotypes. Feuer also found that the corticosteroid content of the adrenals was higher in the MR rats, but lower in the serum. In contrast, Watson (1960) took indirect measures of adrenal activity in the two rat strains, which were body temperature, changes in white blood cell count with stress and adrenal ascorbic acid level, and could not find that MR rats were characterized by greater adrenal activity.

As regards open field findings, on which the Maudsley rats were selected, piebalds defecated more than brown or golden hamsters, but ambulated less than the brown genotype only, and they were almost equal to the golden line on this measure. MR rats defecated more and ambulated less than MNR rats. Possible interpretations of the ambulation measure were discussed in Chapter Eleven. However, the rat findings when other strains, besides the Maudsley lines were involved, do not without exception support a negative correlation between defecation and ambulation (reviewed by Archer 1973). The result that, as MR are to MNR rats, so piebalds are to brown hamsters, may support the description of piebalds as emotional relative to brown hamsters, but how should the golden behaviour be regarded with respect to emotionality?

As discussed in Chapter Eleven, low defecation and high ambulation, although possibly being an expression of non-emotionality may not be the only one, so that non-emotional may also be a fitting description of the golden hamster behaviour.

Reactive rats have also been shown to groom more in the open field (for example, Gray, Levine and Broadhurst 1965), as do piebalds, and to rear less. The conflicting data on grooming was briefly discussed in Chapter Seven and its significance in terms of emotionality is unknown. My results showed no significant differences for rearing in hamsters, which is at variance with the results for Maudsley rats.

Broadhurst and Levine (1963) compared MR and MNR rats on acquisition of an active avoidance response and a conditioned emotional response (CER). MNR rats learned the former more quickly and the latter more slowly than the MR rats, so the authors discussed a possible reason for this. If emotionality led to inactivity, it would impede learning in an active avoidance situation but enhance the decrement in behavioural responses in CER, which is taken as the measure of learning. This response suppression should also facilitate passive avoidance learning where retention of response inhibition is involved, although the evidence from measures of hamster behaviour in this kind of learning situation was inconclusive. Reasons for this were discussed in Chapter Twelve.

Finally, the ulcer findings for the MR and MNR rats are not in agreement with other rat findings relating ulceration and emotionality. Pare (1966) subjected two rat lines, estimated as emotional and non-emotional from open field behaviour, to a four second tone followed by an electric shock, on average every four minutes for 20 hours a day for 22 days. Stomachs were investigated for ulcer incidence and no difference between the two strains could be found, although emotional ones lost more weight and had a lower food intake (mentioned in Chapter Seven).

In my study piebalds were found to weigh less, to take less food into their cages, but among those that died there was a high ulcer incidence. If hamsters were subjected to the same conditions as those used by Pare (1966), more information about ulcer incidence in this animal could be obtained.

Mikhail and Broadhurst (1965) restrained MR and MNR rats for 48 hours and could find no difference when subsequently comparing them for ulceration. They gave the animals an ambulation test and found that rats which ambulated less and were therefore considered to be more fearful, were more susceptible to ulcer formation. The hamster findings showed a relationship between low open field ambulation and high ulcer incidence in the piebald genotype, but the low ambulating golden genotype (as well as the high ambulating brown genotype) showed no ulceration.

Neither the Maudsley nor hamster results agree with Sines' findings (1962) that lesion susceptible rats (SUS) had a higher open field activity score, but piebald findings coincide with some of Sines' other results for SUS rats. Piebalds, like the SUS rats, weighed less than controls, showed a greater open field defecation, and had a smaller litter size and higher infant mortality. Sines also suggested that SUS females ignored their young, as was suggested for piebald mothers by Foote and Foote (1950).

It is possible that the stimulation used by Pare (1966) and Mikhail and Broadhurst (1965) to induce ulcers was too severe to differentiate emotional and non-emotional rats on ulcer susceptibility. In a later experiment, Mikhail (1969) restrained rats for 24 hours and on this occasion found MR rats had more ulcers, which is similar to the increased piebald susceptibility.

However, my findings are not directly comparable with these. A high proportion of piebalds that died had ulcers. Of those that survived

experimentation, an insignificant number had stomach ulcers. Either it could be suggested that piebalds which died were succumbing to the exhaustion phase of the GAS, of which stomach ulcers are a symptom (Selye 1956), or that piebalds as a genotype have a gastric disorder which results in ulcer-like haemorrhages. Either case may or may not be related to emotionality, although it was proposed in the previous section that with regard to piebalds it was. Further work is needed to determine the nature and the significance of piebald stomach ulcers, as the reported study has only shown their occurrence under limited conditions.

Therefore, the pattern of piebald emotionality is somewhat different from that shown by the Maudsley rats. There are two basic differences between these animals. One is the obvious species difference, and the other is that whereas the piebald hamster arises from a mutant one gene effect, the Maudsley rats are selected lines. Therefore, it is not surprising that they show emotional behaviour in different ways. Ginsburg (1954, 1958, 1967) has repeatedly suggested that a given behavioural entity can be due to a variety of distinct genetic pathways. The causal mechanisms responsible for emotional behaviour in the MR rats and piebald hamster are probably different and could be worth investigating as alternative systems of emotionality causation. The unitary emotionality hypothesis would not allow for the occurrence of different systems of emotionality, but if emotionality is a complex state, such differences would not be surprising. Investigation of these likely different mechanisms may, in turn, contribute more knowledge about the nature of emotionality or fear, thus fulfilling an important aim of major gene studies, and presumably of the rat studies on this topic.

H. THE RELATIONSHIP OF BEHAVIOUR IN LABORATORY EXPERIMENTS TO COPING IN NATURAL CONDITIONS

There have been comparisons of the behaviour and physiology of laboratory animals to those in the wild with regard to rats and guinea pigs, and it would not be unreasonable to compare hamster behaviour in laboratory experiments to that in natural conditions. The results would

be particularly interesting since they have ~~only~~ been domesticated for ^{only} 40 years, as opposed to the much longer period of time for rats and guinea pigs.

Unfortunately, little is known about the behaviour of the Syrian hamster in its natural arid environment, although it may be similar to that of the European hamster, which has been studied by Eibl-Eibesfeldt (1953). The only reconnaissance expedition to Syria to study the hamster was carried out by Murphy (1971) who stated that "no gross morphological or behavioural differences between domesticated and wild golden hamsters have been observed so far". Even so, Murphy (personal communication) voiced some scepticism about the use of the domestic variety of hamster for indication of behaviour in the wild. "It is difficult enough to relate laboratory studies to natural behaviour and ecology, without dealing with animals whose ancestors have been in laboratory cages for 42 years". In view of the lack of ethological studies, most behavioural evidence presented does not allow conclusions about its adaptability in the wild, as illustrated below. As golden hamsters are natural inhabitants of Syria, it can be presumed that their behaviour is adaptive enough for survival, so piebald behaviour will be compared to theirs.

One experiment carried out in this thesis which could have relevance to the natural environment of a burrowing, nocturnal animal was the novel situation. Compared to goldens, piebalds had a shorter latency to investigation of exploratory objects, more box and wheel bouts and a longer box and wheel time. The result was that piebalds seemed to investigate exploratory objects more than golden hamsters. However, if it is assumed that the golden behaviour is adaptive, the piebald behaviour may be more, less or equally adaptive. The only firm

conclusion is that piebalds show different patterns of behaviour in the novel situation with indications of increased exploration; but behavioural adaptability cannot be deduced without study of hamster exploratory behaviour in natural conditions.

If reaction to the open field, which is further removed from a real situation, is considered, it can be seen that piebalds and goldens showed equal ambulation and sniffing bouts, but differed in that piebalds showed less sniffing time, more grooming bouts, less time in the corner squares on behaviours lasting five seconds or more and entered the middle squares less. The only measure that would seem relevant to coping with novel, frightening situations in the wild is the entrance to the middle squares, the more exposed area of the arena. The fact goldens entered the squares more would indicate that similar behaviour in the wild could increase their chances of being seen by a predator and killed. However, they may not spend long enough in the middle squares for this to be significant. Piebalds keeping to the edge to a greater extent may prevent their being seen by predators so easily, but if on the other hand they were searching for food, restricting exploration to the edges of a situation would diminish prospects of finding food. Possibly piebalds would starve to death before venturing into exposed areas. It is therefore hard to interpret behaviour even on this measure in terms of adaptability. Once again, it can be concluded that piebalds and goldens show different modes of behaviour in a novel, fearful situation, but whether one is more, less or equal in adaptiveness to the other cannot be deduced from the evidence.

If the food intake experiment is measuring hoarding behaviour as well as ingestion, then a heightened tendency of the goldens to hoard would seem directly to enhance survival, compared to a possibly lower

hoarding rate of the piebalds. However, without further studies, greater hoarding behaviour by golden hamsters cannot be assumed from the findings.

Even the increased withdrawal and fight/escape responses to handling shown by piebalds are hard to interpret in terms of adaptability. If preyed upon in natural conditions by a snake, would the wild goldens show a similarly casual response? Probably not, or they would not be natural inhabitants of Syria. Possibly goldens learn quickly from routine handling from birth, that it is not a threatening procedure. Therefore, either the golden reaction is moderately adaptive in the wild, although there may be some risk of capture, or they quickly learn to discriminate between a relatively harmless stimulus in the environment such as the experimenter, and a predator, such as a snake. Piebalds, by contrast, show fearful reactions to all types of stimuli and learn more slowly which ones are harmless.

The extent to which any behaviour shown by hamsters in the experiments discussed above is related to adaptability in the wild is a human interpretation of an animal situation. Any suggestions must therefore be tenuous.

Daly (1973) pointed out that the only convincing way to argue for the differential adaptiveness of animals is from evidence on disease resistance and survival, rather than behaviour. An organism resisting disease and therefore surviving, must be better adapted to its environment than one that does not. The low piebald viability, high ulcer incidence and hint that these hamsters may be susceptible to parasitic infections indicate poor disease resistance and low adaptability. This is the only strong evidence that compared to goldens, piebalds are less successful in coping with the environment.

The relationship of fear level or emotionality to adaptive success seems complex on the basis of evidence for the hamster species presented in this thesis. In several situations, piebalds behave differently from golden hamsters and it is thought that increased emotionality in piebalds is responsible for their different behaviour patterns. It cannot be deduced whether the piebald pattern is more adaptive than, less adaptive than or equally adaptive to the golden one.

Piebalds could, therefore, be equally or even better adapted to coping with natural conditions than goldens, in terms of behaviour, but their survival in the wild would always be prevented by their unsuccessful breeding and low viability.

J. EXTENT TO WHICH THE AIMS OF THE THESIS WERE FULFILLED

The success of the methodology chosen to investigate emotional behaviour in four genotypes of the golden hamster is reflected in the extent to which the aims of the thesis were fulfilled. The aims were outlined in the Introduction (Chapter One, page 5) and it is concluded that aims one to three were largely fulfilled. Discussion of the fourth and final aim is reserved for the next section.

Aim 1

Merrell (1965) suggested two methods which can ensure that behavioural differences are due to the single gene when this is involved. A common method achieves, through inbreeding, isogeneity at all loci except the one in question. But, Merrell added, when the main concern is with behaviour rather than with a refined genetic analysis, an alternative approach has considerable merit. This procedure involves randomization of the rest of the genotype with respect to the locus under study. This method is the one used in this thesis in connection with developing an understanding of the nature of the behaviour associated with the piebald gene.

It seemed likely from available evidence that piebald behaviour compared to that of the two non-piebald genotypes was attributable to a pleiotropic effect of the piebald gene, although the possibility that a gene closely linked to it was the causal agent cannot be dismissed or resolved from this project; however, there is so far no evidence of linkage (Robinson, personal communication).

Piebald hamsters can justifiably be described as more fearful than either golden or brown genotypes, within the limitations of the usage of the term put forward in Chapter Three. Thus, early reports about the behaviour of the piebald hamster were confirmed.

It is concluded now that the behaviour observed represents a non-trivial effect on a relevant structure and therefore an "interesting psychological function" with its cause not appearing to relate to a peripheral effect of the piebald gene. In 1954, Ginsburg wrote that "... in the light of the growing evidence that behavioural traits ranging from frank abnormalities to subtle shading of temperament and maze performance demonstrably have a genetic basis in a number of commonly used laboratory animals and that these have only in a relatively few cases been demonstrably due to a particular anatomical or physiological factor, we thought it of some importance to investigate a complex genetically controlled behaviour reaction in detail. The objectives of this research are to analyse the genetic basis for a given syndrome as completely as possible and to study the intervening variables that lead to the ultimate behavioural effects".

Ginsburg chose to study audiogenic seizure susceptibility for this purpose and his work represents a valuable approach to the study of single genes. It could be argued that it would be extremely difficult using biochemical, physiological or any treatment method to produce a rodent, which

like the piebald hamster, differs from the normal on a diversity of behavioural and nonbehavioural tests, thus resulting in an animal that may be able to fulfill the most important functions of major gene studies. One of these involves the search for gene-behaviour pathways (as, for example, has been carried out by Ginsburg), which would involve analysis of underlying causal mechanisms and activity in the central nervous system; this would be a next step in the study of the piebald hamster. The other function involves achieving a greater understanding of the behavioural concept unifying different reactions. Comments made in relation to aims two and three should show that this thesis has gone some way towards this.

Aim 2

Consideration of previous work in the field elucidated judicious applications of the terms 'fear' and 'emotionality'.

The Maudsley reactive rats have been described as more emotional than the non-reactive rats. Piebald hamsters were described as exhibiting greater fear than non-piebald hamsters. Yet, it has already been shown that in some fear provoking situations, such as the open field, piebald and non-piebald hamsters behave differently from emotional and non-emotional rats. This does not suggest that 'emotional' or 'fearful' are invalid as loose descriptive terms for either rats or hamsters, but that emotionality is a complex of variables/factors, rather than a unitary state. Consequently, behavioural relationships linked with the expression of fear in the Maudsley rats, can become dissociated when another species is involved - in this case, the hamster.

Aim 3

Description of one rodent sex as more emotional than the other, does not comply with the limitations of the usage of the term and

would appear to be an oversimplification and misleading. The hamster findings do not indicate that a consistent pattern in emotionality is shown by either sex over all tests, and cannot support Gray's proposal (1971a, b) regarding sex differences in emotionality.

Survey of the literature shows that which sex exhibits greater fear on any one occasion depends on a number of variables, for example, species, genetic constitution, internal neuroendocrine state, early experience and other social factors, responses characteristic of the behavioural repertoire, odor detection and other perceptual abilities.

Fear and emotionality, as general descriptive terms leading to predictions about behaviour in various settings, cannot therefore be said to refer to either male or female rodent behaviour. However, they could be used in a restricted way with extreme qualification.

K. FUTURE POTENTIAL OF THE PIEBALD HAMSTER AS AN EXPERIMENTAL ANIMAL

There are a number of ways the present study could be improved. For example, validation of emotionality measures and a larger number of piebalds of both genotypes would allow more convincing conclusions to be drawn.

Also, the existing data could be examined for other results, such as litter effects. Certain litters may show greater emotionality over tests and it could be determined whether this related to their genotypic and sex content. In addition, a piebald born and bred with piebald siblings would be predicted as behaving more emotionally than a piebald reared with non-piebald litter mates.

Although a study involving larger numbers of animals is required to allow separation and correlation of behavioural, physiological and

genetic factors associated with aspects of emotional behaviour, the present findings indicate the usefulness of further work with the piebald hamster.

1. The first of these relates to the single gene effect of the piebald hamster. This condition would allow a search for the biochemical and neurophysiological pathways which lie between the gene and behaviour. Underlying mechanisms responsible for the behaviour may provide an example of how a gene can affect the nervous system to produce heightened emotionality. It is implicit that fear behaviour may result from a variety of genetic pathways, thus agreeing with Ginsburg's findings for audiogenic seizure susceptibility (1958, 1967, 1971).
2. The link between the emotion of fear, and a physiological response, such as gastric ulceration, could be investigated in the piebald hamster. The impression is that piebalds are ulcer-prone hamsters and one straightforward procedure to test for a relationship between ulcer susceptibility and fear would be to compare the extent of ulceration in piebalds subjected to fear provoking procedures and control piebalds not undergoing such procedures. Areas of the brain and neuroendocrine system responsible for this kind of stress reaction could be determined, and drugs and chemicals alleviating the emotion and stress response sought. Information on an association between emotionality and disease resistance may also be forthcoming.
3. Rat findings could be complemented by hamster results when different patterns of emotionality are shown, generalised when there is agreement and reconsidered when there are conflicts. Some re-interpretation regarding claims on rodent sex differences in fear already seems to be a requisite.

4. Fuller and Collins (1970) presented a paper which would seem to bear some relationship to the last aim of this thesis. They emphasized that the study of audiogenic seizures in mice could serve as a parable for research into psychiatric disorders and that the validity of the parable lay in the homology of explanatory ideas and not in an homology of chemical, psychological or genetic mechanisms. Some of the research on the topic of audiogenic seizures was mentioned in Chapter Two, notably Ginsburg's approach. Fuller and Collins (1970) conclude that whatever the physical basis of audiogenic seizure susceptibility may be, it changes during the animals' life cycles in a manner which is characteristic of each strain, but the connection between this view and the activity of the genes at the cellular level is unclear at present, although the continued finding of single responsible loci should aid interpretation of the relationship between biochemistry and seizure phenotype. The authors realize that the problems of psychiatric genetics are more complex at the phenotypic level but believe that the interaction of genetic, environmental and developmental factors follow "similar laws in mice and men" and suggest that the parable can lead to unifying concepts that can be applied to the kinds of data which can be obtained in psychiatric genetics. It is that which my study has taught about the concept of fear, which must apply when studying similar phenomena in other species, that a major part of its heuristic value lies, rather than in the pure description of emotional behaviour in one line of hamsters. Ginsburg (1971) also said that when a single gene approach resulted in an animal model with respect to an underlying behavioural mechanism that may be influenced by environmental changes during development (as

could be the case in the piebald hamster, cf. Chapter Ten, section E), it is then possible to look for homologous situations in other species including man. Therefore, an hypothesis, relating to aim five listed in the Introduction can be made. Based on findings presented in the experimental chapters (Nos. 10, 11 & 12), it can be suggested that the piebald hamster may be an example of an animal with high emotionality, useful for the study of physiological and psychological aspects of emotional behaviour, and which could produce results that had implications for the same involved network in other species.

L. CONCLUSION

In conclusion, it seems fitting to reiterate one particular aspect which has recurred throughout the thesis. Although this study has attempted to discover more about the nature of fear and emotionality, further experiments involving the observation of two direct fear responses, escape and immobile behaviour, may demonstrate that fear can be displayed in many ways, depending on a variety of factors, because it is unlikely to be a unitary condition, and the resulting behaviour patterns may not fall easily on a continuum for intensity of emotionality. A search for different models of emotionality (of which the piebald hamster may be one) should lead to a greater understanding of physiological and behavioural expressions of fear.

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ABSTRACT

The study investigated aspects of emotional behaviour in two piebald and two non-piebald genotypes of hamster, to confirm anecdotal reports that piebald hamsters were more fearful than other types. Behavioural differences were hypothesized to relate to psychological functions and to be associated with the recessive piebald gene, thereby representing a major gene effect which could merit further investigation by a behavioural geneticist.

Limitations on uses of the terms 'fear' and 'emotionality' were acknowledged, and evidence that they were unlikely to refer to unitary states was discussed.

Genetic, maternal and sibling effects were controlled for, so that a single cross could produce the four genotypes in any litter. The hamsters were bred by a geneticist, Roy Robinson. On arrival at four weeks of age they were housed solitarily or in small groups for about three weeks when they were all isolated; experiments began at eight weeks of age.

Behavioural and nonbehavioural tests, designed to measure emotionality, were based on previous work and a priori reasoning. They included reaction to handling, the open field, novel situation, activity, aggressive encounter, passive avoidance learning, and measures of body weight, food intake, adrenal gland weight, gastric ulceration and mortality.

The results from the experiments were subjected to analyses of variance tests; significant genotype, sex and housing differences were discussed. It was concluded that hamsters carrying the piebald gene could be described as more emotional than golden or brown hamsters,



although there was no consistent pattern shown by either sex or differentially housed hamster in terms of emotionality. The piebald hamster may thus provide a starting point for investigations into a gene-behaviour pathway.

The data were compared with other rodent studies on emotionality and how findings contributed information as to whether fear was a unitary condition assessed.

One type of organization responsible for emotionality could be studied in the piebald hamster and this may contribute more generally to literature on physiological and behavioural expressions of fear.