

AN ASSESSMENT OF LEARNING IN DOGS IN
RELATION TO CUES CONVEYED BY HUMANS

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Declaration of Authorship

I declare that all material presented in this thesis is my own and has been generated by me as the result of my own research.

Abstract

In some instances, dogs show proficient skill in search tasks involving object permanence and gestures from humans, yet it is unclear the extent to which they rely on associative learning to solve these tasks. To address this issue, the Mediation Learning Paradigm (Rumbaugh, 1984) was modified to include 1) object cues 2) human communicative cues and 3) non-social physical cues. In the initial discrimination, two containers were presented at locations A and B with reward contingency A+B-. Once a specified performance criterion was met, the rewarded location was switched and three conditions were presented: the original locations (A-B+), and each location paired with a novel location (A-C+, B+D-). Associative learning predicted low performance in A-B+ due to pre-existing tendency to search A and avoid B, where novel location conditions involve only one of these. Alternatively, associative strategy would predict equal performance in all conditions, as search is informed by object cues or human gestures.

In the absence of any cues, dogs relied on associative learning, and the same was true when object cues were presented at the point of reversal. Communicative gestures from humans led dogs to shift away from associative processes, supporting the notion dogs have a comprehension in socio-communication with humans. However, after cue duration was matched with an object cue, dogs were also able to override associative learning without a socio-communicative cue. Additionally, non-social physical cues in the reversal phase were sufficient for dogs to override the effects of associative learning, but dogs were not able to discriminate based on these cues alone.

These results suggest that when food location changes, dogs are prone to search the same location even when there are cues indicating the correct location. Dogs comprehend human pointing cues, but require explicit cues to break away from associative learning as a search strategy. Social cues maximise the chances of searching correctly, but they can also benefit from explicit non-social cues.

Contents

Chapter 1: General Introduction	6
1. The importance of dogs in psychological research	6
I. The unique cognitive abilities of dogs	9
II. Non-social abilities of dogs	18
III. Object Permanence in dogs	19
IV. Accuracy in Object Permanence tasks	23
V. Have socio-cognitive abilities also been overestimated in dogs?	27
2. Associative Learning and the Mediation Learning Paradigm	32
I. The Mediation Learning Paradigm.....	34
II. Considerations for developing a new spatial Mediation Learning Paradigm .	40
III. Aims.....	43
Chapter 2: The Use of Hiding Cues in Dogs' Search for Food Out of Sight	44
Experiment 1: Spatial Mediation Learning Paradigm	47
Experiment 2: Can dogs override learning with object cues?	61
Methods	64
Results	67
Conclusion.....	71
Experiment 3: Can dogs use object cues to search directly?	74
Methods.....	75
Results	78
Discussion	80
Chapter 3: The Use of Spatial Cues by Dogs in the Spatial Mediation Learning	
Paradigm	89
Experiment 4: Exploration of possible confounds in the MLP	93
Methods.....	93
Results	95
Conclusion.....	101
Chapter 4: The Effects of Communicative Cues Conveyed by Humans	106
Experiment 5: Effects of communicative cues conveyed by humans on dogs' search	112
Methods.....	112
Results	115
Conclusion.....	118

Experiment 6: The influence of cue salience on dogs' search	121
Methods	122
Results	124
Conclusion.....	128
Chapter 5: Effects of Physical Cues	133
Experiment 7: Effects of physical non-social cues on dogs' search	139
Methods	140
Results	143
Conclusion.....	148
Experiment 8: Can dogs find bait hidden in plain sight?	150
Methods	151
Results	154
Discussion	155
Chapter 6: Conclusions	157
Appendices	176
Bibliography	180
Glossary of Terms and Acronyms	194

Chapter 1: General Introduction

1. The importance of dogs in psychological research

Domestic dogs have had a prevailing presence in human society for a long time. They have been living together with humans for 14,000 years and were the first animal to be domesticated (Clutton-Brock, 1999). Accordingly, dogs have frequently been the subject of and subject to scientific investigations. Darwin described the effects of artificial selection in domesticated animals as a model for natural selection, and observed the similarities between humans and dogs in their expression of emotions (Darwin, 1859). Later, dogs were used as a model for human behaviour in the first learning studies. Pavlov identified conditioned reflex through glandular response in dogs (Pavlov and Gantt, 1928). He was able to identify relationships between physiological responses to external events, and described for the first time excitatory and inhibitory processes in behaviour (Gantt, 1973). W. H. Gantt continued Pavlov's work with dogs to investigate the role of physiology in behavioural conditioning in dogs (Harvey, 1995). By measuring a number of different physiological systems, Gantt was able to differentiate conditioned reflexes for each system (cited in Harvey, 1995). He also took an interest in the small proportion of dogs that refused to take food during experiments, starting the first studies of individual differences in personality and neuroses (Gantt, 1944). His subsequent work relating to the physiological responses to adverse shocks would lead to the accepted standard of using social reinforcement to train working dogs (Feuerbacher and Wynne, 2011).

The domestic dog also played a role in the development of operant conditioning theory. Although Edward Thorndike's first experiments with puzzle boxes involved cats, he also used dogs in these experiments, as he believed there were no specific differences in the behaviour of the two species (Thorndike, 1898). The pioneers of operant conditioning theory continued to rely on dogs as experimental subjects. Hull, Livingston, Rouse and Barker (1951) investigated the effectiveness of food as a reinforcer and found that food had to reach the stomach to act effectively as reinforcement. Using the operant framework, McIntire and Colley (1967) maximised the effectiveness of training US Army dogs for the US-Vietnam war. McIntire experimented with the best way to maintain a dog 'point' posture following detection of human scent, from telemetered brain stimulation as a reinforcer to tactile human petting (Feuerbacher and Wynne, 2011).

Scott and Fuller (1965) used dogs as a model to study genetic heritability of behaviours. They noted that although there was definite difference between the breeds of dog, expression of genes relating to behaviour were strongly influenced by the conditions in which the animal was raised. This countered the strong belief that aspects of human intelligence are heritable (Dewsbury, 2009). Scott had also used dogs to study the developmental stages in puppies and identified four periods based on types of ingestion, exploration, social interaction, and elimination (Scott and Marston, 1950). The 'socialization period' became an important concept in sensitive periods of development (Bateson, 1979). Subsequently Fox (1964) used the developmental periods described by Scott to track the emergence and disappearance of motor and sensory reflexes, and so linked neurological development with social interaction behaviours.

Following the legacy of Scott and Fuller (1965), Belyaev, a Russian geneticist working in the fur farming industry made an astounding discovery about the origins of the characteristics of domestication and domestic dogs. Belyaev's work initially involved maximising favourable traits in silver foxes for the fur trade. His previous attempts to select directly for reduced stress in handling, large litter sizes, and extended breeding periods had resulted in failure (Trut, 1999). Instead, Belyaev noticed that specifically selecting for tameness resulted in a significant increase in these characteristics. The foxes were classified into three groups according to tameness, from fleeing and/or biting experimenters, Class III, to very tame, Class I. In the first generations of his experiment, Belyaev noted about 10% of the animals fell into the most sociable of the three categories he had created, Class I. These animals were friendly to humans, wagged their tails, and whined. By the 6th generation, a further 'domesticated elite' Class I E was created, as a large proportion of the animals already occupied Class I. This elite class were increasingly "eager to establish human contact" (Trut, 1999) as more generations passed. They increasingly displayed dog-like characteristics: displayed a delayed fear response, and had floppy ears and rolled tails. Some had a loss of pigment in certain areas, leading some to develop markings similar to Border Collies. In addition to phenotypic changes, the late generation tame foxes reached sexual maturation 1 month earlier, had longer mating seasons, produced on average one pup extra per litter, and in some cases produced two litters per year.

It had been generally accepted that characteristics in domestic animals occurred because of chance mutations from persistent inbreeding (Trut, 2001), but Belyaev's experiments demonstrated that physical and behavioural changes occurred due to variation in the regulation of a small number of genes, which lead

to organism-wide effects. These drastic physiological and behavioural changes happened in as little as ten generations, and offer a strong framework for how dogs and other animals became domesticated (Coppinger and Coppinger, 2001) and significantly, as a mechanism through which major evolutionary changes occur (Trut, 2001).

Further research has led to the development of the ‘self-domestication’ hypothesis, which states that a direct selection for reduced aggression (which could have increased access to food in the vicinity of early-human settlements, Coppinger and Coppinger, 2001) in early dogs led to further morphological, neurological and psychological changes (see Hare, Wobber and Wrangham, 2012). Importantly, domestication leads to increased pro-social behaviour (Gariépy, Bauer and Cairns, 2001). In some cases, these changes led to a reduction in abilities: dogs show a lower problem-solving ability than their wild counterparts, and this was also found in other domesticated species (Frank, Frank, Hasselbach and Littleton, 1989; Hare, Wobber and Wrangham, 2012).

I. The unique cognitive abilities of dogs

Despite this wide range of studies in genetics and physiology, until recently researchers considered the cognitive abilities of dogs of little interest due to their artificial selection by domestication. In most cognitive studies, the domestic dog was used purely as a control for the wild canid species such as the wolf, jackal, and coyote (Bekoff, 1977; Fox, 1972; Frank, 1980; Miklósi, Topál, and Csányi, 2004). With increasing numbers of comparative studies examining the development of cognition, subjects were limited to the primate order, because the similar dexterity of humans and non-human primates meant that similar tasks could be used on

children for direct comparisons with monkeys and apes. However, captive non-domesticated species such as non-human primates used in comparative cognition studies may not have displayed natural behaviours. Captivity can overtly alter behaviour (Lickliter and Ness, 1990), and close contact with humans required with complex training paradigms may alter natural behaviour. In a study by Povinelli, Reaux, Bierschwale, Allain, and Simon (1997) the cognitive abilities of children and adult apes were assessed as roughly equal, yet the apes had received considerably more experience with the test procedures than the children had. Domestic dogs' naturally co-habit with humans and are accustomed to regular human contact from unfamiliar people (Gácsi, Györi, Miklósi, Virányi, Kubinyi, Topál and Csányi, 2005; Miklósi, Topál and Csányi, 2007). Unlike other non-domesticated mammal species, dogs are ideal for cognitive research as they require minimal training with test procedures, and their natural behaviour is unaffected.

Researchers came to realise that dogs display unique cognitive abilities that most non-human primate species do not. A study reported dogs' ability to use cues conveyed by humans to locate hidden objects (Miklósi, Polgárdi, Topál, and Csányi, 1998), and this was confirmed by others (Cooper, Ashton, Bishop, West, Mills and Young, 2003; Miklósi, Pongrácz, Lakatos, Topál and Csányi, 2005). In tasks in which dogs search for a hidden piece of food in one of two or four containers, they can use human point and gaze cues to find the food in the majority of cases (Lakatos, Gácsi, Topál, and Miklósi, 2011).

They can also interpret different kinds of pointing including momentary (short duration, delay before search, Miklósi et al., 2005), dynamic (constant movement of pointing and gazing, Tschudin, Call, Dunbar, Harris, and van der Elst, 2001), proximal and distal (Miklósi et al., 2005). They can use the point cues

flexibly in related tasks (Miklósi et al., 1998, Miklósi, Topál and Csányi, 2004, Cooper et al., 2003) and the ability to use them does not change over time (Agnetta, Hare, and Tomasello, 2000; Miklósi et al., 1998; Riedel, Schumann, Kaminski, Call, and Tomasello, 2008; Soproni, Miklósi, Topál, and Csányi, 2001).

In contrast with dogs, primates have great difficulty in using human point and gaze cues. Some individuals of non-human primate species were trained to follow pointing in certain circumstances (e.g. Natale, Antinucci, Spinozzi and Potì, 1986; see Doré and Dumas, 1987 for a review), but chimpanzees performed little better than chance levels. In some cases, they only performed slightly better than controls (Bräuer, Kaminski, Riedel, Call, and Tomasello, 2006; Call, Agnetta, and Tomasello, 2000). It also takes many trials for primates to find an object or food hidden in containers following human gestures (Anderson, Sallaberry, and Babier, 1995; Itakura and Tanaka, 1998) and they cannot extend this understanding when the task is changed (Povinelli et al., 1997; Tomasello, 1996).

One theory for why apes cannot follow human points, is that their survival and selection is directly linked to competition, not collaboration with their conspecifics (Hare and Tomasello, 2004). For example, in a comparison with human infants, Chimpanzees were required to indicate for the experimenter which of two locations contained the target object (Bullinger, Zimmerman, Kaminski and Tomasello, 2011). The Chimps were less likely to indicate the target location if there was no positive outcome for them. However, infants indicated the target no matter whether there was a positive outcome or no positive outcome for them. For this reason, pointing may serve no relevance to Chimps, regardless of whether they are capable of this skill.

This same tendency for cooperation has been linked to a comprehension of human pointing *within* dog breeds. Gácsi, McGreevy, Kara and Miklósi (2009c) compared different groups of breeds on their ability to follow pointing based on the level to which the breeds were selected for cooperation. The ‘independent worker’ breeds included guarding, hound and sled breeds, and the ‘cooperative worker’ breeds included herding and gundog breeds. The cooperative breeds were significantly more likely to choose the correct location following a gaze and point cue. This tendency to cooperate was directly linked to their ability to follow point cues. The authors suggest that domestication has led to selection for using human communicative cues, but also an ability to inhibit their own independent behaviours through cooperation.

Many agree that domestication has led to a change in the socio-cognitive abilities of dogs. Wolves are similar physiologically to dogs (Mech, 2003) but they do not have the same proficiency in following human pointing. In Hare, Brown, Williamson, and Tomasello (2002), dogs were able to follow ‘point’, ‘gaze and point’ and ‘gaze, point, and tap’ cues, but wolves were only able to follow the ‘gaze and point’ cue. In another study, wolves were tested in their ability to use proximal and distant pointing (Miklósi, Kubinyi, Topál, Gácsi, Virányi, Csányi, 2003). Wolves were as likely to choose the wrong container when the distal point was presented, and only half of the wolves could follow the proximal pointing correctly.

It is possible that because dogs spend so much time during development in close contact with humans, they develop these skills, but their genetics also give them a head-start over wolves. In a study comparing dogs with wolves in pointing tasks, Virányi, Gácsi, Kubinyi, Topál, Belenyi, Ujfalussy and Miklósi (2008) found that wolves which have been hand raised by humans, and have also had extensive

training with pointing tasks, can still only perform as well as dogs that are naive to pointing tasks.

Despite their genetic differences, it would be inaccurate to say that heredity is the sole reason for the differences between dog and wolf comprehension of human communicative gestures (Virányi and Range, 2014). In their review of the current understanding of the domestication of dogs, Virányi and Range highlight the fact that there are consequences to socialisation in both dogs and wolves. Dogs that have had only minimal human contact find following human pointing difficult, and that when wolves are raised by humans, they can obtain dog-like abilities in pointing comprehension (Udell, Dorey and Wynne, 2011). However, genetics still clearly play a role in comprehension. In developmental studies, dogs are able to follow human gestures earlier than wolves (Gácsi, Györi, Virányi, Kubinyi, Range, et al. 2009a) and that additional socialisation and training offer little advances in this skill (Gacsi, Kara, Belenyi and Topál, 2009b), suggesting that dogs' genes have created the means through which further socialisation can advance socio-cognitive abilities.

To further understand the effects domestication has endowed pet dogs with socio-cognitive abilities, Miklósi and Topál (2013) developed the concept of 'evolutionary social competence'. This system level approach combines the findings of numerous studies relating to the abilities of socialised and non-socialised wolves and dogs. The theory explains the differences between wolves and dogs' socio-cognitive abilities in terms of the amount of socialisation they have had. As a baseline, dogs need very little socialisation in order to have an ability to follow social gestures from humans, but with more socialisation, such that a pet dog would have, means dogs can obtain a very good ability to follow human

communicative cues. However, wolves need quite extensive socialisation from young ages to obtain similar levels.

What role does associative learning play in dogs following human point cues?

It seems clear that dogs have an advantage over their genetic cousin, the wolf, and also close human relatives, apes, when it comes to communicating socially with humans. However, some researchers have expressed concern for the overestimation of the cognitive abilities of dogs (Elgier, Jakovcevic, Barrera, Mustaca, and Bentosela, 2009; Gácsi, Kara, Belenyi, Topál, and Miklósi, 2009; Hare, Rosati, Kaminski, Broffman, Bräuer, Call and Tomasello, 2010; Lakatos et al., 2011; Udell and Wynne, 2008; Wynne, Udell, and Lord, 2008). The problem is that the underlying mechanisms explaining how dogs process cues from humans are often “neglected or overlooked” (Udell, Dorey and Wynne, 2011, p290). The mechanisms of communicative skills in dogs could fall either into (1) complex cognitive processes, which allow attribution of other-intent as specified by possession of theory of mind or (2) proficient use of associative processes to follow the communicative cues (Elgier et al., 2009). It is still unclear the extent to which dogs rely on associative learning to process cues from humans.

One argument that dogs may be utilising associative learning when following human point gestures is that previous experience with pointing affects the ability to generalise pointing to novel stimuli. Elgier, Jakovcevic, Mustaca and Bentosela (2012) trained one group of dogs to find a piece of food hidden a particular location, which was indicated with a point cue. This was the interference group. Another group of dogs in the control group had to find food, which could be

hidden at either location, together with a point cue towards the correct location. The difference between the groups was that in the interference group the food was always in the same place, whereas in the control group it changed between the two containers. In the final test, both groups were assessed in their ability to follow the pointing cue to search for food, which could be found in either container. The interference group were much less likely to search correctly for the food, whereas the control group were as likely to search correctly, as they were in the pre-test training. These results suggest that the interference group dogs put more emphasis on the location of the food, rather than the pointing cue itself, implying that associative learning played a key role in their search.

Another argument that associative learning plays a role in dogs' search following pointing is that they do improve in their ability to follow human points through their development. Initially, puppies of different ages were assessed in their ability to follow human pointing (Riedel et al., 2008). Puppies at 6 weeks of age were already capable of searching for food following a point and gaze cue 23 cm from the target container. When adult dogs were assessed in the same manner, they were as likely to obtain the food correctly as the 6 week old puppies. In addition, the young puppies did not increase in their ability to follow human pointing over the course of the testing sessions. Following up on this research, Wynne, Udell and Lord (2008) performed a reanalysis of Riedel et al.'s (2008) data, taking into consideration that in the control condition in which no cue was presented, there was no expectation of improvement. Therefore, the control condition was excluded from the analysis. When the analysis was repeated, there was a significant effect of age. Dogs were improving in their ability to follow human points as they aged, and young dogs were more likely to improve in performance towards the end of their

testing session. This reanalysis contradicts Riedel et al.'s hypothesis (2008) and suggests that there is learning involved in dogs following human points, in both long and short term assessments.

Some researchers argue that dogs' cognitive accomplishments might be limited only to the social domain. Bräuer et al. (2006) reported that in non-social tasks, dogs do not perform as well. The tasks involved searching for hidden objects following the presentation of either communicative, behavioural, or physical cues. In the communicative condition, the experimenter performed point and gaze gestures, while in the behavioural cues condition, intentional actions such as 'try to open' and 'reach' were presented by the experimenter but did not feature any purposeful communication. In the physical condition, the cues informed the animals indicated the presence or absence of food based on auditory or visual information. For example, in the 'noise' condition, the baited container was shaken, and in the 'noise empty' condition the empty container was shaken. Bräuer et al. (2006) predicted that dogs would obtain the bait in most trials in the communicative condition, but less in the behavioural and physical condition because although dogs are skilful in using human communicative cues, they do not necessarily understand the "goal-directed actions of others" (p38). This prediction was confirmed, as performance was lowest in the physical cue condition. In fact, in the 'noise empty' condition, in which the experimenter draws attention to the unbaited container by shaking it, in most cases dogs chose this incorrect container over the correct baited container. The dogs seemed to be more interested in the container that the experimenter had interacted with, and did not interpret the causal information in this cue correctly.

Opposing results were found in a study in which dogs performed equally well in a social and a non-social reversal task (Wobber and Hare, 2009). In the social task, two experimenters stood facing the dog with closed fists held out, with one of the experimenters holding food inside their hand. In the non-social task, the same two experimenters held containers that had different features. Only one of the containers contained the bait. The dogs did not see where the bait was hidden and had to discriminate the food location based on the experimenter's identity in the social task, and the features of the container in the non-social task. When the dogs had obtained the bait in 84% of the trials in this discrimination phase, the rewarded stimulus was changed. The dogs may have had more difficulty in the social discrimination if the cues provided by the experimenters were more salient than the non-social containers. Yet the tendency to avoid errors in the reversal phase was equal for both types of cues, suggesting they were considered equally salient by the dogs. Additionally, chimpanzees were also tested in a version of these tasks and outperformed the dogs, particularly so in the social reversal task. Comparing the dogs with the chimpanzee was useful because it highlighted several features of the dogs' behaviour. The chimpanzees were able to use the social information more efficiently than the dogs, suggesting that they were able to process the additional cues inherent in the social task, whereas the dogs were not. Secondly, it appears that the dogs did not differentiate between the two types of stimuli, and consequently both cues had similar influences on their search behaviour. The chimpanzees interpreted that the two stimuli were dissimilar and used this information in different ways. The results suggest that providing social information does not provide any particular benefit to dogs' search, also, even when social cues were presented, dogs still were not able to obtain the food in all trials.

II. Non-social abilities of dogs

It is clear however, that dogs display exceptional cognitive skill in spatial tasks. A study by Cattet and Etienne (2004) showed that dogs are able to form navigational maps of the environment and calculate the most efficient way to a target. Dogs were shown where food was hidden in a large search array. While blindfolded and wearing noise-reducing earphones, they were led along an indirect path to a starting position. When the earphones and blindfold were removed, the dogs were able to find the food using a direct path. Such behaviour requires advanced cognitive processes from the integration of locomotive information into a representational map of the environment, towards a goal-orientated action.

In detour tasks, a fence or obstacle is placed in between the dog and the target, but the target remains visible. Dogs can successfully move away from the target in order to navigate around the obstacle to obtain the target once they have witnessed a demonstration. If an experimenter demonstrates one path around the fence, dogs are equally as likely to take a different equivalent path to the target (Pongrácz, Miklósi, and Csányi, 2001). Dogs will choose a shortcut, even if they have not been shown this route (Chapuis, Thinus-Blanc, and Poucet, 1983).

Dogs are also able to use different types of spatial cues to navigate environments (Fiset, Gagnon, and Beaulieu, 2000). Egocentric spatial information is encoded in relation to the individual's position (self to object), but this information is no longer useful when the individual changes position (O'Keefe and Nadel, 1978). Allocentric spatial information incorporates the relationship between two spatial coordinates (object to object) and allows navigation regardless of changes to the individual's position or the environment. Dogs were able to find

hidden objects when egocentric frames of reference remained valid, but when these were no longer relevant (no search container was present at location), they could also use near-by objects to find the target based on allocentric frames of reference. Dogs could encode and process two different types of spatial information and use these to locate successfully the object in the majority of cases.

Some studies show that dogs were not very good in tasks that require advanced means-ends abilities. In a ‘string pulling task’ a piece of food is attached to a piece of string that leads underneath a barrier towards the dog (Osthaus, Lea, and Slater, 2005). Dogs showed an understanding of the task as were able to pull on the string to obtain the food if there was a single string. However, when the multiple pieces of string were presented, or the string was arranged at an acute angle to the barrier, or strings crossed over each other, most dogs pawed at the barrier close to the food, rather than pulling on the string. A later study presented a similar task to avoid the problem of strings crossing (Range, Hentrup, and Virányi, 2011). Food rested on wooden planks leading under a transparent screen. Dogs could pull the correct plank to obtain the food and even avoided making proximity error when food was placed close to the screen but not on a plank. The initially poor performance in the crossed-string-pulling task in Osthaus, Lea and Slater (2005) may represent dogs’ inability to process crossing paths, which was also reported by Rooijackers, Kaminski, and Call (2009) in an object search task with movements of the containers after the object has been hidden.

III. Object Permanence in dogs

Another type of task is commonly used to assess cognitive abilities in both animals and human children is ‘Object Permanence’ (OP). OP tasks were created to

monitor the development of sensori-motor intelligence in infants (Piaget and Cook, 1954). The range of tasks track the emergence of behaviours that indicate the development of ‘object concept’; the understanding that objects obey principles of causality in relation to the space between them, through the regulation of time, and without the apparent disappearance and reappearance in space. To possess object concept is to reach the “understanding that objects continue to exist even when they are no longer available to immediate perception in the environment” (Fiset, Beaulieu, and Landry, 2003, p1). Piaget described successive stages of OP in terms of abilities and inabilities in interacting with hidden objects. In the first three stages, perception and motor abilities are developed, followed by three further stages in which the concept of object permanence is advanced (Piaget and Cook 1954). In stage III, infants have developed the beginning of object concept, and will reach for objects in view, or objects that are partially covered. However, they do not yet have the ability to assign a constancy to object that goes out of sight. Children at this stage attempt no search for an object that is completely covered, as it is considered to not exist. This is even the case when the object is covered by a cloth, by which the form of the hidden object can clearly be seen.

At stage IV, infants will reach for objects that are completely covered, but they do not display a full understanding of object concept. In ‘A-not-B’ error, children are unable to restrain from repeating search behaviours and they continue to search where the object was previously found despite hand movements, or displacement of cloth covers indicating the correct location. At this stage “the infants seem to think that an object that has been hidden will always be found in the same place” (Bower, 1974, p183). These perseverative or place-errors occur when

children are unable to inhibit the response to search where they have previously found the object.

In stage V, children have almost developed a full object concept, but they find displacements that are more advanced too difficult. They are able to track successfully double visible displacements, that is, they can find objects that have been visibly moved behind inside one container, and then visibly deposited inside a second container. Dogs, along with many other species have demonstrated that they can follow double visible displacements (Triana and Pasnak, 1981) including cats (Gruber, Girgus, and Banuazizi, 1971), chimpanzees (Spinozzi and Potí, 1993), Gorillas (Natale et al., 1986), Monkeys (de Blois and Novak, 1994), Psittacine birds (Pepperberg, 1997) and Magpies (Pollok, Prior, and Güntürkün, 2000).

Yet when objects are invisibly hidden, or are concealed inside a closed fist or displacement device, animals at this stage tend to search where the object was last seen before it disappeared. At this stage, animals are unable to infer that the object's trajectory matches that of the hand, but is separated along the movement trajectory. In the invisible displacement task the object is placed out of sight in an intermediate displacement device (e.g. a container), the container is moved into a container or behind a screen and the object is deposited. After the displacement device is shown to be empty, stage V children will search inside the displacement device again, not in the container where the object was deposited (Bower, 1974).

Some species have demonstrated are able to track single invisible displacements and pass stage VI OP tasks, but the list is shorter than for visible displacements. They include species within the Hominidae family (great apes), and some monkey species (Natale et al., 1986; de Blois and Novak, 1998; Call, 2001;

Barth and Call, 2006; Collier-Baker and Suddendorf, 2006, De Lillo and McGonigle, 1997). Success in invisible displacement tasks means that individuals can “mentally manipulate their own representation (of the objects) to guide their behaviour and actions” (Fiset, Beaulieu and Landry, 2003).

In early studies, results in object permanence tasks indicated that dogs had obtained stage V (Gagnon and Doré, 1992; 1993; 1994) and even stage VI (Pasnak, Kurkjian and Triana, 1988; Triana and Pasnak, 1981) as they could track visible and invisible displacement of objects. Gagnon and Doré (1992) discovered that the development of OP in juvenile dogs matches the stages in child development, although the stages progress more rapidly and not always in the same relative intervals.

The studies that had identified stage VI in dogs carefully controlled for odour cues and for simple rules. It was anticipated that the dogs would also employ associative learning based on the occurrence of certain events, for example, making a choice based on the last screen visited by the displacement device, and designed their procedure accordingly. These rules were excluded because the dogs' performance did not increase over successive tests (Gagnon and Doré, 1992, 1993, 1994). Gagnon and Doré were also careful to minimise the number of test presentations in their studies as they noted that a Japanese macaque's performance benefited from repeated exposure to the invisible displacement task in Natale et al. (1986). The authors concluded from these results that the dogs had indeed solved the tasks based on object permanence and not rule learning.

However, the conclusions based on these results may have to be reappraised. Despite the specially designed procedure, the use of rules by the dogs

may have been overlooked. In a later study (Collier-Baker, Davis, and Suddendorf, 2004), the results of Gagnon and Doré (1992) were reanalysed and the dogs were found to use the rule “search the container nearest to the displacement device” to succeed in the invisible displacement task. When Collier-Baker, Davis, and Suddendorf (2004) systematically controlled the position of the displacement device, rather than measuring performance across trials, the dogs did not pass the invisible displacement task.

IV. Accuracy in Object Permanence tasks

There are other aspects of the dogs’ performance in OP tasks, which suggest that they may be solving the tasks without successfully tracking the movement of the hidden objects. Dogs’ passed both invisible and visible displacement tasks, but they were less likely to pass the invisible displacement task (Collier-Baker, Davis and Suddendorf, 2004; Gagnon and Doré, 1992, 1993, 1994). If dogs were using associative processes to pass these tests they would be less proficient in the more difficult invisible displacement tasks, leading to this pattern of results. Furthermore, Gagnon and Doré (1992) suggest that this may be due to attention problems, and they report that many trials in the invisible displacement condition were discontinued because the dogs “did not visually follow each step of the manipulation” (p65). Dogs that lost interest were excluded from analysis, which may have led to the high performance reported by this study. Collier–Baker, Davis, and Suddendorf (2004) expressed further concern about the order in which the tests were presented in Gagnon and Doré’s assessment of object permanence. They note that previous experience of finding the object significantly increased their performance in the invisible displacement task. In Gagnon and Doré’s study (1992),

the visible displacement task was always presented first, and the tests led up to the most difficult successive invisible displacement task, presented last. The way in which the tests were carried out by humans may also have been the reason why dogs performed so well. By the nature of manipulating the containers, they may have informed the dogs of the correct location, without the dogs fully understanding the task. The procedure in visible and invisible displacement tasks involves container touching and lifting by the experimenter, and may have encouraged local rule learning (Natale et al., 1986).

Due to the disparity in the interpretation of results in OP tasks, Collier-Baker and colleagues (2004) created an object permanence task which removed human body cues altogether to assess whether dogs were taking advantage of subtle movements by the experimenter to locate successfully the hidden object. They presented a condition in which a curtain hung from the ceiling to obscure the experimenter's body from the knee upwards. When the dogs could not see the experimenter performance fell to chance levels. These results led the authors to believe that the dogs were not utilising object concept to locate the hiding location, but were instead using certain body cues from the human experimenter to complete the task. Further studies assessed the impact of whether the experimenter was in view influenced the dogs' performance in object permanence tasks. Fiset and LeBlanc (2007) noted that performance in invisible displacement tasks was increased when dogs could see the experimenter.

In their study, Fiset and LeBlanc (2007) re-examined what the dogs see during visible and invisible displacements. In two conditions, dogs could either see the experimenter hiding an object with a displacement device, or saw only a displacement device with the experimenter hidden with screens. In visible

displacements, the displacements were made with a clear thread; in invisible displacements, the displacements were made with a box without a top or back. The device was attached to the end of a long thin pole. The dogs were videoed during the tests to assess what parts of the apparatus they were looking at. The results showed that the dogs found the object in most of the visible displacement trials, but significantly less of the invisible displacement trials. Additionally, when the experimenter was visible, they were more likely to search correctly. This suggests that seeing the experimenter as well as seeing the object up until the point is hidden is an important factor to the dogs' success. The video footage also showed that in invisible displacements the dogs looked at the array and the experimenter significantly less than in the visible displacement trials. This suggests that the dogs had difficulty tracking invisible displacements.

An analysis of the errors that the dogs made in search also revealed how much the displacement device influenced the dogs' search. The array featured four hiding boxes in a row, and after all the hiding boxes had been visited, the displacement device was left at the end of the array on the opposite side that it started. In all trials, the dogs were permitted to explore the device without this counting as a choice. When the correct box was far away from the resting position of the displacement device, the dogs were less likely to search correctly than if the displacement device was close to the correct box. In fact, in the invisible displacement trials, the dogs were more likely to choose the incorrect box closer to the displacement device than to choose any of the other boxes. The results of this experiment suggest that dogs can pass visible displacement tasks without any cues from humans, but in more difficult invisible displacement tasks, dogs increasingly

rely on visual cues from humans, and are likely to search the last location with which they have interacted.

Another reason why dogs may not have achieved such high levels of OP is the persistence of perseverative 'A-not-B' error. This type of error is committed by infants that are at stage IV OP, but those who reach stage V no longer display this perseverative error. There are instances of dogs committing perseverative error in spatial tasks. Watson et al. (2001) determined that dogs returned back to where they had previously found a hidden toy, despite witnessing it leave with the experimenter before being hidden elsewhere. Topál, Gergely, Erdohegyi, Csibra and Miklósi (2009) determined that specific communicative contexts cause dogs to commit more of these A-not-B errors. Authors no longer accept the possibilities that memory or attention could be the cause of such errors in dogs, but instead maintain that dogs have a 'ready to obey' nature which means they can sometimes overlook the goal for a more immediate target (Sumegi, Kis, Miklósi and Topál, 2009).

Likewise, in spatial detour tasks in which the target was on the other side of a fence, dogs were not able to navigate around this detour (Osthaus, Marlow, and Ducat, 2010). The majority of dogs were able to make it through the gap to the target in the first four trials, but as soon as the gap was moved on the fifth trial, none of the dogs could make it to the target. It was not until the eighth trial that the percentage of dogs reaching the target was similar to the first trial. Dogs continued to move to where they were successful in crossing the barrier, even when they could clearly see that the gap was not there anymore. These inhibitive errors in search further indicate that dogs are not able to pass high level object permanence tasks.

Initially, research reported that dogs were able to pass the highest level of object permanence, and track objects that had been invisibly displaced multiple times (stage 6), but closer examination of the particular arrangements of these experiments revealed that dogs might have been using other cues from the experimenter and the apparatus to predict the location of the hidden object. The dogs may have been able to pass these object permanence tasks not because they possessed the ability to track invisible displacements, but because they could see the experimenter, the displacement device was placed close to the correct location, or more advanced tasks were presented after experience with simpler tasks. In other areas of cognitive research, dogs may have also been overestimated in their cognitive abilities.

V. Have socio-cognitive abilities also been overestimated in dogs?

The cognitive ability of dogs may also have been overestimated in socio-cognitive research. Dogs were able to follow human points to find hidden food where apes were not consistently able to (Miklósi, et al., 1998; Natale, et al., 1986), leading researchers to believe that dogs were able to attribute attentional states of others (Miklósi, et al., 1998).

Pointing in infants is thought to be an important factor in developing social understanding and theory of mind, so therefore if dogs can follow human pointing perhaps they can also attribute attentional states. Yet success in tasks with human pointing and other communicative cues may be achieved by learning associations between the cues and the location of reward (Elgier et al., 2009; Reid, 2009; Udell and Wynne, 2010). Penn and Povinelli (2007) stated that it is unlikely that any non-human mammals, including dogs, possess the mental capacity for theory of mind,

and so it follows that this is not how dogs are processing human pointing cues. When dogs follow human pointing, there may be simpler processes involved. Elgier, Jakovcevic, Mustaca and Bentosela (2009) explored pointing and gaze, which is a particular aspect of point cues conveyed by humans. They presented an extinction procedure in which the experimenter pointed to one of several search locations, none of which was baited. The behaviour to approach the search array was extinguished within around 30 trials and dogs remained at the start position without making a choice. They also found that dogs' response to human gaze in an object choice task was flexible. An object was hidden in one of two containers, and then the experimenter gazed towards the *empty* container. After initially choosing the container that the experimenter was gazing towards, the dogs found it empty. The dogs began consistently searching the container that was not gazed to, and avoided the gaze cue. Elgier et al. (2009b) interpreted that this behaviour was a result of the use of associative processes in following human cues.

Gácsi et al. (2009b) determined that dogs do not consistently follow human points. Although dogs as a whole would follow a human pointing gesture, some had a tendency to search in the same place, or alternate their search, no matter which location the experimenter pointed to. This individual variation suggests that dogs do not have a complete understanding of human pointing.

Additionally, the visual conspicuousness of pointing seems to be more important than the actual content of the pointing cue to dogs. Lakatos, Dóka and Miklósi (2007) presented two containers and performed a pointing gesture towards one of the containers. The pointing cues had varying levels of protrusion from the experimenter's body. The more the hand and arm protruded from the side of the body, the more likely the dogs were to search the correct container. When the

opposite arm was presented in a cross body point, dogs searched the wrong container significantly more than the correct one. Lakatos, Dóka, and Miklósi (2007) also maximised the conspicuousness of different parts of the pointing cue by making the arm and hand contrasting colours to the experimenter's body. Here they found that a point gesture with a conspicuous hand makes dogs more likely to follow it in search.

In pointing, the orientation of the hand can act as an external stimulus through either proximity or directional cuing. Attracting attention towards the relevant stimulus can facilitate dogs in obtaining objects in social situations. Mersmann, Tomasello, Call, Kaminski, and Taborsky (2011) suggested that stimulus enhancement (Spence, 1936) is a mechanism through which learning can take place in social interactions so rapidly for dogs. In their task, a long fence separated the subject from a target object. When the dogs are released to search for the object, they rarely navigated around the fence in order to obtain a visible object as this required moving *away* from the target in the first instance. However, witnessing a human experimenter or another dog move around the fence led most dogs to obtain the object, even if the demonstrator did not move near the object. The dogs even benefited from witnessing an inanimate object move to the edge of the fence, thus attracting attention to the possible route to the object. As is the case with pointing gestures, highlighting the edge of the fence as relevant to the task greatly improves performance.

Other accounts of how dogs' process cues from humans exist. Previous research has shown that dogs are not simply interested in the human hand in point gestures (Kaminski, Schulz and Tomasello, 2012). In this study, dogs were presented with point and gaze cues with conditions varying the level of intent in the

cue. This was done by directing the cue towards either the dog, someone else, or no one else (experimenter alternated gaze between object and wrist watch, or faced away from the dog). The results showed that dogs' performance was highest when the point and gaze cues were directed towards the dogs, suggesting that they need some accompanying ostensive connection between the communicator in order for them to realise that the cue is intended for them.

In Kaminski, Schulz and Tomasello (2012), gaze was a clear determining factor as to whether dogs performed above chance in the search tasks presented to them. Other studies have also highlighted the increased likelihood that a communicative cue from a human will be followed by dogs when it is presented together with gaze towards the dog (Virányi, Gácsi, Kubinyi, Topál, Belenyi, Ujfalussy and Miklósi, 2008).

There is further support for the theory that highlighting an important aspect of tasks involving human communicative cues can help dogs to search correctly. When a non-arbitrary cue object such as a sponge or wooden block is placed in front of the correct container, dogs can successfully find the hidden object in the majority of cases (Riedel et al., 2008; Agnetta et al., 2000). Importantly, the dogs must see the experimenter place or remove the marker in order to succeed. If the marker appears in front of the correct container without any hand contact, or hand movements visible, the dogs search randomly in either container (Agnetta et al., 2000; Riedel et al., 2008). This is similar to the account of Mersmann et al. (2011) of stimulus enhancement. The main feature that the dogs follow in placement of markers is the movement of the human experimenter's hand near the correct container. The same may also be so for when dogs follow human pointing:

movement of the hand in a point gesture is the most important aspect in leading dogs to search correctly.

In recent years the cognitive abilities of dogs have been studied a great deal in order to understand whether the effects of domestication have caused advanced cognitive abilities to emerge in a species outside of the primate group (e.g. Watson, Gergely, Csányi, Topál, Gácsi, and Sarkozi, 2001; Elgier, et al., 2009; Udell, Dorey and Wynne, 2011; Bentosela, Barrera, Jakovcevic, Elgier and Mustaca, 2008). These abilities are often used as a way to assess cognition as they involve complex processes such as theory of mind. Dogs also seem competent in object permanence tasks, but they commit errors that imply that they are using associative processes to complete the tasks. The same may be true when dogs follow human cues. The possibility that dogs may be using associative processes to follow human communicative gestures may mean that dogs' cognitive abilities may have been overestimated. The main objective of this thesis is to assess the cognitive abilities used by dogs in spatial search. This was achieved by contrasting associative learning with the ability of dogs to follow human cues directly. When we establish whether associative learning plays a role in how dogs process cues conveyed by humans, we will better be able to assess their cognitive abilities, and also the effects of their domestication.

2. Associative Learning and the Mediational Learning Paradigm

Association in the context of learning is “the formation and expression of excitatory or inhibitory associations, formed via reinforcement” (Shanks, 2010, p274). The behaviour of animals can be altered or conditioned, based on the exposure to paired events or stimuli. Natural stimuli often lead to an unconditioned response, for example salivating to food as presented by Pavlov (1927). Through conditioning, associations are made between an unconditioned stimulus, food, and a new stimulus, for example a bell. After conditioning, the new unrelated stimulus, the bell becomes a conditioned stimulus, and leads to the activation of the unconditioned stimulus representation (food), followed by the unconditioned response (salivating). This process even occurs in the absence of the conditioned stimulus food. As such, after associative learning, presenting a conditioned stimulus leads to spontaneous behaviours relating to another unconditioned stimulus.

Operant conditioning is a type of learning through which initially spontaneous behaviour becomes reinforced or inhibited through positive or negative outcomes of that behaviour. For example, Thorndike (1898) placed cats inside specially designed puzzle boxes, which opened when an internal lever was pressed and the cat could escape. Initially, the cats were as likely to perform non-effectual behaviours as behaviours that resulted in the box opening. On successive occasions, when the cats were placed inside the box they were more likely to perform the lever pulling behaviour that released them from the box (reward), and were less likely to adopt behaviours that resulted in remaining in the box (non-reward).

The effectiveness of conditioning is influenced by a number of factors. Salience of a stimulus is determined by its biological relevance and similarity to stimuli that animals would encounter in a natural environment (Bevins, McPhee, Rauhut and Ayres, 1997; Kamin and Brimer, 1963; Kriekhaus and Wolf, 1968). Both stimulus intensity and stimulus salience lead to more vigorous responding in conditioning (Domjan, 2003), for example, if an animal is hungry, food is a salient stimulus and conditioning occurs more rapidly.

Thorndike believed that all animal cognition, no matter how advanced, could be explained by increasingly effective use of associative processes. Yet a behaviour that could not be completely accounted for by associative learning was the ability of certain animal species to 'learn to learn', termed 'learning sets' by Harlow (1949). Individuals of a monkey species began in discriminating which stimulus resulted in reward. Yet the more discrimination pairs they were presented with, the fewer number of trials it took before the monkeys chose the correct stimuli consistently after a single trial. Harlow (1949) believed that some animals could learn stimuli problems as the relationship between the elements within the problem, rather than the identity of the stimuli themselves. New problems are learnt not only as the relationship between the elements within the problem, but as a function of previous experience incorporating previous element relationships. The phenomenon was later described as mediating factors, which were defined as "perception(s) of relationships between things" and "representations of things not present" by Rumbaugh and Pate (1984).

To measure the pattern in responses across a number of trials can tell us how animals learn to associate between stimuli. Krechevsky (1932) identified that animals preferentially chose a position or stimulus in an alternating pattern. He

called this pattern of stimulus preference a 'hypothesis'. The difficulty with the discovery of hypothesis learning was that the traditional procedures used to assess learning did not control the use of hypotheses, specifically, to measure how many were in use, and the level to which behaviour was controlled by each hypothesis. Accordingly, Levine (1959) produced a model to analyse simultaneously a number of hypotheses and measured the influence of each hypothesis on pre-solution responses. The task was to discriminate which of one of two stimuli when selected resulted in reward, over three trials. Levine thought of all 32 possible outcome sequences of the three trials, and they were categorised into different hypotheses. The hypotheses included position preference/alternation, stimulus preference/alternation, and a variation of these two, 'win-stay, lose-shift'. In this instance, an animals' response in making a choice between the stimuli was guided based on the outcome of the previous trial. If the stimulus predicted the reward, the response in the proceeding trial was repeated towards this stimulus, and response alternated to the other stimulus if no reward resulted (hence win-stay, lose-shift). A similar strategy was 'lose-stay, win-shift' in which response to stimuli resulting in reward led to response in the proceeding trial towards the alternate stimulus. Of all the hypotheses, 'win-stay, lose-shift' was the most efficient hypothesis as it resulted in reward in the most instances. Only a restrictive number of species can demonstrate this ability, and in general, the large brained ape species display more rule-based learning.

I. The Mediatlional Learning Paradigm

Rumbaugh (1971) was unsatisfied with the current methods of assessing for rule-based strategies, which are involved comparing the rate at which different

species develop learning. He designed a paradigm, which produced quantitatively different results in a reversal task to assess whether animals used stimulus-response associations or mediational rules during learning. In mediational learning, hypotheses are applied to sets of stimuli to maximise the chance of obtaining reward in as few trials as possible, even when the stimuli change (Harlow, 1949). Such hypotheses, or rules may include 'win-stay, lose-shift' (Levine, 1959), and like object permanence are distinct from associative learning as they cannot be accounted for with traditional associative principles.

The task, used by Rumbaugh (1970), was a "modified discrimination-reversal task", later named the Mediational Learning Paradigm (Rumbaugh and Pate, 1984). Based on an assessment of the patterns of performance in three different test conditions, the extent to which animals relied on associations or mediational factors during learning in the prereversal phase was measured. This will form the basis of the first set of experiments.

There was an initial discrimination of a stimulus pair, A and B, in which A was always rewarded and B was not (A+B-). When a response criterion of 84% correct trials was attained, the reward contingency was reversed. Three reversal conditions were presented. Each condition featured a pair of stimuli: 1) the original stimulus pair, the control condition (A-B+), 2) the previously rewarded stimulus substituted with a novel stimulus C (A-C+) and 3) the previously un-rewarded stimulus substituted for the novel stimulus (B+C-).

If mediational learning occurred in the prereversal phase, the animals would have applied a rule such as 'win-stay, lose-shift'. If the choice of a stimulus did not result in reward, the animal would shift search to the alternate stimulus. In the

reversal phase, success would not be determined on whether the animals had made associations with stimuli or not, but would be based purely on the outcome of a particular trial. If choice of a stimulus was successful, the animals would continue to select this stimulus, if it was not successful, choice would shift to the other stimulus.

In the task in the current study, the distinctive features of the two stimuli allow the animal to discriminate which of the two stimuli to select. When further cues (object hiding cues as provided in object permanence tasks) are presented, if animals are able to process this information appropriately, they avoid making errors. Yet if animals are not able to process these cues, they fail to avoid making errors when they are provided with object hiding cues, and performance in the control condition A-B+ will be lower than the other conditions. Unequal performance in the reversal conditions can be interpreted as the animal using mediational learning in the prereversal phase; unequal performance as associative learning in the prereversal phase.

Yet, if the animals were utilising associative learning, animals would respond in a different way in the reversal phase. Animals using associative processes in the prereversal phase, when presented with the stimuli would establish a tendency to select the rewarded stimulus A+ and a tendency to avoid the non-rewarded stimulus B-. At the point of reversal, this tendency would continue. When the condition A-B+ is presented, the animal would make a large number of errors, as they would have to override the tendency to select A and avoid selecting B. In the case of the conditions A-C+ and B+C-, only one of these tendencies would have to be overridden. Thus, if associative learning remains the primary means through which the two stimuli are discriminated in the prereversal phase, then the condition

A-B+ featuring both stimuli from the prereversal phase would be more difficult than the other conditions, which featured only one stimulus.

There are additional interpretations of the Mediation Learning Paradigm based on the relative difficulty of the reversal conditions. The paradigm also indicates the emphasis placed on the inhibitive strength of the incorrect stimulus B compared with associative strength of A (comparison of A-C+ and B+C-). For instance, if the reinforcing effect of food after selecting stimulus A is stronger than the inhibiting effect of not receiving food after selecting stimulus B, overriding selecting A will be more difficult than overriding not selecting B. Performance in condition A-C+ will be lower than condition B+C-. The Mediation Learning Paradigm is also able to demonstrate whether there is a strong effect of novelty. The novel stimulus C is rewarded in condition A-C+, but it is not rewarded in B+C-. If performance in condition A-C+ is higher than B+C-, animals show a preference to select novel stimuli.

Following the development of the paradigm in 1971, many different species have been assessed using the Mediation Learning Paradigm (Rumbaugh, 1971). For example, in a study by De Lillo and Visalberghi (1994) capuchin monkeys were assessed with the paradigm and no evidence of rule mediated learning was found. This conclusion was reached because there was a tendency of the monkeys to score highest in the A-C+ condition, and performance in the control condition A-B+ was the lowest. The results were replicated in a computerised version of the test in rhesus monkeys in a study by Beran, Klein, Evans, Chan, Flemming, Harris..., and Rumbaugh (2008). Here, although none of the monkeys showed a lower performance in the control condition A-B+, there was a significant difference

between the conditions featuring novel stimuli, A-C+ and B+C-. This led them to believe that associative processes must be guiding the rhesus monkeys' responses.

Based on the relative performance in the three reversal conditions A-B+, A-C+ and B+C-, Rumbaugh and Pate (1984) used the Mediation Learning Paradigm to classify different monkey species in terms of their learning mode. The relative proportion of control condition A-B+ trials correct compared to the other two conditions which featured novel stimuli (C+ and C-) indicated which type of learning the animals used in the prereversal phase. If the proportion of control condition trials correct was equal to the proportion of C+ and C- trials correct, then the animals relied on mediational learning in the prereversal phase. This is because in the reversal phase, whether or not the conditions featured novel stimuli, the animals' search was based on the outcome of the previous trial. This group included Gorillas, Chimpanzees, and Orangutans. If the proportion of correct trials in the control condition was significantly lower than the other C+ and C- conditions, this indicated that the animals' search was guided by associative learning in the prereversal phase. This type of strategy meant that the condition was the most difficult in the reversal phase, because to search correctly, animals must override both tendency to approach A and avoid B.

Rumbaugh and Pate (1984) found a correlation between the brain complexity and the likelihood that animals would resort to mediational learning in the task. Figure 1 shows that species with larger, more complex brains are more likely to correctly solve the control condition A-B+, score equally in C- and C+ conditions, more likely to use mediational learning and less likely to rely on associative learning.

	Talopains	Rhesus Adolescent	Lemur	Gibbon	Rhesus	Gorilla	Bright Apes	Chimpanzee
% CONTROL CORRECT	38	41	43	52	65	66	78	86
C+=C-=CONTROL						X	X	X
C+=CONTROL					X			
C-<CONTROL				X				
C+>CONTROL	X	X	X	X				
C->CONTROL	X	X	X		X			
C->C+		X						
C-=C+	X		X					

Figure 1 A recreation of the evolution of learning abilities as presented by Rumbaugh and Pate (1984). The authors ranked the learning mode of various species based on their performance in reversal conditions of the Mediational Learning Paradigm. Control is A-B+, C+ is A-C+, C- is B+C-.

In the second chapter in this thesis, the dogs witnessed the object being hidden inside the correct container in the reversal phase. Unlike Rumbaugh and Pate (1984) this task is spatial. If dogs can use object hiding cues to search correctly for reward, they will avoid errors in the reversal phase, and in this case, performance in the three reversal conditions would be similar. Yet if dogs cannot interpret these object cues, for instance, if they use associative principles in this process, they will not be able avoid making errors in the reversal phase. The associations developed in the prereversal phase will lead to a tendency of the dogs to approach location A and avoid B. If dogs are not able to use the object cues to correctly search for the reward, they will also not be able to override the previously learned associations. This will lead to more errors in the reversal conditions, particularly in condition A-B+, in which the animals have to override two pre-existing tendencies to search locations A and B. The other two conditions only

feature one location from the prereversal phase, and so to search correctly the animals must only override one of these tendencies to search A (in the case of A-C+), or override tendency to avoid B (in the case of B+D-).

II. Considerations for developing a new spatial Mediation Learning Paradigm

For this series of studies, a spatial task was designed. The tasks presented to the various species of monkey in the Mediation Learning Paradigm by Rumbaugh (1971) and others (Rumbaugh and Pate, 1984; Essock-Vitale, 1978; Beran et al., 2008) to assess learning mode were non-spatial. The stimuli were visually and physically discrete objects differing on several characteristics. Although the stimuli were positioned such as to cover wells that could possibly contain food, the left-right position of the correct stimulus was systematically controlled so that it did not become a spatial task. However, the task was modified into a spatial variant for several reasons. Firstly, in order to assess object permanence, tasks must feature physical displacement to different hiding locations. It would be impossible to introduce object displacement cues in a non-spatial version of the Mediation Learning Paradigm. Similarly, in demonstrating directive communicative cues such as pointing to dogs, it would be challenging to maintain the nature of the task without spatial cues becoming central to the dogs' performance.

An interpretation of associative learning, which may be relevant when carrying out spatial tasks, is stimulus generalisation and peak shift. According to Spence (1936), an excitatory gradient is established around a reinforced stimulus and inhibitory gradient around a non-reinforced stimulus. What this means is that new stimuli that are similar to the reinforced stimuli elicit the same reinforced

response, and the more similar the stimuli, the more likely the response elicited. The same is also true for stimuli that are similar to the non-reinforced stimulus eliciting the inhibitory response. As such, new, and completely unfamiliar stimuli can still elicit a response in animals during the test phase. This theory explains how very similar stimuli are more difficult to discriminate.

Kohler (1939) assessed this effect with different colour lights. Chickens were given discrimination training with a pair of coloured cards, light grey (positive stimulus) and dark grey (negative stimulus). A test card, which was an unfamiliar colour to the chickens, was then presented. Although the chickens had no associative or inhibitive tendencies to this lighter colour grey, they responded more than they would have towards the associative stimulus. The associative gradient that was acquired during the training controlled the behaviour during the test. This is because the inhibitive and associative gradients summate so there is a net associative gradient observed with the new lighter grey card. This was named the transposition effect by Kohler (1939).

Hanson (1959) also observed a similar effect in increased responding to a novel stimulus based on the net effects of associative and inhibitive gradients. The study also identified that as stimuli become more similar, the more likely animals will regard a new stimulus as positive stimulus. The associative strengths acquired during training control the training towards the new stimulus in the test because a net associative strength is observed from the overlapping inhibitive and associative gradients.

The generalisation gradient predicts that in the Mediation Learning Paradigm, following discrimination learning (which will occur in the prereversal

phase of the Mediation Learning Paradigm A+B-) excitatory and inhibitory gradients will be established around the rewarded and not rewarded stimulus. When a new stimulus is introduced (as will be such in the reversal phase, A-C+ and B+D-), animals will respond according to the proximity to the familiar stimulus. For example, at the end of the prereversal phase, location A will be a strong excitor (+100), and location B a strong inhibitor (-100). Location C is near to A and so is a weak excitor (+25), similarly location D is close to B and so is a weak inhibitor (-25). According to the associative view, condition A-B+ will be the most difficult condition as the animal needs to convert an excitor into an inhibitor, and an inhibitor into an excitor (A: from +100 to -100; B: from -100 to +100). In the other two conditions, which feature only one of the original stimuli from prereversal, they need only do the following:

- A-C+: the animal needs to convert an excitor into an inhibitor; and a weak excitor into a strong excitor (A: from +100 to -100; C: from +25 to +100)
- B+D-: the animal needs to convert an inhibitor into an excitor; and a weak inhibitor into a strong inhibitor (B: from -100 to +100; D: from -25 to -100)

Consequently, proportion of correct responses in these two novel stimulus conditions will be higher. Associative learning predicts unequal performance in the three conditions. As generalisation gradients predict that the more similar, or closer two discriminators are, the more the animals respond to novel stimuli. It will make a difference whether the novel stimuli are close to or far away from the original stimuli from the prereversal phase, and the experiment design must reflect this.

III. Aims

The aim of this thesis was to assess how dogs guide search in a reversal task. This was achieved by presenting a modified version of the Mediation Learning Paradigm developed by Rumbaugh (1970) to include spatial stimuli, and human body cues at certain points in the experiment. The main reason for using this paradigm was to assess if dogs could use the various types of human cues to override spatial learning.

Firstly, in Chapter 2, the learning mode of dogs was assessed, and this was done without any cues provided during the experiment. Then, the ability of dogs to override learning and follow immediate cues to correctly search for hidden food was used to understand how dogs process object permanence cues. Next, in Chapter 3, communicative cues were presented to assess whether these influence the ability to override associative learning was assessed. Finally, Chapter 5 evaluated the extent to which non-communicative physical cues can be used to override associative learning.

The specific aims of this thesis were to: 1) assess the learning mode of dogs and the relative strengths of reward and inhibition in spatial learning; 2) test whether dogs can use object cues during the hiding process to overcome spatial associations; 3) explore which aspects of human communicative cues are most important to dogs in searching for hidden objects; 4) clarify whether dogs can also use non-social physical cues, as would be presented in an object permanence task, to override associative learning.

Chapter 2: The Use of Hiding Cues in Dogs' Search for Food Out of Sight

Dogs possess very good abilities in following human gestures, yet it is unclear the extent to which they rely on associative processes during search for hidden objects. Dogs have demonstrated good level of skill in Object Permanence (OP) tasks (Gagnon and Doré, 1992, 1993), but later experimenters found that the dogs relied on simple rules using the particular positions of the equipment to predict the correct location (Collier-Baker, Davis and Suddendorf, 2004), in a manner similar to associative learning.

Elgier et al. (2009) explored the possibility that dogs may be using associative processes to follow human gestures but these procedures did not directly contrast associative learning with other strategies. The Mediation Learning Paradigm (Rumbaugh, 1971) can distinguish whether animals are using associative processes or other strategies such as mediational rule-based learning to guide search. The paradigm in a modified version was presented to dogs in this thesis to assess whether associative learning plays a role when dogs follow human gestures to search for food.

The paradigm featured two identical containers at specific locations on a spatial array. Food was hidden inside one of these containers, and as such, we can consider the two containers and their reward contingency 'A+B-'. Over a series of trials, dogs carried out a search of the array; obtained the food following a correct choice, and did not obtain the food in an incorrect choice. The trials were repeated until a performance criterion of 90% correct trials in 10 consecutive trials was reached. When this criterion was met, the reversal phase began and three conditions

were presented. 1) the containers at the same locations, with the previously baited container empty, and the previously empty container with food inside (A-B+) 2) the previously baited container empty and a baited container at a new location (A-C+) and 3) the previously empty container baited, with an unbaited container at a new location (B+D-). In any given trial, there were only two containers on the array.

The performance across the reversal conditions was compared, and it was predicted that if dogs follow associative processes to search correctly in the reversal phase they would have to simultaneously override tendency to search A and avoid B. Therefore, this would be the more difficult reversal condition and performance would be low. The other two conditions A-C+ and B+D-, which featured novel locations, would only require the reversal of only one tendency to approach or avoid and so would not be as difficult as the control condition A-B+. Conversely, it was predicted that if performance across the reversal conditions was equal, this would mean that the dogs could integrate information about the outcome of a single trial, in a strategy such as win-stay, lose-shift.

Experiment 1 assessed whether learning in the prereversal phase is guided by 1) rule-based mediational learning or 2) associative processes. Associative learning is a process through which over repeated instances, animals form tendencies to perform certain behaviours in the presence of stimuli in order to obtain rewarded events, and to avoid non-rewarded events. The probability of obtaining reward is maximised over a series of trials as associative and inhibitory tendencies are established and strengthened. In comparison with children, dogs demonstrated they used associative learning in search tasks that have with successive searches (Watson et al., 2001). Following an incorrect search, the period before the dogs made the next search for an object hidden behind one of several

screens increased with every unsuccessful search. Watson and colleagues interpreted this result as a decreasing tendency to search, and consequently that dogs were using associative learning to search. The children on the other hand, increased in the rate at which they made a choice and performed a search, suggesting that they were using deductive reasoning and not associative learning to guide search.

In Experiment 2, the spatial Mediation Learning Paradigm was presented again with a slight variation to the procedure. At the point of reversal, a cue conveyed by a human (witnessing the experimenter placing food inside the baited container) was presented indicating the location of food. The dogs witnessed the experimenter placing the bait inside the correct container. To correctly search in the reversal phase of the paradigm, dogs had to utilise the cues conveyed by the experimenter and override spatial associations. If they can use cues conveyed by the experimenter to correctly search for the food, this was shown by an equal performance in all reversal conditions. However, an inability to inhibit learned responses from the prereversal phase will indicate that the dogs were not able to use effectively the cues conveyed by the experimenter, and continued to rely on associative processes. In this case, there will be more errors in condition A-B+, in which both locations present from the prereversal phase are presented to the dogs.

Experiment 1: Spatial Mediation Learning Paradigm

Method

Subjects

Ten healthy dogs were recruited from the customers of a commercial boarding kennels in an opportunistic sample. Ethical approval for all experiments was obtained from the University of Leicester. Customers who made a booking during the period that the experiments were carried out were contacted at the time of booking, or on dropping off their dog(s). None of the dogs had taken part in any other studies, nor were any dogs working dogs. All of the dogs had received basic obedience training only. All subjects of experiments 2-6 were recruited in the same manner.

Dogs were assessed for suitability for the experiment, namely, sufficient interest in food and absence of signs of anxiety. If they refused to take food from the hand of experimenters, then from inside the container, or displayed posture indicating anxiety such as tail between hind legs, avoidance and growling, they were excluded from the testing. Four dogs failed such tests for lack of interest in food and one for anxiety. Ten dogs were recruited and passed behavioural assessment, they were five males, and five females with a mean age of 4.44 years (range 2-6). The dogs were of the following breed types: two Labrador retrievers, three Collies, one Spaniel, one large cross breed, one Dalmatian, one Bull Mastiff, and one Weimaraner. During the second testing session, one dog displayed very elevated signs of anxiety and so was excluded from the experiment. After the completion of the study, the male Weimaraner breed dog was diagnosed with epilepsy, and so was withdrawn from the data.

There were two experimenters who were responsible for daily care of the animals, such as husbandry, exercising and feeding, and so had some familiarity with them. Dogs had access to water at all times during testing.

Apparatus

Testing took place indoors in a separate building to the kennels facility. The search array comprised of a semi-circular line of 12 circles approximately 2 cm in diameter, marked in white paint on a rubber mat, with dimensions 2 metres by 4 metres, which provided grip for dogs during testing. The circles were 20cm apart and 1 metre from the dog starting position, which was marked in white as a rectangle 20cm by 30cm (Figure 2 section a.).

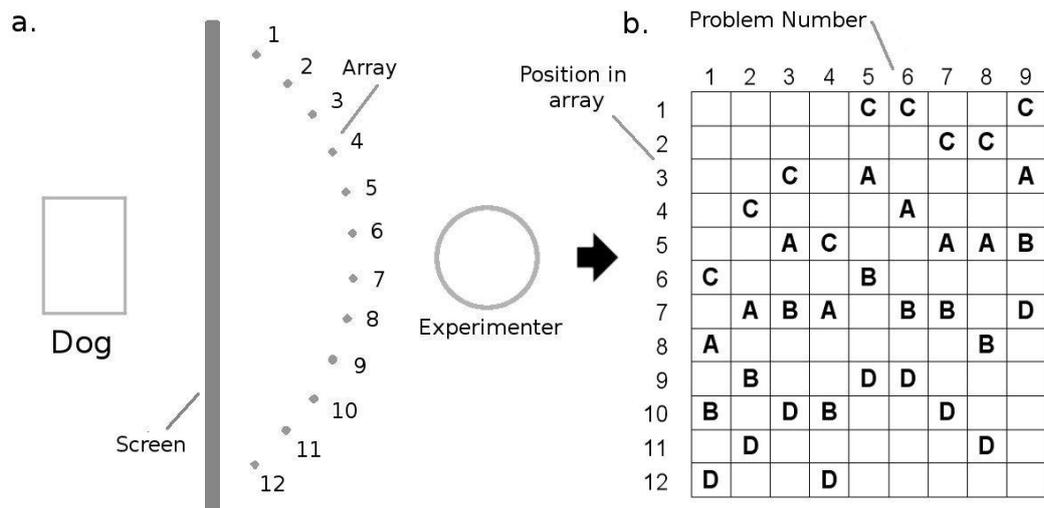


Figure 2 The apparatus used in the spatial Medial Learning Paradigm. Section a. displays bird's eye view of the search array, screen, and dog starting position. Section b. displays the locations used in the various spatial problems (described below).

To obscure the experimenter and prevent transmission of body cues, a screen was placed between the dog starting position and the array. The screen was taller than the experimenter and wider than the array, and had a fabric section in the top half. The lower half was open and permitted free movement of dogs

underneath. The fabric was blue cotton weave and was of thickness 700g per square metre. A roll-blind of the same fabric the width of the screen hung from the bottom of the screen so that when lowered, the whole of the experimenter and the array was hidden.

There were two containers and each one comprised of two plastic 10cm diameter plant pots of a brown colour stacked together. Bait was placed inside the lower pot and the second pot was stacked on top so that scent cues were provided at both containers from this inaccessible bait. The inaccessible bait also created a sound to replicate the sound of baiting in the unbaited container.

Bait was one meat flavoured dog biscuit approximately 2g. Dogs were not starved prior to the testing period. The experiments were video recorded to ensure that trials were coded accurately.

Procedure

Familiarisation

There were two experimenters present during testing, the first experimenter performed the baiting of the containers and operated the screen. The second experimenter controlled the position of the dog and recorded the outcome of a trial.

Immediately prior to the first testing session, dogs were released to explore the testing room and apparatus (without any containers or bait) for a short time, typically 3 minutes. The first and second experimenters were present during this period. During this time, the curtain was raised and lowered until the dogs became accustomed to the action. Dogs wore a slip lead during the experiment to prevent search at both locations and to facilitate repositioning at the starting position at the start of a new trial by the second experimenter. The second experimenter restrained

the dog by the collar at the starting point, ensuring that the dog was facing forward towards the array. They were positioned kneeling to the right of the dog so that the camera's view of the dog was not blocked.

Three warm-up trials were presented in order to inform the dogs that the containers contained bait. A piece of bait was placed centrally on the array without a container present and the dog was released to obtain it by slackening the lead. When it had located and eaten the bait, it was brought back to the starting point by the lead. In a second and third warm-up trial, the bait was placed next to and then inside a centrally placed container. When the baiting had taken place, the second experimenter released the collar but held onto the slackened lead. When the dog had made one choice and had sufficient chance to search inside the container, the second experimenter brought the dog back to the starting point using the lead. Data was not recorded in this phase.

Test Phase

Each dog was presented with three testing sessions, each with a different spatial discrimination reversal problem (spatial problem). Each session had two phases: the prereversal phase and the reversal phase. Data was recorded for both phases. A spatial problem was chosen at random and determined the location of two containers at two different locations on the array (see Figure 2, section b.). These locations remained constant throughout the testing session. The distance between the two locations was between 40 and 60cm apart so that they were both within the dog's visual field but not so close that dogs could see inside both containers from a central point. The containers and the baiting contingency was referred to as A+B- (A baited and B not baited).

In the testing phase of Experiment 1 the dogs did not witness the baiting at any time. When the dog was at the starting position, the curtain was lowered and only raised when search was to take place. Only two containers were placed on the array in any given trial. Baiting took place away from the array and both containers were positioned at the same time. Once the containers had been placed on the array, the first experimenter stood in between and slightly behind the containers, and looked straight forward to the screen, with hands placed behind the back. A trial was recorded as a correct response if the dog obtained the bait from inside the baited container with its mouth, or indirectly by knocking over the container so the bait fell out. An incorrect response was recorded if the dog approached and investigated inside the unbaited container. This included positioning its head above the container so it had direct line of sight of the inside of the unbaited container.

Each testing session had two phases: the prereversal (acquisition) phase and the reversal phase. A spatial problem consisted of two containers at two fixed locations on the array, A and B, the baited location referred to as +, and unbaited location -, i.e. A+ and B- in the case of the prereversal phase. The testing sessions were randomised so that some featured the baited A location as the left container, and others as the right container.

The number of trials presented in the prereversal phase is determined by the number of correct trials. Once a performance criterion of 90% correct responses within 10 trials was obtained the reversal phase began (see Rumbaugh and Pate, 1984; De Lillo and Visalberghi, 1994; Beran et al., 2008). The proportion of correct responses was calculated during the testing so that the number of prereversal trials presented could be adjusted accordingly.

In the reversal phase, the reward contingency was switched so that the bait was not hidden in location A again. There were three conditions, which each featured containers at two locations: the locations A and B from the prereversal phase, and also two new locations C and D. The same reversed reward contingency applied to all conditions. Specifically, the conditions featured the following locations and contingencies: 1) A-B+; the locations from the prereversal phase with B rewarded instead of A, 2) A-C+; the rewarded location from prereversal empty, and novel location C baited, 3) B+D- the non-rewarded location from prereversal now rewarded, presented with novel location D, empty.

The locations A-D were specified by the spatial problem, chosen at random from a pool of possible combinations (Figure 2 section b.). The number of possible locations was limited by 1) the minimum/maximum distance of 40-60cm between locations as outlined above and 2) location pairs within a condition had to be positioned adjacently so that the first requirement was met (i.e. A next to B, A next to C and B next to D). This was to account for the effects of variable responding to novel stimuli as predicted by stimulus gradients (Hanson, 1959).

In the reversal phase, one trial of each condition was presented in a random order. These trials were excluded from analysis, as in similar studies (for example De Lillo and Visalberghi, 1994). Following these trials, six trials of each condition were presented in a random order. The order of trials in the reversal phase is presented in Table 1.

Table 1 Order of trials in the prereversal and reversal phase of the spatial Mediation Learning Paradigm

Prereversal phase 9/10 correct criterion	Reversal phase (Trials 1 to 3 in random order)	Reversal phase (Trials 4–21 in pseudorandom order)
A+ B-	A- B+ (no novel, 1 trial) A- C+ (novel S+, 1 trial) B+ D- (novel S-, 1 trial)	A- B+ (6 trials) A- C+ (6 trials) B+ D- (6 trials)

When a dog had completed a testing session they were returned to their kennel. Testing typically took place in three sessions over two days: morning, afternoon and the following morning. All testing was completed during a single stay at the kennels so there was no more than one day delay between sessions. A session lasted approximately 15 minutes.

In the prereversal phase, the number of trials to reach a criterion of 90% correct within 10 consecutive trials (TTC) was measured. TTC was recorded as number of trials. TTC was analysed in a separate data set. In the reversal phase, the proportion of correct responses (PCR) was calculated for each condition. The first trial of each reversal condition was excluded from the analysis, as typical in Mediation Learning Paradigm studies (Rumbaugh and Pate, 1984).

Data Analysis

The outcome of the familiarisation phase was not recorded. Data in the prereversal phase analysed included the proportion of correct responses (PCR) and the number of trials to reach performance criterion (TTC). In the main testing phase, only the PCR was recorded as the number of trials in the reversal phase remained constant. The PCR in the first instance of each condition was excluded from the main analysis, as these trials were considered as informing the dogs that the reward contingency had changed. This type of procedure is used in other

mediational learning studies (Rumbaugh and Pate, 1984; De Lillo and Visalberghi, 1994). In the prereversal phase, the data were assessed as not normally distributed (see results and Appendix 2), therefore non-parametric Freidman's test was used to test whether there was any change in TTC in the prereversal phase from session 1 to session 3. The same non parametric tests were used in this phase of the experiment in the analysis of all following experiments.

The data in the reversal phase was also assessed for normality (see Appendix 2) and was found to be normally distributed. Accordingly, the PCR in each reversal condition was compared using a one-way repeated measures ANOVA. To assess how the conditions differed, post-hoc independent sample t-tests were used, with Bonferroni adjusted alpha level. To assess whether any learning took place in the reversal phase, the PCR of session 1 was compared to session 3 with a paired samples t-test.

Results

Prereversal Phase

The mean number of trials in which the dogs obtained the learning criterion in the prereversal phase (trials to criterion, TTC) was 15.07 (95% CI=12.52, 17.61). In the first session, dogs achieved criterion performance in 16.80 trials (95% CI=13.02, 20.58), in the second session 16.20 trials (95% CI=9.90, 22.50), and 12.20 trials in the third session (95% CI=8.81, 15.59). A Kolmogorov-Smirnov test was used to test for normality on the main dependent variable TTC. Although session 1 ($D(9)=.22$, *ns*) and session 2 were normally distributed ($D(9)=.32$, *ns*), session 3 was not ($D(9)=.47$, $p<.05$), therefore non-parametric tests were used for the

prereversal phase of the experiment. The same non-parametric tests were used in all proceeding experiments.

To test the hypothesis that the dogs applied the use of rules between sessions to decrease the number of trials before the prereversal criterion was met, the number of trials to reach criterion (TTC) in the three sessions was compared using Friedman's test. If there was a decrease in the number of TTC over the three sessions, the dogs were using the spatial problems to form advanced rules, or 'learning to learn'. However, no such decrease was found. There were no differences between TTC in session 1, 2 and 3 ($\chi^2(2, N=3)=3.47, ns$).

Reversal Phase

The mean proportion of correct response (PCR) in the reversal phase for each condition in Experiment 1, in which the hiding process was not visible and no cues were conveyed by the experimenter are displayed in Figure 3.

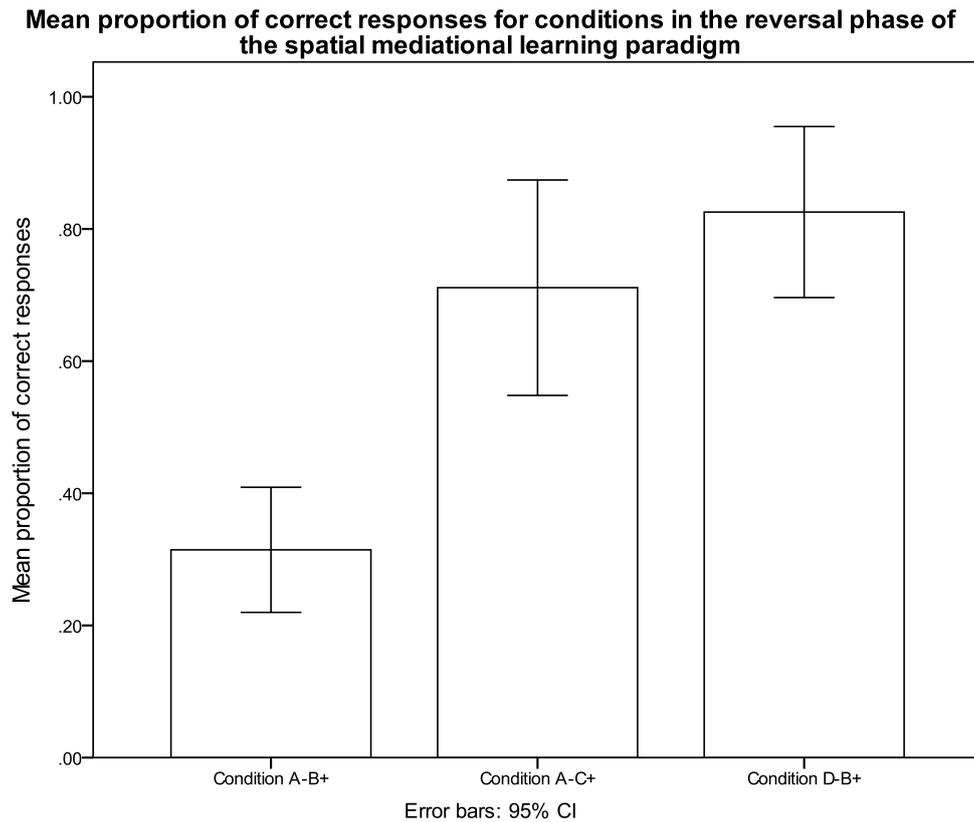


Figure 3 Mean proportion of correct responses in the three reversal conditions of Experiment 1, in which cues conveyed by the experimenter were not visible at any time during the experiment. Error bars represent 95% CI.

To test the hypothesis that dogs were able to overcome the learned associations between location and reward from the prereversal phase, search correctly in the majority of the reversal trials, by using the object cues, the proportion of correct responses were compared between reversal conditions. The three conditions featured: both locations from prereversal (AB), the previously rewarded location paired with a novel location (AC) and the previously unrewarded location together with an additional novel location (BD). All three conditions matched the reversed contingency (A-B+, A-C+, D-B+). If the dogs were able to learn using rules such as ‘win-stay, lose- shift’ in the prereversal phase, they would perform equally in all conditions, as search would occur without taking into account associative or inhibitive weights of the stimuli. However, the level of

performance in the conditions would be *unequal* if the dogs were using associative learning to guide search in the prereversal phase. Specifically, there would be significantly lower level of performance in the reversal condition featuring the locations from the prereversal phase, condition A-B+ as associative learning predicts that correct search requires simultaneous inhibition of response to A and inhibition of response to avoid searching B. The other two conditions, which feature only one location from the prereversal phase, would require only one of these two operations.

To test the hypothesis explained above, the PCR of the three reversal conditions was compared using a one-way repeated measures ANOVA. There was a significant difference between the conditions ($F(2,16) = 17.98, p < .001$, partial $\eta^2 = .69$). The differences were assessed with further analysis using independent samples t-tests with Bonferroni adjusted alpha level of .016 per test (.05/3). Condition A-B+ PCR was lower than the other novel location substituted conditions (A-B+ and A-C+, $t(8) = 3.91, p < .016$; A-B+ and B+D-, $t(8) = 6.89, p < .016$). The comparison between conditions A-C+ and B+D- did not show a significant difference ($t(8) = 1.50, ns$). The performance across the conditions was unequal; therefore, the dogs used associative learning in the prereversal phase.

Learning in the reversal phase

To assess whether dogs improved in their performance in the reversal phase of the experiment, the proportion of correct responses in the first and last test was compared. The proportion of correct responses (PCR) in session 1 was .59 (95% CI = .49, .68), and in session 3 it was .62 (95% CI = .54, .70). A paired samples t-test was carried out and there was no significant change in performance over the course

of the experiment (mean difference = $-.04$, $t(8) = -.77$, *ns*), therefore no learning took place in the reversal phase.

Conclusion

The aim of this experiment was to assess if dogs use mediational learning or associative processes to guide search in a spatial learning discrimination task. This was achieved by presenting the Mediational Learning Paradigm, which features first a spatial discrimination (A-B+). Once a performance criterion had been met, the reward contingency was changed. In the reversal phase, two additional locations were introduced. Three conditions were presented: a condition with the original locations A-B+, a condition with the previously unrewarded location substituted for a novel location A-C+, and a condition with the previously rewarded location substituted for a novel location B+D-. The relative performance in these three conditions indicated whether dogs were using mediational learning or associative learning in the prereversal phase to solve the discrimination. If the dogs were using mediational learning, they would need only one trial in which to realise the correct location of the hidden food, by implementing a rule such as 'win-stay lose-shift'. As a result, performance in the three reversal conditions would be equal. However, if they relied on associative processes, pre-existing tendencies to search in the previously rewarded location and avoid the previously unrewarded location would continue to guide the dogs' search in the reversal phase. Performance in the A-B+ condition which featured both locations from the prereversal phase would be the most difficult as correct search would require simultaneously overriding the incorrect tendency to avoid B and search A. The other two conditions would require overriding only one of these tendencies as novel locations have no pre-existing

associated tendencies to search or avoid. As a result, if the dogs were using associative learning the performance in the A-B+ condition would be relatively low compared to the other two conditions.

The performance in the three reversal conditions was compared and it was found to be dissimilar, therefore dogs used associative learning to guide search in the prereversal phase, and continued to rely on these learned associations in the reversal phase. Consequently, they made most errors in condition A-B+.

Dogs have not been tested in this way using the Mediation Learning Paradigm before but they have been found to rely on associative learning in other spatial tasks. Watson et al. (2001) used an invisible displacement task to test for the presence of inferential reasoning by negation. The authors designed the task to compare the rate at which dogs search successively. They predicted that if dogs used inference to guide search, following incorrect choice, the proceeding search would have a more rapid response time as the dog had greater certainty about the location of food in the remaining unsearched locations. Conversely, associative learning would lead to a slower rate of search following an incorrect search, as general commitment to search decreased with each unsuccessful search. Dogs refer to associative processes not inferential reasoning to guide search (however there are criticisms of this interpretation, which are outlined in Chapter 1).

Other species assessed with the Mediation Learning Paradigm have also demonstrated an associative learning mode, including talopins (Rumbaugh, 1971), rhesus and stump-tailed macaques (Essock-Vitale, 1978) and tufted capuchins (De Lillo and Visalberghi, 1994).

In Experiment 1, there were no cues conveyed by the experimenter or information about the location of the reward. To search correctly in the reversal phase, dogs' search had to be guided by the outcomes of previous searches. In the next experiment, the ability of dogs to utilise the sight of the reward being hidden in the reversal phase was assessed. In Experiment 2, the dogs did not witness any cues about the reward location in the prereversal phase and were obligated to form associations between location and food.

It was apparent from the results of Experiment 1 that dogs do not form rules about the location of food by using mediational learning, but most likely use stimulus response associations to maximise their chances of finding hidden food. The main aim of Experiment 2 was to assess whether, when provided with object cues conveyed by the experimenter in the reversal phase, dogs can overcome the effects of associative learning.

Experiment 2: Can dogs override learning with object cues?

Research has demonstrated that dogs can perform well in tasks that involve complex socio-cognitive abilities, in most cases better than non-human primates (Miklósi et al., 1998; Cooper et al., 2003; Miklósi, Topál and Csányi, 2004). They also show a high level of skill in Object Permanence (OP) tasks, which require advanced spatio-temporal abilities (Triana and Pasnak, 1981; Gagnon and Doré, 1992; 1993). Yet in these tasks, which require the inference of an object's location from a series of displacements, performance is directly linked to how much of the body of the human experimenter they can see (Collier-Baker, Davis and Suddendorf, 2004; Fiset and LeBlanc, 2007). This led researchers to believe that dogs were using associative learning rather than specific spatio-temporal abilities, OP, to solve the task. The dogs may have been directly following subtle body cues such as head gaze or proximity of hand near the baited container to correctly search for the bait.

The ML paradigm assessed whether dogs perform well in OP tasks because they notice object cues during hiding, and are able to process object permanence, or whether they form associative tendencies based on the cues. In the following experiments, a 'hiding cue' (the action of the food being placed inside the baited container) was presented in the ML paradigm. To correctly search in the reversal phase of the paradigm, dogs had to utilise the hiding cue and override spatial associations.

Based on their performance in other types of cognitive tasks, they may be successful in the ML paradigm with object cues. Dogs have demonstrated high

levels of skills in various kinds of spatial tasks (Fabrigoule and Sagave, 1992; Pongrácz, Miklósi and Csányi, 2001; Chapuis, Thinus-Blanc and Poucet, 1983) and can use a demonstration from another individual to learn how to complete object manipulation tasks (Osthaus, Lea and Slater, 2005). Yet others have argued that basic levels of cognitive processing may account for dog's apparent abilities in cognitive tasks. They may simply be proficient in the use of associative processes (Elgier et al., 2012), or have a heightened sensitivity to humans and their body signals (Wobber and Hare, 2009). For example, in object permanence tasks, the likelihood that dogs found the hidden object was related to the final resting position of certain manipulating apparatus, and not necessarily OP ability (Collier-Baker, Davis and Suddendorf, 2004). Additionally, a task was designed by Watson et al. (2001) to distinguish between associative processes and inferential reasoning when presented with object cues in search task. In this case, dogs demonstrated a tendency to rely on associative processes, as those dogs, which successively searched incorrectly, took longer to search in their next chosen location. This slowing in search was interpreted as associative processes guiding search as with each incorrect search decreased the tendency to search. In comparison, 4 to 6-year-old children sped up in their search of multiple locations, until they successfully found the object. The children took less time to make a decision about which location to search as they based their search on deduction and were able to infer the location of the hidden object based on the object cues.

In Experiment 2, cues about the object's location were presented to dogs in the spatial ML paradigm in order to assess whether they rely on associative learning, or are able to interpret the human cues to locate successfully the food in the reversal phase. If they use the object cues about the location of food, this will be

evident as a high performance in the reversal phase of the task. However, an inability to inhibit learned responses from the prereversal phase will indicate that the dogs were not able to effectively use the object cues conveyed, and continued to rely on associative processes. In this case, there will be errors in the reversal phase and particularly in condition A-B+, in which both locations present from the prereversal phase are presented to the dogs.

The aims of Experiment 2 were: 1) to assess whether, given object cues conveyed by the experimenter dogs can overcome a tendency to perform a learned response and 2) to assess whether they alter search behaviour based on the presence of object cues. It was apparent from the results of Experiment 1 that dogs' learning of the location of food is not mediated by the formation of rules, but rather based on associations. This strategy was effective in the prereversal phase but dogs made many errors in the reversal phase. This was evident because dogs made most errors when the stimuli from the prereversal phase are presented with reversed reward contingency, but not when novel stimuli are presented.

In the absence of any information to guide their search, dogs may have expressed learned responses from the prereversal phase as the best strategy to find food in the reversal phase. Given dogs' abilities in OP tasks, witnessing the hiding event should provide sufficient information to find the hidden food in the reversal phase of the task. In this case, performance in the reversal discrimination can be expected to be equal in all reversal conditions. Conversely, a significantly lower performance in condition A-B+ will indicate that the dogs, in the reversal phase, expressed the learned response from the prereversal phase. The dogs may be unable to override such learned responses, regardless of whether or not they have seen

object cues, or they may choose to ignore the experimenter cues completely (distinguishing which of these is the case will be explored in Experiment 3).

Methods

Subjects

10 dogs, aged from 2-6 years (mean 4.44 years), took part in the experiment. There were five males and five females of the following breeds: two Dalmatians, four Labrador Retrievers, two Alsatians, one Pointer, and one small cross-breed. The dogs had not been used in behavioural testing before and had received basic obedience training only.

Apparatus

The same apparatus as in Experiment 1 was used (rubber mat, screen, two containers and bait). As in previous experiments, scent of bait was present at both containers.

Procedure

The same familiarisation phase was presented as in Experiment 1. The prereversal phase of Experiment 2 was also identical to that of Experiment 1: spatial problems specified the position of the two containers on the spatial array, and were selected from the same pool of nine spatial problems. The dog faced the experimenter and the array with the screen in between the two. The screen obscured the top half of the experimenter's body, and during baiting the curtain below the screen was lowered to hide the search array and experimenter from the dog. The bait was placed in the correct container away from the array and both containers

were positioned on the array at the same time (with reward contingency A+B-). The curtain was raised and the dog was released and allowed to search. A response was scored when the dogs moved close enough to the container to see the contents inside. Once a response was chosen, the other container was removed to prevent the dog from performing a second search in the same trial. The dogs were permitted to eat the bait if a correct choice was made, or were given several moments to explore the empty container if an incorrect choice was made. Then the dog was led back to the starting position on the other side of the screen ready for the next trial to begin.

When the dogs had obtained 90% of correct responses within 10 consecutive trials, the reward contingency was switched and the reversal phase began. In the reversal phase, the two locations from the prereversal phase, plus two new locations C and D were used as possible positions for the containers in three different reversal conditions. The reversal conditions had matching reward contingencies that opposed the prereversal phase: A-B+, A-C+ and B+D-. The first three trials presented in the reversal phase were one of each condition in a random order, and were excluded from main analysis, as is standard practice for the Mediation Learning Paradigm (Rumbaugh, 1971; Rumbaugh and Pate, 1984; De Lillo, and Visalberghi, 1994), and then followed six trials of each reversal condition in a random order. These final 18 trials formed the main testing phase of the experiment.

Unlike Experiment 1, cues conveyed by the experimenter were presented in the reversal phase to indicate the correct location of the bait. After the prereversal phase had ended, the curtain on the bottom of the screen was raised so that the lower half of the experimenter's body was visible. The cue consisted of the following: the experimenter stood in the middle of the two containers holding one

piece of bait in the hand closest to the container to be baited. The experimenter then performed the following two actions: 1) the bait was placed inside the container or 2) the empty container was manipulated with the empty hand to produce a sound similar to that of the bait placement (the inner plastic pot was raised and dropped). The reason this 'sham bait' action has been included into the design is that previous research has demonstrated that dogs can use the 'last visited' rule in object search tasks (Fiset and LeBlanc, 2007). Additionally, when the experimenter touches or lifts apparatus in the experiment they may be encouraging local rule learning (Natale et al. 1998). The objective of these two actions is to convey the correct location of the bait whilst providing an equal amount of manipulation of both locations. The comparison of performance in the two trials should also give insight into the extent to which dogs rely on this information.

The order of these bait and sham-bait actions was determined prior to testing in a counterbalanced way: no more than two consecutive trials could occur in which the bait was positioned first or vice versa. Trials were determined before testing as 'bait last' or 'sham bait last' and performance on these two types of trials was compared to assess whether dogs were using the rule of searching the location last visited by the experimenter.

The baiting actions required the experimenter to bend at the waist but her head was not visible to the dog when this occurred. When these actions had been performed, the experimenter looked centrally forward into the screen and the dog was released and allowed to search. Dogs were presented with three spatial problems (which featured a prereversal and reversal phase) chosen at random from the pool of problems.

Data Analysis

As in Experiment 1, data from the prereversal phase was not normally distributed, therefore non-parametric tests were used. However, the reversal phase data were normally distributed, therefore parametric tests were used (see Appendix 2). In the prereversal phase, Freidman's test was used to compare the PCR across the three sessions. In the reversal phase, a one-way ANOVA was used to compare the PCR in each reversal condition. Post-hoc tests to compare specific reversal conditions were carried out using paired samples t-tests with Bonferroni adjusted alpha level. Any learning that took place during the course of the experiment was assessed using a paired samples t-test with PCR in session 1 and 3. Finally, to assess whether the dogs were searching based on where the experimenter had visited last, PCR in bait last trials were compared with that of sham bait last trials using one-way ANOVA.

Results

Prereversal Phase

It took dogs an average of 16.13 trials to reach criterion performance (TTC; 95% CI=13.51, 18.76). For each session the TTC were as follows: session 1=12.20 trials, session 2=18.40, session 3=17.80 (95% CI: 9.87<lower bound<12.55; 14.53<upper bound<24.25).

To find out if the dogs increased in their performance in the prereversal phase and reduced the number of trials to criterion across the three sessions, Freidman's test was carried out on the TTC from session 1-3. The test showed that there was no change in TTC across sessions ($\chi^2(2, N=3)=.42, ns$).

As both Experiments 1 and 2 had identical prereversal phase procedures, a similar equal TTC across sessions as in Experiment 1 was predicted. This was tested with a one-way ANOVA. There was no difference between the TTC in the three sessions between Experiment 1 and 2 (session 1 $F(1,18)=3.30$, *ns*; session 2 $F(1,18)=1.01$, *ns*; session 3 $F(1,18)=.08$, *ns*).

Reversal Phase

The proportion of correct responses (PCR) in the reversal phase in each condition were compared to test whether dogs used the cues conveyed by the experimenter to override learning from the prereversal phase. If they did follow the cues, the performance in the reversal conditions will be equal, but if they continue to use associative learning, performance across the conditions would be unequal. Specifically, condition A-B+ would be the lowest as it is the most difficult when associative learning guides search. The PCR in condition A-B+ was .34 (95% CI=.27, .41); in condition A-C+ it was .86 (95% CI=.81, .91) and in condition B+D- .86 (95% CI=.80, .91). The values were compared with repeated measures ANOVA and there was a significant difference between the PCR values in each reversal condition ($F(2,18)=26.42$, $p<.05$, partial $\eta^2=.75$). The differences between the specific conditions were assessed with independent samples t-tests using the Bonferroni adjusted alpha of .016. PCR in condition A-B+ was significantly lower than the other conditions (A-B+ and A-C+, $t(9)=5.43$, $p<.16$; A-B+ and B+D- $t(9)=6.33$, $p<.016$). The other two conditions A-C+ and B+D- were not significantly different from one another ($t(9)=.24$, *ns*). Therefore, the dogs used associative learning to guide search in the reversal phase and they did not follow the object cues conveyed by the experimenter.

The second hypothesis was that dogs benefit in their search from witnessing the object cues conveyed by the experimenter. If this were the case, performance in the reversal phase in Experiment 2 would be higher than in Experiment 1 when no cues were presented. The comparison of PCR in each reversal conditions in Experiment 1 and 2 is presented in Figure 4.

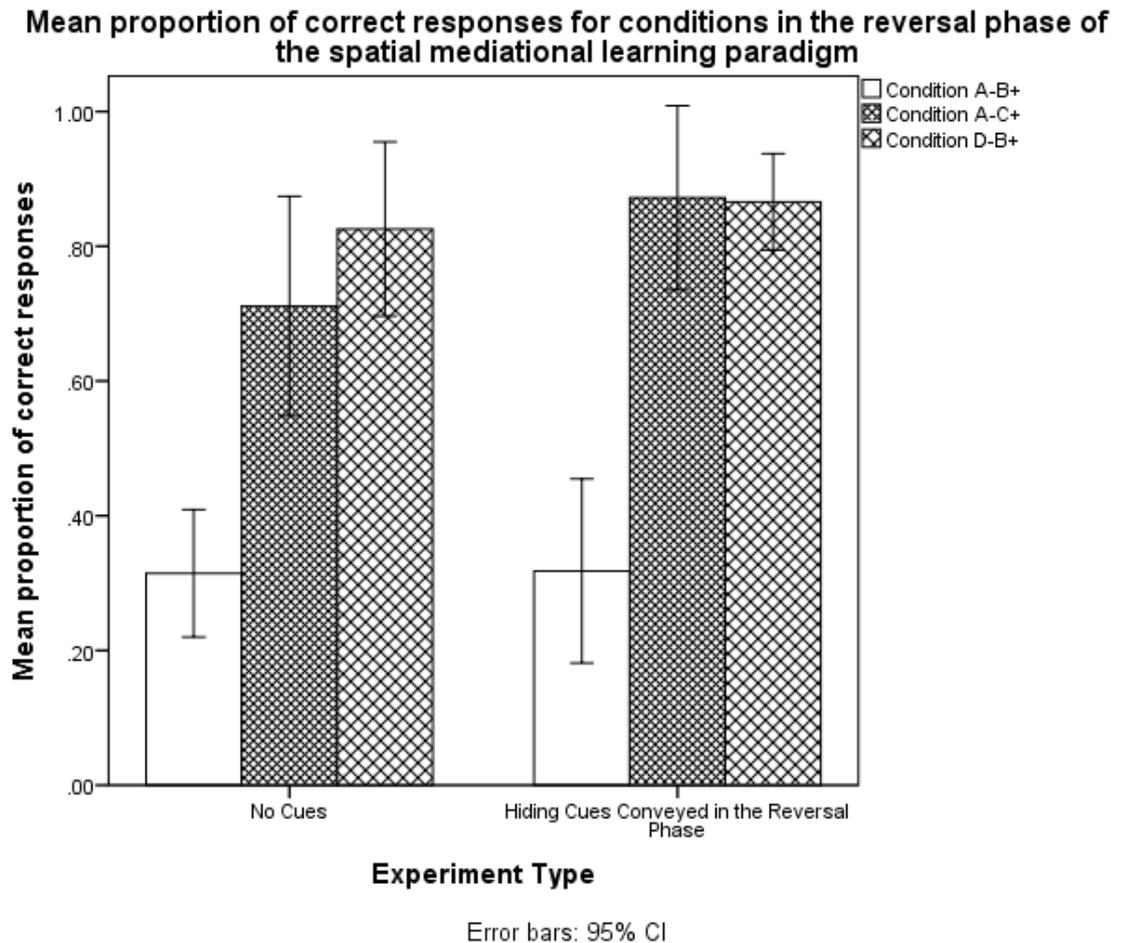


Figure 4 A comparison of the PCR (proportion of correct responses) in each condition following the presentation of no cues (Experiment 1, no cues) and cues conveyed by the experimenter post-reversal (Experiment 2, cues conveyed in the reversal phase). Error bars signify confidence intervals of 95% level.

A repeated measures ANOVA was used to test this hypothesis, with proportion of correct responses in the three conditions as dependent variable, and Experiment (1 and 2) as the independent variable. There was no difference between the experiments (Reversal x Experiment $F(2,34) = .87, ns$). The dogs' search

behaviour remained the same whether there were cues conveyed by the experimenter or not in the reversal phase.

Learning in the reversal phase

The dogs were presented with three tests. In the first test, dogs' proportion of correct responses (PCR) was .63, (95% CI=.57, .69), and in the third test it was .72 (95% CI=.68, .75). Paired samples t-tests were carried out to assess for change in PCR from session 1 to session 3. There was a significant difference in performance across the experiment as a result of witnessing the hiding cue in the reversal phase (mean difference=-.09, $t(9)=-2.65$, $p<.05$, 95% CI=-.16, -.01).

Proportion of correct responses rose from session 1 to session 3.

Use of simple rules

In order to assess whether the dogs were using the rule of searching the location last visited by the experimenter, performance in the 'sham bait last' and 'bait last' reversal trials were compared. In the 'sham bait last' trials, the experimenter placed the bait inside the correct container, then lifted and dropped the empty container. In the other 'bait last' trials, this procedure was reversed so the reward was placed inside the correct container after the empty container had been lifted. The PCR in the 'sham bait last trials was .60 (95% CI=.54, .65), and in the 'bait last' trials it was .78 (95% CI=.73, .83). To test if there was a significant difference between the PCR in the sham bait last and bait last trials, a one-way ANOVA was carried out, and it was significant ($F(1,539)=22.23$, $p<.05$, partial $\eta^2=.04$). Dogs were more likely to obtain the bait in trials in which the experimenter visited the correct container last.

Conclusion

The spatial Mediation Learning Paradigm was designed to assess if dogs have the ability to use cues conveyed by the experimenter to search directly and override learned associative responses when reward location changes. The first experiment was presented to dogs to establish as baseline to assess whether they used mediational learning or associative learning. The current experiment obliged dogs to use trial and error in order to identify the correct location to search in the prereversal phase. This led to the establishment of learned associative responses to the baited location. In the reversal phase, these learned responses were no longer relevant, yet the experimenter conveyed cues directly relevant to the location of the bait. When the reversal conditions featured *both* the locations from the prereversal phase (i.e. condition A-B+), dogs were not able to correctly search for the bait in the majority of cases. They continued to rely on no longer relevant prior associative learning to guide search despite witnessing the experimenter hiding the bait.

These results are consistent with Watson et al. (2001), which contrasted associative learning with inferential reasoning. An object was hidden behind a series of screens and only the trials in which the dogs looked behind the correct screen last were counted. In the task, the rate at which dogs performed sequential searches got slower, indicating a decreasing tendency to perform a search following unsuccessful searches. This indicates that the dogs were using associative learning. The rate of search would have increased if the dogs were using another type of search strategy, reasoning by deduction.

The dogs were not able to override learning by following the hiding cues in Experiment 2. If they had overridden the associative tendencies formed in the

prereversal phase, this would indicate they are capable of using more advanced strategies such as object permanence, which lie separate from cue-learning. The fact that they also relied on the 'last visited rule' and searched the last location manipulated by the experimenter also supports the notion that they were not able to use more advanced search strategies such as object permanence.

Two possibilities arise as to why dogs behaved in this way in Experiment 2: 1) dogs were not able to simultaneously override both the tendency to approach A and the tendency to avoid B in the reversal phase, 2) or they were not able to interpret the movements of the human hiding the bait as relevant predictors of the location of reward. The first possibility is likely, as the same pattern of errors was observed in Experiment 1 in which dogs had no access to cues conveyed by the experimenter. Yet it largely appears from comparing the results of Experiment 1 and 2 that witnessing the human hiding the bait led to no changes in the dogs' behaviour during Experiment 2. However, the search behaviour was influenced by the cues conveyed by the experimenter, as the dogs were more likely to obtain the bait when the trials featured the experimenter visiting the correct location last. Although dogs were not able to reduce errors equally across the conditions, this difference between the two types of trials (sham bait last vs. bait last) indicates that they did in fact notice the experimenter's actions.

Even though the dogs did not use the cues conveyed by the experimenter in the reversal phase, they may still have noticed that the cues were presented. It may be that the dogs had such a strong tendency to follow the learned spatial associations from the prereversal phase that they could not override them.

This experiment forced the dogs to rely, in blind trial and error, to establish the location of food in the prereversal phase. This may have induced the formation of associations between the location and reward. To assess whether dogs can use object cues, such as those that would be presented in an object permanence task, before any learning has taken place, object cues were presented from the start of the prereversal phase. It may be that the dogs do not form any associations between location and reward, and search based on the object cues alone. In this case, they will make few errors in the reversal phase, as the same object cues were presented. Or, if the dogs form spatial associations as well as follow the object cues, performance in the reversal phase will be affected. If dogs were using associative learning, there will be a lower performance in condition A-B+. Additionally, a secondary analysis is possible if we compare the number of trials to reach criterion in the prereversal phase. If presenting the object cues in the prereversal phase affects the ability of dogs to search for the food, there will be fewer numbers of trials to criterion in Experiment 3.

Experiment 3: Can dogs use object cues to search directly?

In Experiment 2, dogs were not able to utilise cues conveyed by the experimenter effectively in the reversal phase of the spatial Mediation Learning Paradigm. They continued to use associative principles and commit errors even though all the relevant information to correctly search for the reward was provided for them. In Experiment 3, cues were conveyed by the experimenter from the start of the prereversal phase. From the beginning of the prereversal phase, dogs were given the opportunity to search directly without learning associations between the location and food. The same hiding cue was presented in the reversal phase. The cue corresponded with the correct location of food in both the prereversal and the reversal phase of the experiment. One of, or a combination of the following predictions may have occurred. Prediction 1: dogs searched where they saw the human hiding the food, without forming any associations, Prediction 2: dogs formed associations between location and food, facilitated by cues conveyed by the experimenter in the prereversal phase, and Prediction 3: dogs formed spatial associations between the location of food in the prereversal phase based on the spatial *location* and ignore cues conveyed by the experimenter. In the case of prediction 1, performance in the three reversal conditions would be similar, as dogs follow cues conveyed by the experimenter to obtain the food. Prediction 2 also expects equal performance in the reversal conditions because the cues conveyed by the experimenter continue to indicate the location of reward. Prediction 3 expects a lower level of performance in reversal condition A-B+, which features the containers at the same locations in the prereversal phase. This is because according to associative principles, this control condition A-B+ requires the dog simultaneously override the tendency to approach A and to avoid B, making this the

most difficult condition. The other two conditions A-C+ and B+D- require only one of these processes, and so the dogs make fewer errors.

A second indication that dogs' search performance was influenced by cues conveyed by the experimenter is that dogs would reach the performance criterion in the prereversal phase in fewer trials than if they did not see any cues in the prereversal phase. This possibility is very likely if we take into consideration that dogs' performance in detour tasks is improved if they witness a human perform the detour (Pongrácz, Miklósi and Csányi, 2001), and also that dogs' performance in search tasks is better when social cues are provided, rather than physical cues relating to object properties (Bräuer et al., 2006).

In this third experiment, dogs were presented with cues conveyed by the experimenter about the location of hidden reward in the spatial Mediation Learning Paradigm. The cues were presented in both the prereversal and the post-reversal trials. This procedure was designed to assess whether dogs could detect cues conveyed by the experimenter and use them to increase the likelihood of searching correctly for the hidden reward when the reward contingency changed.

Methods

Subjects

Ten dogs that did not take part in any previous tests participated in Experiment 3. The mean age of the dogs was 5.00 years, with a range of 2 to 8 years. One dog was withdrawn from testing because it displayed an increasing level of anxiety towards the end of the tests for this experiment. The remaining dogs comprised of five males and four females of the following breeds three Collies, one

Great Dane, one Golden Retriever, one Alaskan malamute, one Labrador-Poodle cross, one Doberman, and one Irish terrier.

Apparatus

The apparatus used was identical to that of Experiments 1 and 2.

Procedure

The familiarisation phase was presented to the dogs as in previous experiments. The general procedure of Experiment 3 was very similar to the experiments carried out previously. The main difference was that in Experiment 1, no cues were presented, and in Experiment 2, hiding cues were conveyed by the experimenter in the reversal phase. In Experiment 3 the hiding cue was presented both in the prereversal phase *and* in the reversal phase. Three spatial problems were selected from the pool of nine as before, specifying the location of the two containers on the array. Throughout the experiment, the screen remained in place but the curtain was permanently raised so that the hiding cue could be seen.

The same cue as presented in the reversal phase of Experiment 2 was presented in the prereversal phase: the experimenter stood in between and slightly behind the two container locations holding bait in the hand closest to the container to be baited. The experimenter either baited the correct container and then performed a manipulation of the empty container to mimic the noise produced in the first action, or performed these two actions in the opposite order. The sequence was decided prior to testing and was counterbalanced so that three consecutive trials were not presented in the same order. Once the bait was placed inside the container, the experimenter looked to the middle of the back of the screen. The

dogs were permitted to search one location and then brought back to the starting position. This was repeated until the dog reached a criterion proportion of correct responses of 90% in 10 consecutive trials, after which the reversal phase began.

In the reversal phase, there were three conditions. These conditions specified the location of the two containers used in any given trial. In condition A-B+ the containers were placed on the locations from the prereversal phase with reward contingency reversed, and the other two conditions featured one of these locations substituted by a novel location, C or D. The reward contingencies of all conditions were the same and featured both absence of bait at A and presence of bait at B, or only one of these features (A-B+, A-C+, B+D-). One trial of each condition was presented in a random order in the first three trials of the reversal phase (termed informative trials, excluded from the main analysis), and then six trials of each condition were presented in a random order. In the prereversal phase, the number of trials to criterion and proportion of correct responses was recorded. In the reversal phase, only proportion of correct responses was recorded, as there were a fixed number of trials.

Data Analysis

The data for the prereversal phase was assessed as not normal (see Appendix 2), therefore non-parametric Freidman's test were used to assess whether there was any change in the number of trials to reach criterion before reversal. In the reversal phase, which was assessed as normally distributed, a one-way ANOVA was used to assess whether there was a difference in performance between the three reversal conditions. Specific condition performance differences were assessed using Bonferroni adjusted t-tests. Learning in the reversal phase was assessed by

comparing the performance from the first to the last session, using a paired samples t-test. Finally, in order to assess whether the dogs were using a simple strategy of searching the last location the experimenter's hand visited, the PCR in trials in which the correct location was baited last was compared to those in which the incorrect location was sham baited last. This comparison was done using a one-way ANOVA.

Results

Prereversal Phase

In Experiment 3 in the prereversal phase trials to criterion (TTC) was 13.57 (95% CI=11.41, 15.73). The TTC in session 1 was 11.56 (95% CI=9.71, 13.40) in session 2 11.00 (95% CI=8.97, 1.03) and in session 3, 1.22 (95% CI=9.71, 1.73).

K-S tests demonstrated that the data for the prereversal phase was not normally distributed (see Appendix 2), therefore, non-parametric tests were used.

To assess if there was any change in TTC across the sessions, Friedman's test was carried out on TTC in each session. There was no significant difference between the three sessions ($\chi^2(2, N=3)=2.95, ns$).

In order to find out if the dogs changed their behaviour in the prereversal phase as a result of witnessing the hiding cue (in Experiment 3), the TTC in Experiments 1, 2 and 3 were compared using Independent Samples Kruskal-Wallis test. The test found that there was a significant difference in the distribution of mean TTC across Experiments ($p<.05$), therefore, witnessing the object hiding cue altered the likelihood of searching correctly in Experiment 3.

Reversal Phase

In the reversal phase PCR was .64 (95% CI=.60, .68). Condition A-B+ had a mean PCR of .20 (95% CI=.05, .35), A-C+ was .80 (95% CI=.52, 1.08); B+D- was .75 (95% CI=.54, .96). It was predicted that if dogs used cues conveyed by the experimenter in the prereversal phase there would be equal performance in all the reversal conditions. However, if the dogs were using associative learning in the prereversal phase, there would be a significant drop in the performance in condition A-B+. This is because if the dogs were using associative learning, they would have to simultaneously override the tendency to approach A and avoid B as acquired in the prereversal phase. The other two conditions would require only one of these processes and so would be relatively easy.

The difference between the PCR in each condition was assessed using a one-way repeated measures ANOVA. There was a significant difference between the conditions ($F(2,16)=26.42, p<.001, \text{partial } \eta^2=.79$). Further analysis of the differences in PCR between the specific conditions was assessed using independent samples t-tests with Bonferroni adjusted alpha level to .016. A-B+ was significantly lower than the other two conditions (A-B+ vs. A-C+ $t(8)=6.05, p<.016$; A-B+ vs. B+D- $t(8)=6.93, p<.016$), but there was no significant difference between the two novel-location conditions A-C+ and B+D- ($t(8)=.87, ns$). A difference between the reversal conditions indicates that dogs were using associative learning in the prereversal phase when object cues were presented. It also indicates that when the reversal phase began, dogs were not able to use the object cues to avoid making errors, thus there was a lower performance in condition A-B+.

Learning in the reversal phase

To assess whether there was any change in performance in the reversal phase because of witnessing the hiding cue in both the pre- and post-reversal phases, the PCR from session 1 was compared to session 3. The mean PCR in session 1 was .60, (95% CI=.49, .72), and in session 3 it was .71 (95% CI=.62, .81). A paired samples t-test revealed that there was a significant difference between these two values (mean difference=-.11, $t(8)=-3.23$, $p<.05$, 95% CI=-.18, -.03), therefore performance increased when the dogs witnessed the cues in the prereversal and reversal phases.

Use of simple rules

Dogs have relied in the past on simple rules such as ‘search the location last visited by the experimenter’. To test for use of such a rule, the trials in which the sham bait was performed first, baiting last, were compared to the trials in which the baiting was performed first and then sham baiting last. If dogs were using the ‘last visited rule’ they would only be successful with this rule in the ‘bait last’ trials. In the ‘sham bait last trials’ the PCR was .59 (95% CI=.53, .65), and in the ‘bait last’ trials it was .69 (95% CI=.63, .75). To assess whether there was a different PCR in the sham bait last and the bait last trials, a one-way ANOVA was carried out, and it was significant ($F(1,484)=4.99$, $p<.05$, partial $\eta^2=.01$). Dogs were more likely to obtain the bait in trials in which the human hand visited the correct container last and were likely to be using the 'last visited rule' to search.

Discussion

Dogs acquired associations more rapidly in the prereversal phase, as the number of proportion of correct responses was lower when dogs witnessed the cues

conveyed by the experimenter in the prereversal phase. No matter whether cues conveyed by the experimenter were introduced in the reversal phase, or from the prereversal phase, dogs use associative learning and made more errors in condition A-B+. In this condition, dogs were unable to simultaneously overrule the tendency to approach A and avoid B, and so committed the most errors in this case. Dogs noticed cues conveyed by the experimenter in the prereversal phase of Experiment 3, and so could have acquired learned associations relating to these cues. Then in the reversal phase, the conditions presented would effectively not feature any reversal, as the cues conveyed by the experimenter continued to indicate the correct search location. This result indicates that dogs have a strong inclination to acquire associations based on spatial cues, rather than human gestures, despite the fact that dogs are able to use object cues to search for hidden objects (e.g. Gagnon and Doré, 1992; 1993).

The spatial Mediation Learning Paradigm differs from the OP tasks, but can offer some insight into the spatio-temporal abilities of dogs. In the spatial mediational learning task, there are multiple numbers of trials in the prereversal phase to encourage the animal to form some kind of learning, however in OP tasks, it is assumed that learning does not take place over the course of the experiment. Also, although the 'A-not-B' task features a change in position of the target across trials, most tasks, if they feature a number of trials, control the location of the target so that it is not consistently in the same place. Although the two types of task are slightly different, the Mediation Learning Paradigm can tell us about the perseverative error and the ability to track hidden objects using object cues. The reversal of the location of reward resembles the visible displacement task, in which an object is hidden inside a container. Stage III infants are able to successfully

locate these hidden objects, but are differentiated from stage IV infants because they commit 'A-not-B errors' (Piaget and Cook, 1954). When the location of the hidden object is changed, they cannot ignore their previous success, and despite witnessing the hiding event, search at the empty location. In Experiment 2 and 3, dogs were unable to ignore their previous success at the A location in the prereversal phase. When the food changed location in the reversal phase, they made a large number of errors, which suggests that they are unable to inhibit search where they have previously been successful, in a similar way to stage III infants.

Dogs were found to rely on the simple strategy of searching the location where the experimenter had moved her hand. In the 'sham bait last trials' performance was lower than in the 'bait last' trials, as this strategy was only effective in the 'bait last' trials. This result indicates that the dogs were using cues conveyed by the experimenter in some way, but conversely it also suggests that they consider the cues conveyed by the experimenter as potential stimuli to predict reward. Further, the large number of errors in the reversal phase of Experiment 3 suggests that cues conveyed by the experimenter are considered secondary predictors of reward to spatial associations, as dogs continued to rely on spatial associations even when they had the opportunity to learn the cues conveyed by the experimenter.

The Mediational Learning Paradigm was modified into a spatial task so that it could be used to assess the ability of dogs to override prior learning with object cues. First, the learning mode of dogs was assessed in the absence of any object cues in Experiment 1 and found that they rely on associative processes. They also do not override these learned associations when the reward contingency changes in the reversal phase. From the results of Experiment 2, it is apparent that dogs also do

not use cues conveyed by the experimenter to override spatial associations, and continued making errors in the reversal phase when they witnessed the bait being hidden elsewhere. Experiment 3 was conducted to assess whether dogs noticed the cues conveyed by the experimenter presented in Experiment 2. The cues were presented from the beginning of the prereversal phase, before any associative learning had taken place. If dogs noticed the cues, but were unable use them to override learned associations in the reversal phase, then the dogs would have behaved differently in both the prereversal and reversal phase of Experiment 3. The dogs may have been able to avoid making errors in the reversal phase if they were presented with object cues in the prereversal phase. However, the pattern of performance in the reversal phase remained the same as in previous experiments.

The possibility that dogs were ignoring the object cues presented in the reversal phase of Experiments 2 and 3 was tested by examining the effects of the number of trials to reach criterion in the prereversal phase. In Experiment 2, in which no object cues were presented in the prereversal phase, dogs took significantly more trials to reach criterion performance than in Experiment 3, in which object cues were presented. The dogs were able to use the cues to reduce the number of trials to reach criterion, so it is clear that they did notice the cues.

Two new issues arise because of presenting a spatial version of the Mediation Learning Paradigm: 1) the use of spatial frames of reference in relation to the environment; and 2) overlapping associative and inhibitive gradient effects in the space surrounding the stimuli. Dogs could either conceptualise the position of objects in the environment relating to an allocentric frame of reference (object to object, AR), or relating to an egocentric frame of reference (self to object, ER, see Fiset, Gagnon and Beaulieu, 2000). This issue becomes important when the

discrimination becomes a reversal task if dogs prefer considering object position as egocentric. This is because groups of objects that have been shifted within the environment, but retain their general organisation will be regarded as the same as the first position. Consider a pair of containers, A and B. The dog has a tendency to search A which is in the middle of the array and positioned to the left of B. If B container is moved to the other side of the array, it now becomes the left-hand container. Dogs utilising AR will continue to search the container in the centre of the array, A; with ER, the tendency is to search the container on the left, now B.

The second consideration is the discriminability of the two stimuli.

According to Spence (1936), during discrimination learning an excitatory gradient is established relating to the rewarded stimulus. Similar stimuli may also elicit an excitatory response, and the more similar the new stimulus to the initially rewarded stimulus, the more likely a response will be elicited. The same is so for an inhibitory gradient relating to a non-rewarded stimulus inhibiting a response. Thus, reinforced and non-reinforced stimuli that are very similar to one another will be very difficult for the animal to discriminate as they may elicit both the excitatory and inhibitory response. In the context of the Mediation Learning Paradigm, conditions that have containers far apart will be easier to discriminate than those that are close together. Further, response towards a container at a novel position introduced in the reversal phase of the task will be directly influenced by the distance from the rewarded and non-rewarded containers. In the first series of experiments, the paradigm presented specifically controls the distance between the container pairs so that it remains constant between conditions. In later experiments, this distance will be systematically varied so that both the effects of spatial frames of reference and associative gradients can be assessed.

Considering the importance of spatial information to dogs during associative learning, further assessment of how dogs use this information in the spatial Mediation Learning Paradigm is needed. This was not an issue encountered in previous studies using the Mediation Learning Paradigm, as the discrimination problems were non-spatial and thus stimulus position was systematically controlled (Rumbaugh and Pate, 1984; De Lillo and Visalberghi, 1994). In the spatial Mediation Learning Paradigm developed for this study, the influence of human gestures on search behaviour was assessed. If we consider that dogs can code two different types of information in spatial learning: orientation based on landmarks in the environment (allocentric) and orientation of the target in relation to the dog's position (egocentric) then there may be more than one way to learn spatial associations. Dogs can utilise both egocentric and allocentric spatial cues (Fiset, Gagnon and Beaulieu, 2000).

The frames of reference may influence the results of the spatial Mediation Learning Paradigm. The interpretation of data from the spatial Mediation Learning Paradigm relies on the comparison of the relative difficulties of the three reversal conditions. A lower performance in condition A-B+ specifically predicts the use of associative principles as guiding search as opposed to mediational strategies. If one condition is more difficult than the others are then this interpretation may no longer be supported. In Experiments 1-3, reversal of the reward contingency of the spatial problems used was based on allocentric (absolute location), but not egocentric (location relative to position of dog) frames of reference. Egocentric frames of reference may also be compared to position responses, which Spence (1936) described as "by far the most common systematic responses made by animals when first introduced to the discrimination problem"

(p439). Spence lists position responses as one of the pre-solution hypotheses animals may try before they make a successful connection between excitatory or inhibitory components in the task.

In allocentric frames of reference, or object to object cues, location A was, for instance, the fifth location on the array, approximately 60 cm from the screen, 20 cm from the edge of the mat, and so on. Location B was on another location on the array and had different distances from the various landmarks in the room. Associations based on these cues would follow as 'search/avoid container at a certain location on the array, a certain distance from the screen, wall, and edge of the mat'. However, cues based on egocentric frames of reference, self to object cues, A was for instance, the container on the left-hand side of the two containers. B was the right-hand container.

This distinction between allocentric and egocentric cues becomes important when the reversal phase begins. For allocentric cues, in all reversal conditions, the containers that were considered baited, are now empty, and vice versa. For egocentric cues, this is not so. In condition A-B+, the right-hand container is baited, so the association of the container on the left hand container, and inhibition of the right-hand container is now reversed. This is a reversal of the cues learned in the prereversal phase. But the other two containers do not follow this reversal of cues. The arrangement of the containers on the array means that in reversal condition A-C+ and B+D-, the baited container is on the same left hand side as the prereversal phase. If dogs used self to object cues and egocentric frames of reference, there was no reversal of the stimuli in condition A-C+ and B+D- in Experiments 1-3.

This procedure was a balance to ensure that each condition had relatively equal distance between the container locations. This concept is illustrated in Figure 5, but note that this does not accurately depict the distances between the containers. From the figure, in conditions A-C+ and B+D- the correct location is on the left, whereas condition A-B+ it is on the right.

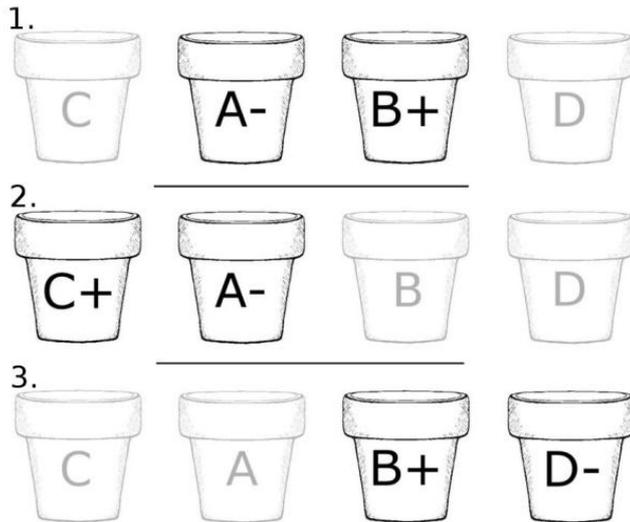


Figure 5 A representation of the arrangement of the spatial problems for Experiments 1-3. Faded containers indicate that a container was not present at this location within this reversal condition. This figure does not accurately depict the distances between the containers, which changes depending on the spatial problem.

For this reason, the nature of the spatial problems may have led to the high performance in conditions A-C+ and B+D-. This is because if dogs were primarily using egocentric frames of reference (e.g. search the container on the left) in the prereversal phase, the conditions A-C+ and B+D- would not be considered a reversal of the original reward contingency. The particular constraints involving the possible locations of the containers on the array in the pool of spatial problems specified that only condition A-B+ featured a reversal of the reward contingencies in respect to the left or the right of the animal approaching the pair of containers. It may be that only that only this condition was affected by a negative transfer of

learning, and that consequently in condition A-C+ and B+D- did not require the dogs to override associative learning to search correctly.

In order to ensure that the results in Experiments 1-3 matched the prediction that a unequal proportion of correct responses in the reversal conditions was due to the dogs being unable to override associative learning, a different kind of experiment was designed. In Experiment 4, Experiments 1 and 2 were replicated but with a variation in the arrangement of container locations to ensure that there was a transfer of learning from the prereversal phase to the reversal phase in all conditions.

Chapter 3: The Use of Spatial Cues by Dogs in the Spatial Mediation Learning Paradigm

In the previous chapters, three experiments were conducted to assess whether dogs could use cues about objects to avoid making errors in the spatial Mediation Learning Paradigm. The paradigm features the ability to distinguish whether animals override associative learning in the reversal phase, indicated by an equal performance across reversal conditions, or continue to rely on associative learning, indicated by unequal performance in the reversal conditions. The results of Experiments 1-3 found that 1) dogs use associative learning and not mediation learning (Experiment 1); 2) they cannot use object cues post-reversal to override associative learning when the hiding location changes (Experiment 2); and 3) they cannot use object cues in the prereversal phase to search for hidden food, and thus continue using associative learning (Experiment 3).

Dogs which witnessed the baiting cue at the time of acquisition in Experiment 2 were equally likely to make errors in the reversal phase to the same extent as those that did not in Experiment 1, raising the question whether they even noticed the cues conveyed by the experimenter. Yet dogs formed associations more rapidly in the prereversal phase when they had access to the cues, in Experiment 3. We can assume from these results that although the dogs witnessed the object cues in the prereversal phase, they were not able to override associative learning in the reversal phase.

The purpose of the next experiment is to replicate these results in a paradigm, which was altered to account for the possibility that the effects of

learning would not be transferred from the prereversal phase to the reversal phase equally in all conditions. For instance, in the prereversal phase, the dogs may have formed a tendency to search location A because it was always on the left. In the reversal phase this tendency to search on the left would still apply in condition A-C+ and B+D-. Consequently, these two conditions would be much easier than the test condition A-B+. The main premise of the spatial Mediation Learning Paradigm is to assess whether animals can override associative learning in the reversal phase using the cues provided and search correctly, but they may also have successfully found the hidden food because they could continue using the same tendency to search from the prereversal phase in these two particular conditions. This was not an issue encountered in previous research using the Mediation Learning Paradigm such as Rumbaugh and Pate (1984), as the discrimination problems were non-spatial and thus stimulus position was not systematically related to the position of the reward. In the spatial Mediation Learning Paradigm developed for this study, stimuli are discriminated based on their position on the array. In this way the effect of witnessing object cues relating to a particular location so dogs' search behaviour could be assessed.

In the spatial problems, the distance between the containers varied systematically within the different conditions. There is strong evidence to suggest that proximity plays a role in influencing dogs' search (Osthaus, Lea and Slater, 2005; Wobber and Hare, 2009; Pongrácz, Miklósi and Csányi, 2001). However, controlling the distance between the containers in Experiments 1-3 meant that in conditions A-B+ the baited container was on the right, and the other conditions were always on the left. Milgram, Adams, Callahan, Head, Mackay, Thirlwell and Cotman (1999) established that dogs use allocentric (landmark-based) cues in

spatial search tasks, so it was predicted that in the case of the spatial Mediation Learning Paradigm, all reversal conditions would be equal difficulty despite the alternating side of baiting. Further, Milgram et al. (1999) also remarks that dogs' reliance on these cues diminishes with growing distance from landmarks, meaning that unequal distance between containers would *encourage* egocentric coding. For these reasons, the spatial problems in Experiments 1-3 were arranged to systematically control for distance between the locations.

In Experiment 4a and 4b the pool of spatial problems was altered. The four possible locations used in the spatial problems remained the same but the arrangement of locations A to D was changed. Up until now, locations A and B had been located in the two central points of a spatial problem, and the novel locations on the outer points (from left to right C-A-B-D). This meant that each condition featured a pair of locations that were adjacent to each other, and no conditions would feature a 'gap' in between container locations where another container location may have been found on a previous trial (C-A, A-B, B-D). In the new arrangement of spatial problems, the containers were arranged in the order of A-C-D-B. In this new arrangement, the baited container was always on the same side in all conditions.

Experiment 4 assessed further the results obtained in Experiments 1 and 2, in two sub experiments 4a and 4b. Dogs were not able to override learning in the reversal phase of Experiment 2 because the performance in condition A-B+ was significantly lower than the other conditions. Experiment 4 assessed whether this difference between the conditions was because dogs had more difficulty in overriding learning in condition A-B+ than they did in A-C+ and B+D-, or, whether they did not transfer the negative effects of learning to these last two conditions. In

Experiment 4a, as in Experiment 1, no cues were presented in any trials, and in Experiment 4b, object cues were presented in the reversal phase to replicate Experiment 2.

Experiment 4: Exploration of possible confounds in the MLP

Methods

Subjects

20 dogs were recruited from the same boarding kennels as previous experiments. 10 were chosen at random and assigned to Experiment 4a. This group was comprised of four males and six females with a mean age of 4.00 (range 1 to 9 years). The breeds of the dogs were one Doberman, five Labrador Retrievers, two medium sized cross breeds, one Staffordshire terrier, and one Weimaraner.

The other 10 dogs were assigned to Experiment 4b and were five males and five females, age from 1 to 9 years. The breed types were one Border collie, one Great Dane, one German shepherd, two Labrador Retrievers, two medium sized cross breeds, one Pyrenean Mountain Dog, and two Spaniels.

Apparatus

The same apparatus used in previous experiments was used in Experiments 4a and 4b (rubber mat, screen, containers and bait).

Procedure

The familiarisation phase was the same as Experiments 1-3. The procedure of the main experiment was very similar to Experiment 1: there was a prereversal phase with two locations A and B specified by the spatial problem, and the number of trials in the prereversal phase was determined by a performance criterion of 90% in 10 consecutive trials. As in Experiments 1-3, in the reversal phase, there were

three conditions, condition A-B+ featured the locations used in the prereversal phase, and conditions A-C+ and B+D- substituted novel locations C and D in the place of one familiar prereversal location.

The revised spatial problems now featured locations A and B on the outer two locations so that from left to right the containers were arranged A-C-D-B. This meant that in each reversal condition the baited container was consistently on the left or right, and that it was opposite side to that of the prereversal phase. Condition A-B+ featured locations that were relatively far apart however, and so analysis to compare the performance in this condition in both the 'allocentric assumed' and revised 'both allocentric and egocentric assumed' spatial problems (see conclusions section of previous chapter) was carried out in the results section.

The proportion of correct responses was recorded in the prereversal phase together with the number of trials to criterion. In the reversal phase, the performance was measured as the mean proportion of correct responses in each condition of the 18 reversal trials. The first three informative trials, that were presented immediately after the reward contingency was reversed, were excluded from the main analysis as in other Mediation Learning Paradigm studies (Rumbaugh and Pate, 1984). Performance in the reversal phase was also assessed across sessions 1-3. Effects of bait order were not calculated for Experiment 4a as the hiding cue was not witnessed. To assess whether dogs were using the rule 'search container last visited', trials in which the correct container was baited last were compared with sham bait last trials.

Data Analysis

Non parametric tests were used in the prereversal phase, as the data were previously assessed as not normal (Appendix 2); parametric tests were used in the reversal phase as this data was normally distributed. Firstly, in the prereversal phase, the change in performance from session 1 to 3 was assessed using Friedman's test. In the reversal phase, the PCR in each reversal condition was compared using a one-way ANOVA, followed by post hoc t-tests with Bonferroni adjusted alpha level to compare specific condition differences.

Given the possibility that dogs may have not considered certain conditions a reversal of the original prereversal discriminus, an assessment was carried out on the PCR in the initial trials of the reversal phase. These trials had previously been omitted from the data analysis, as is common practice with the Mediatonal Learning Paradigm. The PCR in the initial reversal trials of Experiment 4 were compared with Experiment 1-3 using a one-way ANOVA. Finally, to assess the use of simple rules by searching the location last visited by the experimenter's hand, PCR in bait last trials were compared with that of sham bait last trials using a one-way ANOVA.

Results

Prereversal Phase

In Experiment 4a, in which no cues were provided at any time during the experiment, the number of trials to reach criterion (TTC) of 90% correct was 13.57 trials (95% CI=12.11, 15.02). Dogs obtained TTC in 13.40 trials in session 1, 13.30 trials in session 2, and 14.00 trials in session 3 (95% CI=9.80<lower bound<11.52,

15.21<upper bound<18.20). K-S tests demonstrated that the data for the prereversal phase was not normally distributed (see Appendix 2), therefore, non-parametric tests were used.

To assess whether there was any learning from the first to last session, the TTC of Experiment 4a was compared using Friedman's test. There was no difference between the first and third session for TTC ($\chi^2(2, N=3)=.19, ns$)...

In Experiment 4b, an object cue was conveyed by the experimenter in the reversal phase, but the prereversal phase was identical in procedure to Experiment 4a. Dogs obtained the TTC in 12.63 trials (95% CI=11.57, 13.70). In session 1 the mean number of TTC was 13.40, session 2 12.30 and session 3 12.20 (95% CI=1.39<lower bound<1.90, 13.50<upper bound<16.16). The change in performance from the first to last session of the prereversal phase was assessed for TTC using Friedman's test. There was no significant difference between session 1 and 3 TTC ($\chi^2(2, N=3)=.00, ns$). Therefore, in both Experiment 4a and 4b there was no learning across the prereversal phase

Reversal Phase

When presented with no cues post-reversal (Experiment 4a), dogs obtained a proportion of correct responses (PCR) of .50 (95% CI=.45, .54) and when hiding cues were conveyed in the reversal phase the PCR was .51 (Experiment 4b, 95% CI=.47, .56). The proportion of correct responses in each condition for the two experiments is displayed in Figure 6.

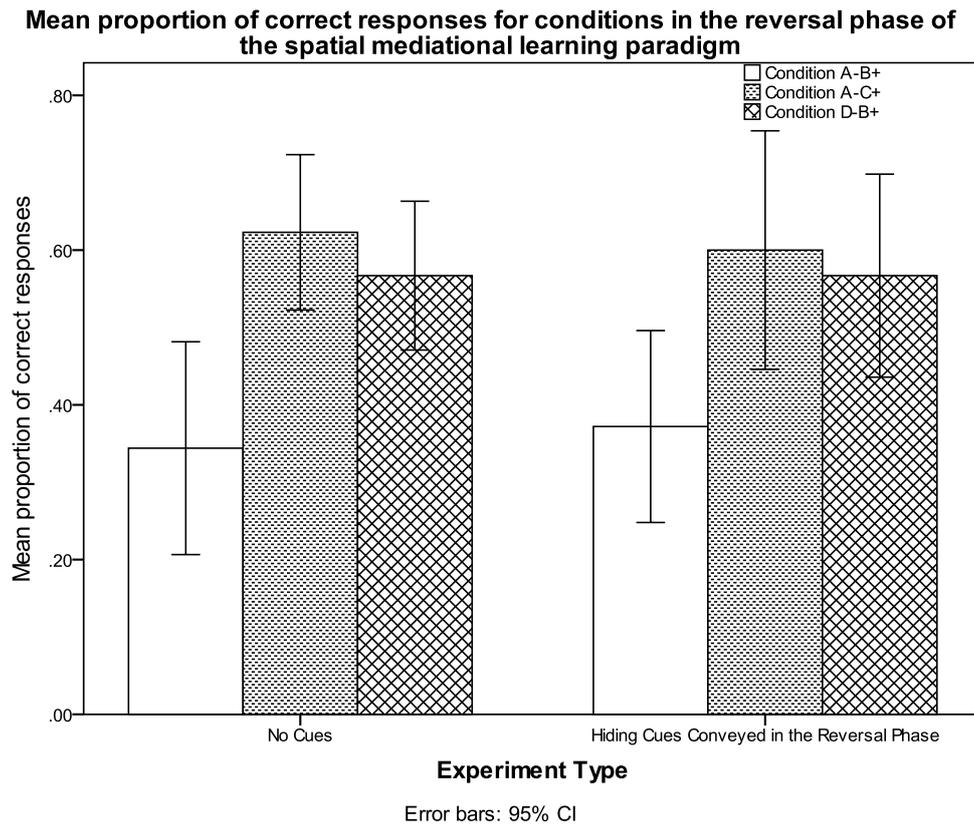


Figure 6 Proportion of correct responses following no cues (Experiment 4a) and cues conveyed by the experimenter (Experiment 4b) in reversal trials.

In previous experiments, dogs were found to rely on associative learning in the prereversal phase in Experiment 1. This is because the PCR across the reversal conditions was different. The same was true even when an object cue was presented in the reversal phase in Experiment 2.

However, the arrangement of the containers may have led some dogs to rely on choosing a location on a particular side. For instance, in the prereversal phase if the food was always found in the container on the left, in the reversal condition A-B+ the correct location is on the right. In the other two conditions, the correct location remains on the left, the same as the prereversal phase. In this case, conditions A-C + and B+D- are less difficult than A-B+. Experiments 4a and 4b were carried out to ensure that the difference between the proportion of correct

responses in the reversal phase Experiment 4 were due to the type of search strategy used, and not because the arrangement of the containers meant that some conditions in the reversal phase were not a reversal of the original discrimination. A different type of spatial problem was presented in Experiments 4a and 4b. All conditions in the reversal phase feature the correct location on the opposite side to the prereversal phase. However, the distance between the containers in each condition does not remain equal.

The proportion of correct responses (PCR) across the reversal conditions in each experiment was compared using one way repeated ANOVAs to find out if the pattern of performance from Experiments 1 and 2 remained the same with this modified arrangement of containers. In Experiment 4a, there was a significant difference of PCR among the reversal conditions ($F(2,18)=1.69, p<.05$, partial $\eta^2=.54$). Specific differences between the three reversal conditions were assessed using independent samples t-tests with Bonferroni adjusted alpha level of .016. In Experiment 4a, condition A-B+ was significantly lower than the other two conditions (A-B+ vs. A-C+ $t(9)=2.50, p<.016$; A-B+ vs. B+D- $t(9)=2.38, p<.016$) but A-C+ and B+D- did not differ ($t(9)=.27, ns$). Dogs continued to associative learning when the position of the correct stimulus was controlled.

In Experiment 4b, object cues indicating the location of food were conveyed by the experimenter in the reversal phase. As in Experiment 4a, the position of the correct container was controlled. The difference between the reversal conditions was assessed using one-way repeated measures ANOVA and there was a significant difference, ($F(2,18)=4.94, p<.05$, partial $\eta^2=.36$). Post-hoc tests were used to assess specific differences between each of the conditions using pairwise t-tests with Bonferroni adjustment. Although there was a significant difference

between the PCR in each condition, this was not demonstrated in the post hoc tests (A-B+ vs. A-C+ $t(9)=2.39$, ns; A-B+ vs B+D- $t(9)=2.07$, ns; A-C+ vs B+D- $t(9)=.34$, ns).

Learning across the reversal phase

In order to assess whether dogs increased in performance from the beginning to the end of the experiment, the proportion of correct responses (PCR) from session 1 and 3 was compared. Previously, in Experiment 1 and 2, in which the distance between the stimuli was controlled but the correct stimulus alternated side, the PCR remained the same throughout the experiment. This was true even when object cues indicating the location of food were conveyed in the reversal phase of Experiment 2. In Experiment 4a, in which no cues were presented, the PCR in session 1 was .42 (95% CI=.28, .57), and in session 3 it was .49 (95% CI=.34, .65). A paired samples t-test revealed that there was no significant difference between the two tests (mean difference=-.07, $t(9)=-.78$, ns) therefore no learning took place. In Experiment 4b, in which hiding cues were conveyed in the reversal phase, the mean PCR in session 1 was .45, (95% CI=.35, .55). In session 3 mean PCR was .59 (95% CI=.50, .68). This difference was approaching significance (mean difference -.14, $t(9)=-2.00$, ns, 95% CI=-.30, .02), however no learning took place in Experiment 4b.

Immediate performance following reward reversal

The immediate trials following reversal were excluded from analysis, as is the norm for the Mediation Learning Paradigm. However, the difference in performance in these trials in Experiments 1-3 and Experiment 4 may tell us more about the search behaviour of the dogs. In Experiment 1-3, if certain conditions were not considered reversals of the initial discriminus, then the performance in

these initial trials will be relatively high. Initial reversal performance in the Experiments 4a and 4b will be relatively low if dogs consider this new arrangement of stimulus as reversal of the original discrimination. The proportion correct responses for each experiment of the initial trials of the reversal phase are presented in Figure 7.

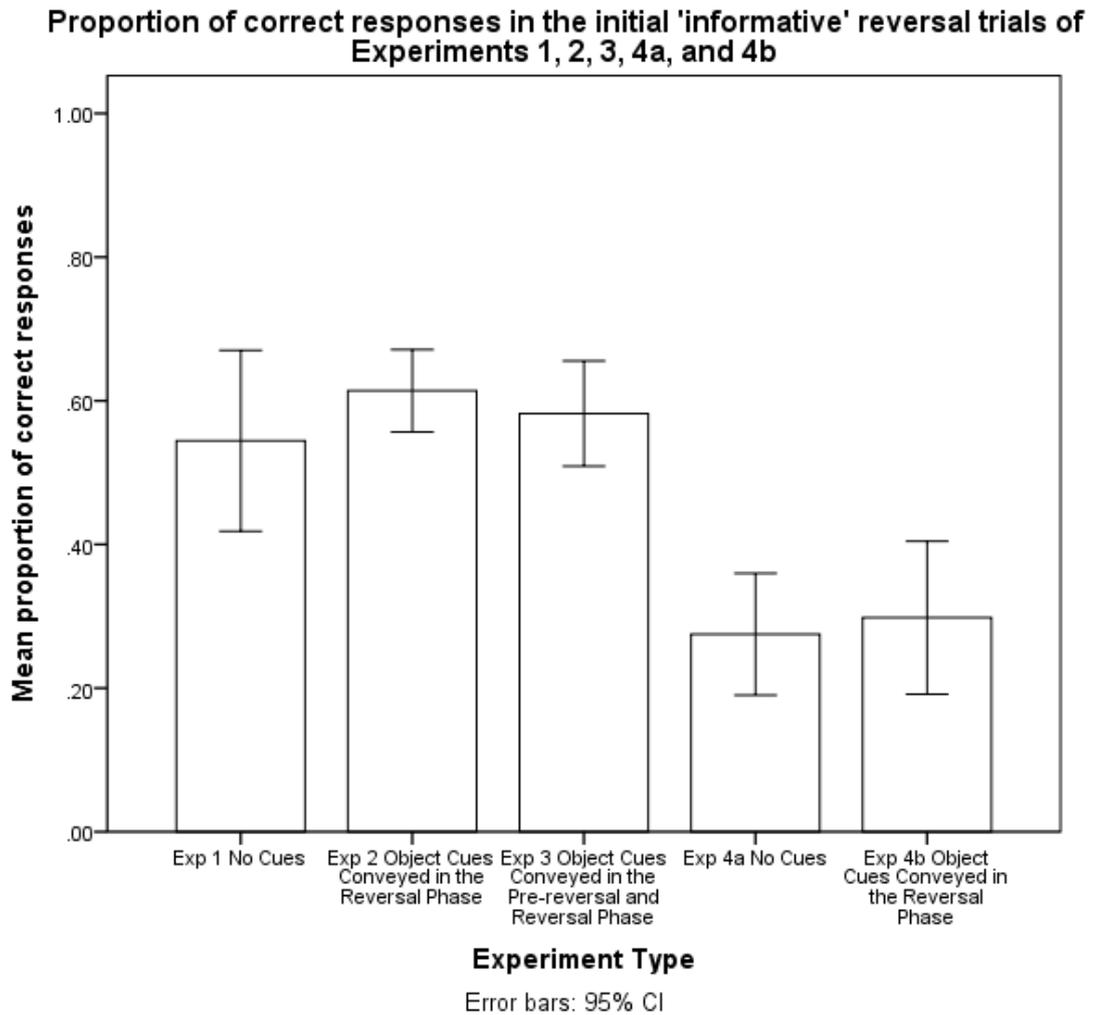


Figure 7 PCR across experiments in the initial 'informative' reversal trials. Experiments 1-3 feature spatial problems, which have equivalent distances between locations in all conditions. Experiments 4a and 4b present a revised spatial problem with a reversal of the left-right location of reward from prereversal to reversal phase

A one-way ANOVA was carried out on the PCR of initial reversal trials to assess for differences between Experiments 1, 2, 3, 4a, and 4b, and to assess whether the arrangement of locations in the spatial problems used in Experiment 4 and 4b affected initial reversal performance. There was a significant effect of Experiment ($F(4,43)=16.63, p<.05$, partial $\eta^2=.58$).

Use of simple rules

If the dogs were using a simple rule such as ‘search last location visited by human hand’, there would be more errors on those trials in which the correct location was baited first and the incorrect location sham baited last (this is only a possibility for Experiment 4b as in Experiment 4a the dogs did not witness the experimenters hand hiding the bait). The PCR in sham bait last trials in the reversal phase was .46 (95% CI=.40, .52) and in the bait last trials it was .56 (95% CI=.50, .62). To test for the use of this rule, one-way ANOVA was carried out on the proportion of correct responses in the bait last and the sham bait last trials. There was a significant difference between the two types of trial ($F(1,539)=5.48, p<.05$, partial $\eta^2=.01$) therefore, the dogs searched based on the last location visited by the experimenter’s hand.

Conclusion

There was a possibility that the difference in difficulty between the reversal conditions in Experiments 1-3 was due to the arrangement of the locations, rather than the pre-existing tendencies to search and avoid, as predicted with associative learning. The difference in difficulty across the conditions is the main means in which animals are assessed in their ability to override associative learning in the Mediational Learning Paradigm. If there is another reason that there is a difference

in difficulty between the reversal conditions, this could cloud the results. For this reason, Experiment 4a was conducted to replicate the results of Experiment 1, but accounting for the fact that dogs may have transferred negative effects of learning in all conditions. In Experiment 4a, dogs were presented with the spatial Mediation Learning Paradigm, with no cues at any time during the experiment. The possible locations the food could be hidden was changed to that of previous experiments to ensure that the results of Experiments 1-3 were a reflection of whether or not dogs could override associative learning.

Without any other additional cues conveyed by the experimenter, dogs were not able to override associative learning as they made more errors in condition A-B+ in Experiment 4a. Therefore, the reason that there was a difference between the performance in the reversal conditions in Experiments 1-3 was because dogs were not able to override associative learning in the reversal phase. There was a smaller difference between the conditions in Experiment 4a than there was in Experiment 1. This becomes important if we consider that egocentric frames of reference lead dogs to form tendencies to always search on a particular side in the prereversal phase, say for instance on the left. In the reversal phase, to search correctly they must override this tendency and search on the right. However, in Experiments 1-3, in conditions A-C+ and B+D- the correct location continued to be on the same side. Therefore, if dogs used egocentric frames of reference, conditions A-C+ and B+D- would be easier than condition A-B+. In all experiments from this point on in the thesis, *the correct location in the reversal conditions will always be on the opposite side of the array to the prereversal discrimination.*

Importantly, the conclusion that was reached in Experiment 1 that dogs do not use mediational learning is upheld in Experiment 4a. Further, Experiment 2 was

replicated in Experiment 4b, when the new altered spatial problems were presented to dogs again, this time with object cues presented in the reversal phase. In this case, as in Experiment 2, dogs were not able to use the object cues to override associative learning in the reversal phase. This result is important as dogs have demonstrated an ability to succeed in invisible displacement tasks (Gagnon and Doré, 1992; 1993; 1994), but this result was later refuted. Dogs were found to be using simple strategies such as following displacement devices, learning over successive tasks, and deriving information from the visible body parts of the experimenter (Collier-Baker, Davis and Suddendorf, 2004). The results of all the experiments so far support the notion that dogs use associative learning in object permanence tasks, as they are not able to override associative learning with the use of object cues.

Collier-Baker and colleagues (2004) were aware that associative learning may have been the reason for dogs' success in their object permanence task and monitored the change in performance across sessions. They found that there was little change in the performance from the beginning to the end of the testing sessions. In Experiment 4b, there was no difference between the proportion of correct responses in the first test to the last test. This suggests that dogs were not using associative learning in relation to the object cues. Additionally, it appears that dogs developed a simple strategy. There was a tendency to search the location last visited by the experimenter in Experiment 4b. This is not a new discovery (Collier-Baker, Davis and Suddendorf, 2004; Gagnon and Doré, 1992; 1993; 1994). However, this is not the only way in which dogs were able to solve the task: even the 'sham bait last' trials in which the location visited last was empty led to an above chance PCR, so dogs were able to use other strategies to find food. Only a

few dogs may have been relying on this strategy, but this is unclear from the results.

It has been suggested that the reason for dogs' skills in the use of cues conveyed by human may originate from sensitivity to human body gestures, paired with an ability to rapidly form associations (Collier-Baker, Davis and Suddendorf, 2004). In Experiments carried out in this thesis, dogs failed to use the object cues as part of a learned association to predict the location of the food. They continued to make errors in the A-B+ control condition, despite seeing the experimenter place the food in the correct container. This is resonant with perseverative error that children, who are yet to reach stage IV object permanence, also commit. Dogs persist in searching where they have previously been successful, even in cases where they are provided with all the information necessary to search in the correct location.

Topál et al. (2009) replicated this situation in a search task. The experimenter repeatedly hid a toy behind screen A and allowed the dog to search for it. Then the toy was hidden behind the other screen, screen B. In three conditions, the experimenter hid the toy whilst carrying out either ostensive-communicative cues, no cues, or hid the toy by manipulating devices without any human interaction. Dogs in the non-human interaction condition had a preference to choose the B screen, and correctly search for the toy. However, dogs in the ostensive-communicative condition persisted in searching the A screen, despite seeing the experimenter explicitly hide the toy behind the B screen. These dogs, which had been presented with overtly communicative cues, committed more perseverative error than those dogs, which had seen the toy move on its own behind the screen. This suggests that it is the communicative nature of the cues presented

at the time of hiding that leads dogs to commit perseverative errors, and that with communicative cues removed, dogs are better able to inhibit a prior response to search where they were previously successful.

It is unclear whether associative learning plays a role when dogs follow *communicative cues* from humans. In addition, there are mixed views about whether dogs perform better in social or non-social tasks. Up until this point, Experiments 2-4 have featured object cues, whereas the following experiments will explore the influence of communicative cues on the ability of dogs to override learning. Experiment 5 was carried out to assess whether dogs can override associative learning by using communicative cues presented in the reversal phase.

Chapter 4: The Effects of Communicative Cues Conveyed by Humans

One interpretation of why dogs have such a good ability to use human cues to find food is that the animals form associations between the hand and correct location of hidden food (Elgier et al., 2009; Reid, 2009; Udell and Wynne, 2010). Experimenters assessed whether dogs used associative learning to follow human communicative cues in several ways. One study, the results of which initially endorsed the idea that dogs can follow human communicative cues without associative learning, indicates the opposite when the results are fully explored. Agnetta, Hare and Tomasello (2000) suggest that the skill of dogs to use human gestures *does not* stem from learning because dogs they tested were able to search correctly when a marker object (a sponge), was placed in front of the object hiding location. Agnetta and colleagues expected that the dogs would be able to interpret this ‘marker only’ placement as a communicative gesture. Agnetta, Hare and Tomasello (2000) interpret their findings to mean that dogs follow markers as communicative cues, and because the marker sponge is a totally novel cue to the dogs, that they must not be using associative learning in search.

However, in conditions in which the human experimenter was not seen to manipulate the marker, rather that it ‘appeared’ behind a screen, the dogs were not able to follow this marker cue. The authors stated that the marker was the object that the dogs interpreted as communicative, but this ‘marker appears’ condition suggests that it is the movement of the experimenter’s hands that the dogs followed. Therefore, we cannot claim that dogs follow totally novel cues, marker objects, as

communicative cues. Agnetta, Hare and Tomasello (2000) still affirm that their hypothesis is supported even though in the marker appears condition, which was presented before and after the other marker conditions, performance was significantly below chance.

In fact, in a later study, Riedel, Buttleman, Call and Tomasello (2006) systematically reduced the contact of hand with marker, and recorded a fall in search performance in marker search tasks. Dogs saw either a whole human placing a marker, the hand placing the marker, or the marker on its own next to the correctly baited container. The less of the experimenter the dogs could see, the lower their performance was. This suggests that dogs could not interpret the marker as communicative, as suggested by Agnetta, Hare and Tomasello (2000). However, these marker search tasks do not seem to be able to claim conclusively that dogs do not use associative learning in search.

The interpretations of the marker studies rely on the assumption that if dogs can follow inanimate marker objects such as a sponge block, they can also follow human communicative cues without associative learning. However, the results of these studies are confusing, or do not support the theory that dogs can follow marker objects.

More complex forms of human gestures have been used to assess whether dogs utilise simple rules, or associative learning in following human cues to find food. In Lakatos et al. (2011) there were multiple individuals presenting pointing gestures indicating the correct container. The task featured four containers, with two experimenters standing at the array each pointing at a different container. Only one experimenter indicated the correct location of the hidden object. The dog's

owner stood next to the dog facing the array and pointed to the experimenter who pointed to the correct container. Only 5 of the 23 dogs tested with this procedure were successful at searching the correct location at a level of performance above the chance level of 25% correct. The dogs were able to follow their owners and searched near the correct experimenter, but could not always select the container that the experimenter pointed towards. Of the dogs that correctly followed their owner's pointing towards the correct experimenter, there was no preference to choose the correct container. This experiment was interesting as it introduced a series of interconnected pointing gestures, and could potentially assess whether dogs were able to interpret the gestures, or if they used simple strategies. However, even if the dogs were able to interpret the communicative cues, they may not be able to piece together all the relevant information in a meaningful way. This type of procedure also does not adequately answer whether dogs use associative learning in following human gestures.

Research suggests that dogs' skills in object search are limited when there are no communicative cues present. Dogs were not able to distinguish whether a task was social or non-social in nature and successfully use this information to help them complete the task. A reversal discrimination was performed in either a social or a non-social version, and was tested on both chimpanzees and dogs (Wobber and Hare, 2009). In the social version of the task, bait locations were distinguished by two different experimenters holding identical bowls. The non-social version featured two bowls, which differed in colour. The findings suggest that dogs cannot use social information to find successfully food, and that learning takes place even in tasks that provide social information. Both species took the same number of trials to reach criterion in the prereversal phase of both tasks. However, in the reversal

phase the chimpanzees found the food in more trials in the social task than in the non-social task. The dogs, who found the food in trials less overall than chimpanzees, performed equally in the reversal phase of the social and non-social task. The dogs were equally as likely to find the food in the trials in which the information provided in the task was social or non-social. The chimpanzees performed better in the reversal phase when the information provided was social in nature than when it was non-social. Further, learning analysis of the first and last 10 trials of the reversal phase demonstrate that the chimpanzees did not increase their performance in the social condition, but they did increase performance in the non-social condition. For dogs, the performance in *both* non-social and social conditions increased from the first to the last ten trials of the reversal phase. This indicates that even in the social phase learning took place in dogs. For the chimpanzees, their performance remained constant throughout the reversal phase, suggesting that no learning took place and the chimpanzees processed the social information from the very beginning. It would appear from these findings that the ability to process social information from humans in dogs may be formed on the basis of associative learning.

Interestingly, the non-social and social conditions did not differ because the dogs could not tell when the context had changed. If this is the case, the fact that chimpanzees did have a different reversal performance suggests that unlike dogs, they are more sensitive to changes in the social situation. According to the results of this study, dogs are as likely to override learning when communicative and object cues are presented in the reversal phase of the Mediation Learning Paradigm.

The experiments reported in this chapter use a variation of the spatial Mediation Learning Paradigm described in the previous chapters to elucidate the relative role of human communicative cues and associative processes in dogs search for hidden objects. Using a procedure similar to that adopted in the studies in chapter 1, dogs were obliged to form spatial associations between location and food hidden in one of two containers, with no other cues available. Then once the reversal phase began and the food was hidden in the other location, dogs were presented with a communicative cue indicating the correct location of the food.

In the previous series of experiments, it was apparent that dogs could not overcome the effect of previously acquired spatial associations even when they witnessed the baiting of a different container in the reversal phase of the spatial Mediation Learning Paradigm. These cues conveyed the action of baiting (the sight of the bait, the hand holding the bait moving inside the container, and emerging from the container empty) and as such provided all the information necessary to successfully locate the hidden bait. Yet the dogs persisted in searching where they had previously been successful despite witnessing the bait being hidden elsewhere. The purpose of Experiment 5 is to assess whether communicative cues from humans during the reversal phase of the Mediation Learning Paradigm allow dogs to avoid overriding the effects of associative learning observed in the experiments reported in previous chapters.

In the next experiment, communicative cues were presented post-reversal. No cues were visible to the dogs in the prereversal phase, and the baiting of containers took place behind a screen. The screen was raised to allow the dog to search correctly. Once a criterion performance was met, the reversal phase began and the three reversal conditions A-B+, A-C+ and D-B+ were presented. In the

reversal phase, the baiting of the containers was now witnessed by the dog. Also, during the reversal phase, a communicative cue was presented at the time of baiting. If dogs were able to use the communicative cue to override associative learning in the reversal phase, performance in all the reversal conditions would be equal. However, if the dogs persisted in using associative learning, performance in the condition which featured the locations from the prereversal phase, A-B+ would be significantly lower than the other two conditions.

Experiment 5: Effects of communicative cues conveyed by humans on dogs' search

Methods

Subjects

As in previous experiments, 10 dogs were recruited from a commercial boarding kennels. There were 6 males and 4 females with a mean age of 4.00 (range 1 to 9 years). The breeds of the dogs were 1 German Sheppard, 1 Terrier, 1 Boxer, 1 Lurcher, 1 Spaniel, 3 Labrador Retrievers and 2 medium sized cross breeds. One dog was taken ill before the final test could be administered and this dog's data was not included. The dogs in these experiments did not take part in any previous experiments

Apparatus

The apparatus was the same used in all previous experiments, and featured 12 points marked in a semi-circular shape on a black rubber mat, a screen with retractable curtain in the lower section, and two identical containers. Inaccessible bait was located in each container in the way of a pair of stacked containers. Manipulation of the unbaited container occurred as before. The screen remained in place for the duration of the baiting and search and prevented involuntary body cues such as posture and gaze from the experimenter from being conveyed to the dog.

Procedure

The procedure was similar to Experiment 4. Dogs were permitted to explore the equipment for 3 minutes. Over three trials dogs were familiarised with obtaining the bait from inside one of the containers and also with the movement of the curtain. During the experiment, correct search was recorded when the dog retrieved the bait from inside the baited container using either mouth or paw, or if the dog positioned its head above the container to look inside. An incorrect search was recorded if the dog placed its mouth or paws in contact with the container, or looked over the top of the container to see inside. Following an incorrect search, the dog was taken back to the starting position and was not permitted to search in the remaining correct container.

There was a prereversal phase and a reversal phase. Spatial problems specified which 4 of the 12 points on the array were used, and also identified specific points as A-D. Problems were selected from the same pool of 9 used in previous experiments. In the prereversal phase, the two containers were placed on the A and B locations of the array. In the reversal phase all four locations were utilised as part of the reversal conditions.

In the prereversal phase the curtain was lowered during the hiding cue so it was not witnessed by the dogs, and then it was raised for search. The performance criterion was 9 out of 10 correct responses in 10 consecutive trials. When the criterion was met the prereversal phase ended and the screen was removed from the testing area.

In the reversal phase a communicative cue was presented (see Appendix 3 for all the different types of cues used in this thesis). A point and gaze cue towards

the to-be baited container was performed immediately prior to the hiding cue, which was also witnessed. In the cue, the pointing hand protruded sideways approximately 15cm from the body and approximately 15cm from the container. The non-pointing hand was held flat against the side of the body. The cues were presented for approximately 2 seconds, then the hiding cue took place (placing the food in the baited container and manipulating of the non-baited container in a randomised order, but in the same order on more than 2 consecutive trials). During the hiding cue the experimenter looked at the relevant container whilst it was being baited or manipulated. Once the hiding cue was finished, the experimenter looked towards the dog. The dog was then released and allowed to search. Three informative trials were presented, one for each condition (A-B+, A-C+, B+D-, randomised) and then the test phase of 6 trials of each condition was presented. Conditions were presented not more than twice consecutively.

Data analysis

As the data collected during the prereversal phase was found to be not normal (see Appendix 2), non-parametric Friedman's test was used to compare the performance across the three sessions. In the reversal phase, of which the data was normally distributed, a one-way ANOVA was used to compare the PCR in the three reversal conditions. As in the prereversal phase, chance in PCR across the three sessions was compared to assess for learning throughout the experiment. This was done using a paired samples t-test. Finally, use of the simple strategy 'follow the last location visited by the experimenter's hand' was assessed by comparing the PCR in bait last and sham bait last trials, using a one-way ANOVA.

Results

Prereversal Phase

In the prereversal phase of Experiment 5, no cues indicating the location of food were conveyed by the experimenter. The mean number of trials to criterion (TTC) in the prereversal phase was 15.72 (95% CI=13.26, 18.19). In session 1 the mean TTC was 16.50 (95% CI=1.54, 22.46), session 2=17.00 (95% CI=12.45, 21.557), and session 3=13.00 (95% CI=1.26, 15.74). The data was assessed for normality using K-S tests and it was found to be not normal, therefore non-parametric tests were used for the main assessment (see Appendix 2). To test whether there was any change in performance over the three sessions, Freidman's test carried out on TTC in sessions 1-3. There were no significant differences between the three sessions ($\chi^2(2, N=3)=2.51, ns$).

Reversal Phase

In the reversal phase, the mean proportions of correct responses for each condition are displayed in Figure 12. To assess whether dogs were able to override prior learning in the reversal phase by following the communicative cue, the PCR of the three reversal conditions were compared. If the PCR in the three conditions was equal, this would signify that the dogs used the communicative cue, as there was equal difficulty whether the conditions featured locations from prior learning in the prereversal phase, or if the conditions featured novel locations. If, however the dogs continued to use associative learning to guide search and were not able to follow the communicative cues, the control condition A-B+ would be more difficult than the other two conditions. Therefore, if the PCR across the conditions is equal

the dogs were able to override associative learning, but if the PCR is unequal, associative processes prevailed as the search strategy.

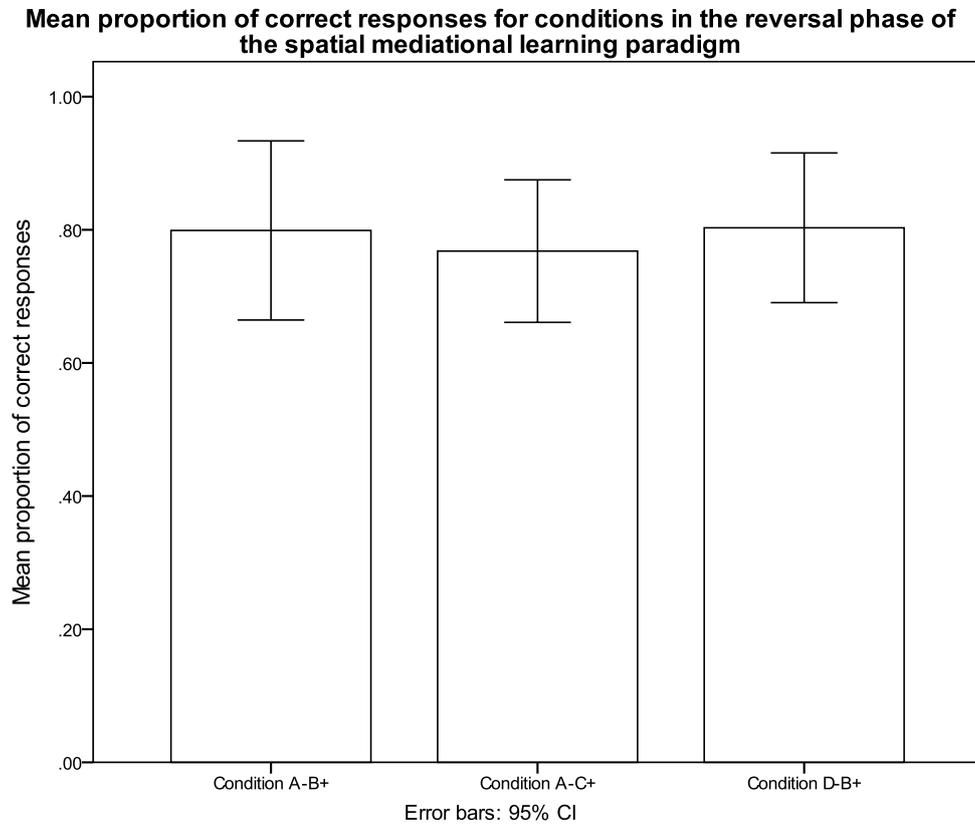


Figure 8 Mean proportion of correct responses when presented with a communicative cue.

The difference in PCR across the conditions was compared with paired sampled t-tests. There were no significant differences between the conditions (A-B+ and A-C+ mean difference=.03, $t(9)=1.00$, *ns*; A-B+ and B+D- mean difference=-.00, $t(9)=-.09$, *ns*; A-C+ and B+D- mean difference=-.04, $t(9)=-1.05$, *ns*). The dogs were able to override associative learning and follow the communicative cue.

Learning in the reversal phase

Three test sessions were presented to each dog. To assess whether there was any change in performance over the course of the sessions a result of witnessing the

communicative cue, the proportion of correct responses in the reversal phase of session 1 was compared to that of session 3. The mean PCR in session 1 was .92 (95% CI=.86, .97) and in session 3 it was .77 (95% CI=.57, .97). A paired samples t-test was carried out on the PCR of session 1 and 3 to assess for differences and it was not significant (mean difference=.15, $t(9)=1.65$, *ns*).

Immediate performance following reward reversal

The first trial in each condition of the reversal phase was excluded from the main analysis, as is standard practice for the Mediation Learning Paradigm (Rumbaugh and Pate, 1984). However, these trials may indicate whether dogs followed the communicative cue from when it was first presented, or if they gradually began to follow the cue when they were unsuccessful in search. If the dogs continued to use associative processes and ignored the communicative cue in the first trials, the PCR will be significantly below chance. The PCR in the first three trials was .59 (95% CI=.43, .75). A one-way ANOVA was carried out on this figure to assess whether it differed from Experiment 4b, in which a non-communicative object hiding cue was presented. It found there was a significant difference $F(1,19)=12.08$, $p<.05$, partial $\eta^2=.40$). Dogs were much more likely to find the bait in the very early reversal trials when they saw the communicative pointing cue, than when they saw the object hiding cues in Experiment 4b.

Use of simple rule 'last location visited by human hand'

To test the possibility that dogs may have been searching based on the last location visited by the experimenter's hand, the proportion of correct responses (PCR) in trials in which the correct container was baited last was compared to the trials in which the incorrect container was sham baited last trials. The PCR in 'bait last' trials in the reversal phase was .83 (95% CI=.78, .87) and in 'sham bait last'

trials it was .81 (95%CI=.76, .86). A one-way ANOVA revealed that there was no difference between PCR in sham bait last and bait last trials ($F(1,522)=.28, ns$).

Therefore, the dogs were not searching based on the last location visited by the experimenter's hand.

Conclusion

This experiment was carried out to test whether communicative cues from humans would be sufficient for dogs to overcome spatial associations. Previously, it has been shown that object cues conveyed by the experimenter alone are not sufficient to achieve this. It was predicted that with a communicative component included in the cue, dogs would ignore the no longer relevant learned associations and correctly search for the bait. Incidentally, we know that they had acquired associations in the prereversal phase, as they obtained the training criterion of 9 out of 10 trials correct in 10 consecutive trials, as in previous experiments.

This prediction was confirmed by the fact that the performance in the three reversal conditions was equal. Regardless of whether the condition featured locations from the prereversal phase, or featured novel locations the dogs performed the same in the reversal phase. The additional cues provided to them were the communicative point and gaze cue. The dogs were able to use these cues to override the learning that had taken place in the prereversal phase.

One illuminating finding was the performance in the first informative reversal trials. In these three trials, dogs were informed that the reward contingency had changed. In the baseline experiment, in which no cues were presented in the reversal phase, the dogs only had the outcome of the trial to inform them of the change. As a result, the informative trials were below chance performance, as the

dogs had not had enough instances to redress the learned associations. In Experiment 4b, where object cues were presented in the reversal phase, performance in the informative trials at the beginning of the reversal phase were the same as when no cues were presented. Dogs continued to behave in the same way as when no cues were presented. Either they did not notice the object cues, or they were not able to change their behaviour accordingly.

In the case of Experiment 5, when communicative cues were presented in the reversal phase, dogs had immediate cues as to the new location of food, and could search correctly from the very early trials. In the first informative trials of the reversal phase of Experiment 5, the dogs performed above chance levels.

Further, in Experiment 5 with communicative cues, there was no increase in this performance across sessions 1-3. This suggests that this ability was at its peak from the very beginning of session 1 and remained the same throughout the experiment. This is a further difference between the dogs who saw object cues in Experiment 4b, and those who saw communicative cues in Experiment 5.

In summary, the findings from Experiment 5 were as follows. There was equal performance across the conditions in the reversal phase, which means that when presented with a communicative cue, dogs considered all conditions equal difficulty. They were able to override the spatial associations they had made in the prereversal phase. There was no learning across the three sessions and also performance was high from the very first trials. This suggests that the processes dogs use when following human communicative cues do not involve learning.

What it is about the communicative cue that allows dogs to overcome the spatial associations, where they were not able to with non-social object cues

conveyed in Experiment 4b? We must consider the possibility that the two types of cues were not of the same duration, and this may be the reason why dogs behaved differently in the reversal phase. The communicative cue presented in Experiment 5 was longer than the object cue, and so this may be the reason why dogs were able to override learning in Experiment 5. The next experiment will present an object cue of the same duration as the communicative cue to assess whether the length of cue was the reason why dogs could override learning. If dogs presented with an object cue of a longer duration can override learning in the reversal phase of the Mediation Learning Paradigm, then we must reassess the results of Experiment 5. In this case, dogs may not discriminate cues based on whether they are communicative or non-communicative, but the salience of the cue, for instance cue duration. In the next experiment, a non-communicative object cue of the same duration as the communicative cue in Experiment 5 was presented in the reversal phase of the Mediation Learning Paradigm.

Experiment 6: The influence of cue salience on dogs' search

In the following experiment, we can achieve three aims using the spatial Mediation Learning Paradigm as a tool: 1) to assess whether dogs can overcome spatial association with a non-communicative cue, 2) to assess the strength of human gaze as a cue, and 3) to test whether the longer duration of the communicative cue in Experiment 5 was the reason for dogs' ability to override learning.

The first aim will be achieved by presenting a non-communicative cue post reversal. If dogs can override learning with non-communicative cues, can use immediate information to make decisions about where to search, and can ignore no-longer relevant associations, the performance across the reversal conditions will be similar. It may be however, that the process of domestication has equipped dogs with a special human cue-sensitivity, and that this ability (witnessed in Experiment 5) is limited to the communicative domain only. If this were the case, when presented with a non-communicative cue of the same duration, dogs will not attain equal performance across the reversal conditions.

Closely linked to the first aim is 2) in which the upper body of the experimenter will be hidden during the baiting phase, in order to gauge the contribution of the gaze cue towards the high performance in Experiment 5. Without the gaze cue, we may see the performance in this experiment fall, as we have seen from the literature review that gaze alone is not sufficient to indicate the location of food, but that provided together with a point cue, it augments the strength of the communicated message. Also, it is apparent that responsiveness

towards the gaze cue increases over time, as learning was seen in the reversal phase of Experiment 5. In the following experiment, we may see an absence of this increase in performance across trials, within or between sessions, as there is no gaze cue provided.

Aim 3) is intended to match the circumstances of the communicative cue in Experiment 5, in order to assess whether the longer duration of the communicative cue in Experiment 5 was in fact the reason for high performance, and not the communicative nature of the cue. The cue presented in this experiment will be of the same duration as the cue in Experiment 5, but will be non-communicative in nature. If it is the longer duration of cue that provides sufficient information for dogs to overcome associations, we will notice equal performance across the conditions; if it is the communicative context of the cue, we will notice dissimilar performance.

Methods

Subjects

10 dogs were recruited from the same commercial boarding kennels as in Experiment 1-5. There were 3 males and 7 females, with mean age 5.3 years (range 1 to 10). The dogs were of the following breeds: 2 Border Collies, 2 Dalmatians, 1 Great Dane, 2 Retrievers, 1 medium cross breed and 2 Spaniels.

Apparatus

The apparatus was the same as described in experiments 1-5, including the rubber mat with 12 locations marked in a semi-circular array, the screen and

baiting-obscuring curtain and 2 opaque plastic containers with inaccessible bait at the base to provide olfactory cues.

Procedure

The locations chosen for the spatial problems were the same pool as previous experiments, and the outer two of these four were used in the prereversal phase. The same performance criterion of 90% in 10 consecutive trials at which point the reward contingency switched (and the reversal phase began) was used. As before, in the reversal phase there were 3 conditions, 1 condition featuring the original prereversal pair, and two others featuring novel locations paired with each of the original pair.

The procedure for the familiarisation and prereversal phase were the same as Experiment 1-5. In the prereversal phase, the curtain was lowered during baiting so that no cues were provided as to the location of food. Baiting was visible in the reversal phase. In Experiment 5, in order for the full body communicative cue to be witnessed, the entire screen was removed from the room. In this experiment, the screen remained for the duration so that only the lower section of the experimenter was visible for baiting.

The 'explicit object cue' for this experiment was as follows: the experimenter stood in between the two containers facing the dog. The bait was held in the hand the same side as the container to be baited. Either the baited container was baited first or the unbaited container was manipulated first. For the baiting, the bait was held with fingers and thumb in clear sight of the dog 15cm above the container (and the same distance from the body of the experimenter) for 2 seconds. This was the same duration and position as the pointing cue in the communicative

gestures of Experiment 5. In the manipulation of the unbaited container, the inside pot was picked up and dropped to make a sound similar to the baiting of the baited container. The order that these two trials were presented was controlled so that one type of trial did not occur more than twice consecutively.

Data Analysis

As in previous experiments, the data in the prereversal phase was not normally distributed, therefore non parametric a Freidman's test was used to assess change in performance (PCR) across the three sessions. In the reversal phase, the PCR across the reversal conditions were compared using a one-way ANOVA. Change in performance in the reversal phase was assessed by pair samples t-tests to compare PCR in session 1 and session 3. Immediate performance in the reversal phase was compared with previous experiments using a one-way ANOVA. Finally, to assess the possibility that dogs may have simply been searching the last location visited by the experimenter, PCR in bait last trials was compared with that of sham bait last trials using a one-way ANOVA.

Results

Prereversal Phase

The mean number of trials to criterion (TTC) and proportion of trials correct in Experiment 6 was 16.13 (95% CI=13.51, 18.76). In session 1 the mean TTC was 22.30 (95% CI=14.16, 3.44), session 2=14.30 (95% CI=1.03, 18.57), and session 3=13.60 (95% CI=11.52, 15.68). To test whether there was any change in performance over the three sessions, Friedman's test was carried using TTC in

sessions 1-3. There was no significant change in performance ($\chi^2(2, N=3)=1.14$, *ns*).

Reversal Phase

The mean proportion of correct responses (PCR) for each condition is displayed in Figure 9 (right hand cluster). In order to assess whether the dogs were able follow the explicit object cue and override prior learning, the PCR across the three reversal conditions of Experiment 6 were compared. If, as in Experiment 4a, in which no cues were presented, the dogs continued to rely on associative processes, the reversal conditions would have unequal difficulty. Alternatively, if dogs can use the explicit object cue to search correctly, the performance across the reversal conditions will be equal. To find out which of these strategies the dogs were using in search, a one-way ANOVA was carried out to assess for differences across the reversal conditions. There were no significant differences between the PCR of the three conditions $F(1,9)=.62$, *ns*). Therefore, the dogs were able to override associative learning with the explicit object cue.

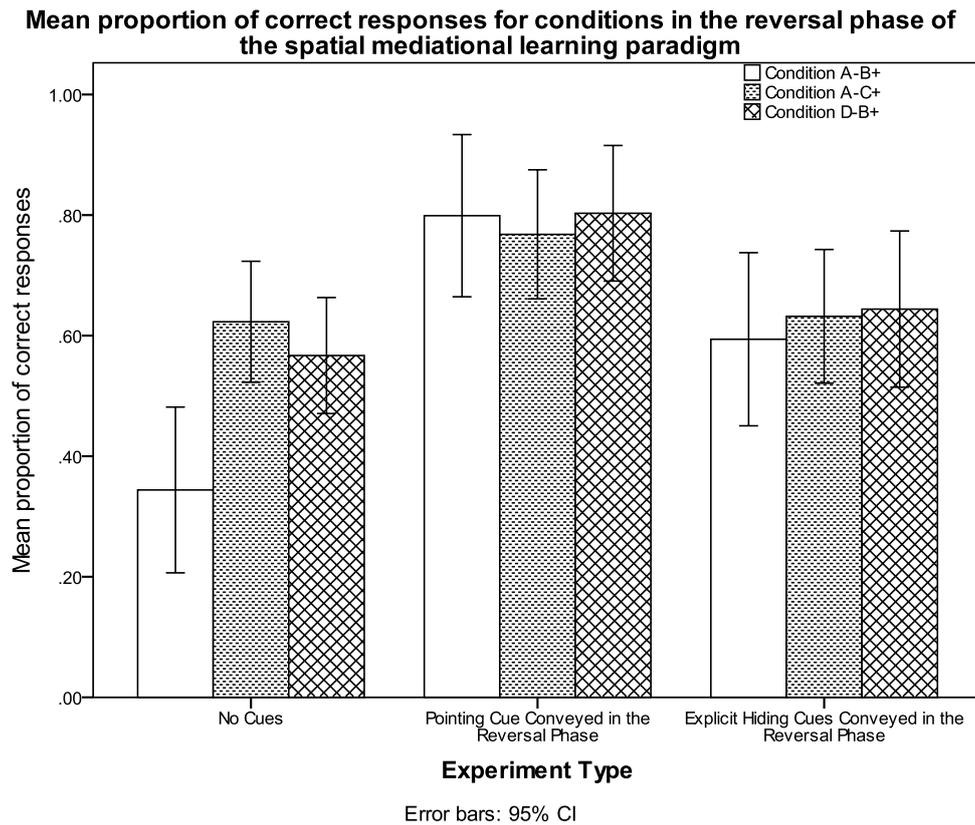


Figure 9 A comparison of the proportion of correct responses in Experiment 4a (no cues), Experiment 5 (communicative cue post-reversal) and Experiment 6 (Explicit hiding cue in reversal phase).

Learning in the reversal phase

In the first session of Experiment 6, the mean proportion of correct responses was .66 (95% CI= .53, .78), and in the final session it was .58 (95% CI=.47, .68). A paired samples t-test was carried out to assess whether there was a change in performance over the course of the experiment, and therefore if learning took place. The test was not significant (mean difference=.08, $t(9)=1.50$, *ns*). No learning took place over the course of the experiment when the dogs witnessed the non-communicative explicit object cue.

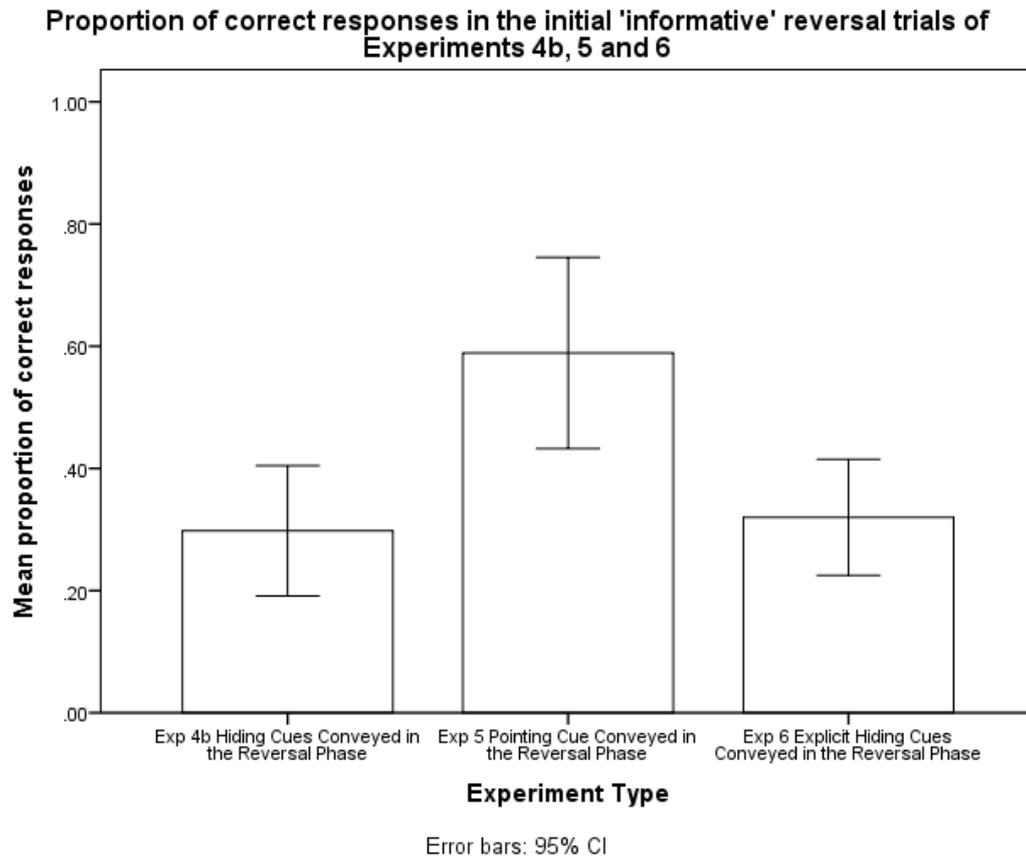
Immediate performance following reward reversal

Figure 10 Graph representing the PCR in the initial reversal trials following the presentation of object cues (Exp 4b), pointing cues (Exp 5) and explicit hiding cues (an object cue with the matched duration of the pointing cue, the current Exp 6).

In order to assess the effect of presenting an explicit object cue on the initial trials of the reversal phase (which were excluded from the main analysis), a one-way ANOVA was carried out on the PCR of the initial trials of Experiments 4b (object cue, same spatial problem), 5 (pointing cue) and 6 (the current experiment). There was a significant effect of Experiment type on PCR ($F(2,29)=8.98, p<.05$, partial $\eta^2=.07$). Post-hoc LSD tests revealed that Exp 6 was significantly different to Exp 5 (mean difference=.27, $p<.016$) but did not differ from Exp 4 (mean difference=.02, *ns*). Therefore, dogs' performance was much higher from the very beginning of the reversal phase when they witnessed a pointing cue, but

performance in comparison was very low following either an object hiding cue or explicit object hiding cue.

Use of simple rule 'last location visited by human hand'

In order to test whether dogs were guiding search based on a simple rule to search the location the experimenter's hand had visited, the proportion of correct responses (PCR) in bait last and sham bait last trials was compared. The PCR in sham bait last trials was .64 (95% CI=.58, .70) and in bait last trials it was .61 (95% CI=.55, .67). A one-way ANOVA revealed that there was no significant difference between these two values ($F(1,539)=.64, ns$), therefore the dogs were not following last location the experimenter's hand visited.

Conclusion

The purpose of this experiment was threefold: 1) to assess whether dogs could overcome associations with a non-communicative explicit object cue, 2) to weigh up the strength of gaze as a cue from humans, and 3) to match the duration of the communicative cue with a hiding cue alone to test whether this was the reason for dogs' high performance.

The first point was resolved when it was found that the performance across the reversal conditions was equal. When presented with the non-communicative explicit object cue, of the same duration as the communicative cue, performance in the three conditions was equal. In other words, in the presence of explicit object cues, dogs were both able appreciate that the cue presented was more relevant to the search and to ignore the associations formed previously. On a parallel, this finding also indicates that dogs were able to avoid making A-not-B errors, where previously, when presented with object cues conveyed by the experimenter alone in

Experiment 4b, they were not able to. This suggests that in the case of explicit object cues conveyed by the experimenter, dogs are able to ignore their previous success and follow more relevant cues.

This was the same pattern of performance as in Experiment 5, when dogs were presented with a communicative cue: the performance across the conditions was equal. However, the overall performance dropped in Experiment 6 when a non-communicative cue was presented. This could be for a number of reasons, namely, that the explicit hiding cue did not feature gaze. The head of the experimenter was blocked by the screen both during the hiding cue and also during the search when the dog was released. In the previous experiment, in which the gaze cue was presented, the experimenter used the gaze cue to draw attention to the baited location, and gazed towards the dog during search to continue the communicative exchange. This may have impressed on the dog that something of interest was in this container, and that the dog had to perform some action to obtain the food. Without this gaze cue, the dog may have not appreciated fully that the explicit object cue was indicating something of interest, but was merely conveying the sight of the bait. Witnessing the cues conveyed by the experimenter may have been sufficient for the dog to overcome the spatial associations and lead to equal performance in the conditions. But the further elevated performance we saw in Experiment 5 may have been as a result of the extra communicative information, in which the dog was more motivated to search for the food.

Secondly, the drop in performance in this experiment following the absence of a communicative cue may have been as a result of the lack of directional information in the point cue, and to a lesser extent, the gaze cue (gaze cues alone are only sufficient for a small proportion of dogs to follow, McKinley and

Sambrook, 2000; Miklósi et al., 1998). The communicative cue also indicated direction which the explicit hiding cue did not. This could be the reason for the drop in performance, perhaps because the dogs resorted to the old spatial associations in some cases when they could not interpret specific information in the cue to guide them to the correct location, only that they interpreted something of importance in the hiding cue.

The type of cue presented affected the number of trials required to reach reversal criterion in the prereversal phase. When the cue presented in the reversal phase was communicative, the number of trials to criterion in the prereversal phase did not change across sessions. We may have expected that if dogs see a communicative cue they may either a) come to rely on the cue in the reversal phase, not form spatial associations and thus acquire associations in the next session quicker; or b) expect to be presented with an immediate informative cue in the prereversal phase, not rely on the outcome of a trial, and subsequently take more trials to acquire the association. However, it was the prereversal phase of Experiment 6 in which a change in TTC was recorded. When the dogs saw the explicit object cues in the reversal phase, they reached the training criterion more rapidly towards the end of the experiment. It is unclear why this result was observed, but can perhaps be taken as an indication that the explicit object cue was considered differently to both the communicative cue of Experiment 5 and the shorter object cue of Experiment 4b.

It is unclear the extent to which whether or not the cues conveyed by humans in Experiment 5 and 6 were communicative influenced the ability of dogs to override associative learning and correctly search for the hidden food. It may be that the communicative cue in Experiment 5 conveyed more 'social information',

and for this reason led the dogs to perform well in the reversal phase. Or, it may be that the dogs were not able to distinguish that the point cues in Experiment 5 were communicative and the extended cue conveyed by experimenter in Experiment 6 was not, and the difference in performance in the reversal phases of these experiments was simply due to the salience of seeing the whole body of the experimenter. This may also explain why dogs were able to override associative learning in the experiments in Experiments 5 and 6, where they were not able to in Experiments 1-4: the cues in the latest experiments were longer in duration and provided more information for the dogs to override the associations.

Reducing the communicative component of the explicit object cue in Experiment 6 led to the same pattern of results in the reversal phase as in Experiment 5. When a non-communicative explicit object cue was presented however, the overall performance was lower. Because both the cues were conveyed by humans, they may have been perceived by the dogs as communicative. In fact, in Wobber and Hare (2009), the dogs did not differentiate between ‘social’ and ‘non-social’ conditions. The experimenters differentiated between the conditions based on the information that the humans provided, yet both conditions featured humans as interacting with the apparatus.

In experiments in this thesis, the experimenter’s body was obscured by a screen from the waist upwards, but the lower half of the body and particularly the arms were visible. It may be that dogs succeeded in correctly searching in the majority of the reversal trials because they used the proximity of the extended hand to the baited container, even though in this case the cues were designed to minimise social cues. For this reason, the following experiments will *remove social cues*

entirely to assess the ability of dogs to utilise non-social cues to override learned spatial associations.

The next experiment will assess the ability to override learning when presented with purely non-social physical cues. The cues featured in the next experiments will not feature any cues conveyed by humans, but will convey the location of the hidden food by using transparent containers in the reversal phase.

Chapter 5: Effects of Physical Cues

In the previous experiments reported in this thesis, the ability of dogs to overcome associative learning using a variety of cues conveyed by humans has been explored with a modified spatial version of the Mediation Learning Paradigm. Dogs were unable to override associative learning using object cues presented, but when communicative cues were presented, the dogs were able to override prior learning. What was the nature of these cues that led dogs to avoid making errors in most of the trials? Some researchers suggest that it is the social characteristic of these cues that makes dogs' search performance so effective when they witness pointing and other types of social gestures (Brauer et al., 2006). Bräuer et al., (2006) developed a series of experiments assessing the effectiveness of social and causal cues in dogs and apes. The dogs were most effective in correctly searching for food when they had to follow explicitly communicative cues conveyed by humans such as 'point' and 'look'. However, they were less effective in utilising causal cues, for example, when the experimenter shook the empty container to show that it did not make any rattling noise. These results suggest that dogs rely heavily on the social characteristics of cues.

In other tasks, dogs' search performance is also adversely affected when social cues are controlled. Collier-Baker, Davis, and Suddendorf (2004) performed an invisible displacement task with systematically controlled (but not removed) social cues. For example, in one condition the displacement device was removed completely from the search array area. Dogs' performance was drastically reduced, indicating that one of the primary cause of success was to use a rule based on where the experimenter had left the displacement device. Similarly, in 'social dog-causal

ape' study of Bräuer et al. (2006), dogs showed a strong preference for searching containers that the human experimenter had manipulated. In the 'noise empty' condition, the empty container was picked up and shaken to produce no sound. Instead of searching the correct container, most dogs searched the empty container that had been touched.

Research has also demonstrated that it is ostensive-communicative information in cues from humans, which leads dogs to make *more* errors. Topál et al. (2009), the A-not-B error was induced in dogs by repeatedly hiding a toy behind screen A, and then hidden behind screen B in a test phase. When the toy was hidden by the experimenter, and accompanied with ostensive social cues, dogs committed perseverative error and continued to search behind the A screen even when they had seen it being hidden behind the B screen. However, another condition featured the toy being hidden without any human interaction with the object or screens, and in this case in the B trials, the dogs search correctly without making perseverative errors. Presenting the ostensive-social cues meant that the dogs were unable to inhibit tendency to search where they had previously been successful.

In Experiment 5 of this thesis, dogs benefitted from ostensive communicative cues. They were able to override associative learning when they witnessed communicative cues. Unlike the Topál et al. (2009) study, the dogs were able to inhibit tendency to search at the A location. Interestingly, when the communicative cue was removed, but a non-communicative object cue with the same longer duration was presented, dogs were still able to override associative learning. This outcome suggests that cues with a communicative component improve the ability of dogs to inhibit associative learning.

Object permanence (OP) tasks with transparent screens or containers have been used to characterise different cognitive requirements of OP tasks (see Shinskey and Munakata, 2001). Piaget and Cook (1954) established that infants under the age of 12 months failed to search for objects hidden by a soft cloth and in turn interpreted that infants were unable to maintain a perception that the object existed once it was no longer visible, or in other words, ‘out of sight, out of mind’. Yet Bower and Wishart (1972) elaborated on this interpretation by presenting visible ‘hidden’ objects behind transparent barriers. Children that had failed to search for objects hidden with opaque containers succeeded in the same task with transparent containers. A second experiment was carried out in which objects were initially visible to infants, and then the lights were turned off. All 12 infants, who had previously failed to reach out for an object covered with an opaque container, reached out in the dark for the object. Based on the results of these two experiments, it was concluded that ‘out of sight out of mind’ is not an accurate interpretation of why young infants are unable to search for hidden objects (Bower and Wishart, 1972).

From the results of Experiment 2 and 4b, in which object cues were presented in the reversal phase, it appears that dogs are not able to process object cues. This is because they were unable to override associative learning in the reversal phase using the object cues. They may have been using associative learning to solve the OP tasks presented by the early researchers who initially rated them very highly (Gagnon and Doré, 1992, 1993, 1994; Triana and Pasmak, 1981). The implication from Topál et al. (2009) is that social information can negatively affect the ability of dogs to inhibit prior responses as they commit more perseverative errors when humans perform the object displacements in OP-like

tasks. Perhaps if the instance of human interaction was removed in the Mediation Learning Paradigm, dogs will be able to override learning in the reversal phase by using object cues. An ideal type of cue to use is hiding objects behind transparent barriers, such as presented in Bower and Wishart (1972).

Transparent barriers have been used to assess the ability of dogs to track objects hidden behind transparent barriers, however there are only a small number. Only one unpublished study (cited in Miklósi, 2007) has tested dogs in a non-social transparent containers discrimination. Dogs were presented with a search task with two identical transparent containers, in which bait was hidden randomly inside one or the other. In the small number of trials (fewer than 20), dogs were not able to successfully obtain the food in the majority of cases. They rapidly formed a preference to search in one of the containers as this resulted in success in approximately half of the trials. This is consistent with the results of the experiments of this thesis, as dogs rapidly formed spatial associations in fewer than 10 trials. Yet it is unclear how dogs use the visibility of bait inside transparent containers in a reversal paradigm.

Another study was carried out to assess dogs in following the sight of food behind transparent barriers; however, this paradigm involved social cues. An experiment by Kunder, De Los Reyes, Arbuthnot, Allen, Coshun et al. (2010) was designed to assess if dogs could ignore dishonest points and find food hidden behind transparent barriers. The containers were either transparent or opaque, and the human experimenter conveyed points in a dishonest manner towards the empty container. To correctly search for the bait on the visible trials, dogs had to ignore the dishonest point gestures, and follow the sight of the bait inside the correct transparent container. Or, on the more difficult not-visible trials, ignore the point

cue, infer that the transparent container was empty, and the food hidden in the opaque container. Results were mixed: the dogs were more likely to find the bait when it was placed in transparent containers than opaque containers, when a short duration dishonest point was made. However, when the dishonest pointing gesture conveyed was longer the dogs were as likely to choose the empty container. Importantly, in the conditions in which no cue was presented, dogs were more likely to choose the correct container when the containers were clear and the bait was visible. It appears that this information takes precedence over human pointing, but only when the point gestures conveyed are of a short duration.

We have seen from Experiments 1-3, that dogs show a strong preference for spatial association as a means to search for hidden objects. They are able to utilise human gestures, particularly pointing to override these learned associations to avoid making errors when the reward contingency is reversed. However, the extent to which dogs require the presence humans to be able to effectively use the cues is not clear. In the following experiment, a completely non-social cue indicating the correct location of hidden food was provided to dogs in the reversal phase of the spatial Mediation Learning Paradigm. Dogs could either 1) continue to utilise associative learning established in the prereversal phase, in which no cues were provided as to the correct location, or 2) override the no-longer relevant learned associations and follow the cue of the bait visible through transparent containers. In the case of 1), dogs would need to simultaneously overcome a tendency to both approach A and avoid B, making the reversal condition featuring both these locations the most difficult. In the instance of 2) performance in all reversal conditions should be similar as the visible cue of the bait in all conditions is equally indicative of the presence of food at the baited location.

In addition, to assess whether dogs utilise the visible cue of the bait inside the transparent container via associative learning, the procedure includes three enclosure conditions. The level to which the bait is contained within the transparent container is varied from completely enclosed, partially enclosed, to not enclosed. If dogs are unable to perceive objects as existing once they are enclosed within other container, the more the bait is enclosed within the container, the more difficult the reversal phase of the task will be. Dogs may learn to associate the sight of food inside the transparent container as a predictor of food, in which case we can predict an increase in performance in the reversal phase from the first to the last session. However, if dogs consider the food as hidden behind a transparent barrier and can use this to override associative learning, from the very early trials dogs will make few errors from the very early reversal trials.

Experiment 7: Effects of physical non-social cues on dogs' search

The spatial Mediation Learning Paradigm was modified to include transparent containers in order to assess whether dogs could use the sight bait to override associative learning. This is an alternative method used to assess tracking of objects in early object permanence (OP) tasks in infants (Bower and Wishart, 1974). It is also an opportunity to assess whether dogs are able to override associative learning when there is no human interaction involved in the procedure. In the prereversal phase, the containers were opaque (bait not visible) so that associations we made between the location and reward in the absence of any cues. In the reversal phase, the containers were transparent so that the food became visible from the dog's location. The dogs did not witness the food being hidden and so the only cue available was the sight of food visible through the containers. If dogs are able to find the food from this cue, they should be able to override associative learning and search correctly in all reversal conditions. However, if the dogs cannot follow this cue to find the food and they continue to rely on associative learning, they will make most errors in condition A-B+.

In addition, we assessed whether dogs noticed the transparent barrier at all. There were three conditions in which the food in the reversal phase was either fully enclosed, partially enclosed, or not enclosed. In the 'Fully Enclosed' condition, the bait was placed inside one of the containers at the base, in the 'Partially Enclosed' condition the food was placed on a ledge so that half the piece of food protruded from the top of the container, and in the 'Not Enclosed' condition, the bait was placed directly in front of the container on the rubber mat. This type of cue is similar to those provided in very early level OP tasks, in which infants are assessed

in their ability to reach for visible objects. This condition should be the most likely condition for dogs to override associative learning. The ‘Partially Enclosed’ condition reflected mid-level OP tasks in which the ability of infants to track partially obscured objects is assessed. Dogs may be able to override associative learning in the reversal phase of this condition if they are able to track partially hidden objects.

Methods

Subjects

Due to time limits and the large number of conditions presented to each dog, only five dogs were tested, of which two were females, and three males. The mean age was 5.80 years (range 7.00 years). The breeds were one Dalmatian, two Great Danes, one Boxer and one Rough Collie.

Apparatus

The rubber mat, with white semi-circular spatial array marked in white, was used, as was the screen to obscure the experimenter during the hiding phase of each trial. The containers were plastic clear circular tubs 15cmx15cm purchased from a florist supplier. Covers were constructed out of white laminated paper, which was wrapped around the sides of the pot to completely hide all the internal contents. These covers could easily be removed in the reversal phase of the experiment in which bait was required to be visible. At the base of each container was a perforated white laminated circle, which hid a piece of inaccessible bait. Additionally, two clear circular laminated sheets could be fitted inside each of the containers to create an internal shelf to elevate the bait outside the top of the

container for certain conditions. The clear shelves were attached with clear tape to the inside of the white laminated covers.

Bait was large, flat, soft meat flavoured dog treat 2cm x 6cm. Inaccessible bait was hidden inside each container to provide scent cues at each location.

Procedure

All dogs had taken part in previous experiments involving the spatial Mediation Learning Paradigm, but not in the experiments involving pointing cues. The dogs were familiar with the equipment so no familiarisation phase was presented beyond three minutes of free exploration of the room where the testing took place.

The spatial Mediation Learning Paradigm was presented using opaque containers (not clear) in the prereversal phase and transparent containers in the reversal phase. A screen obscured the experimenter from the waist up, and was lowered during the baiting of the containers. Dogs wore a collar with a 1.5m lead attached, and were positioned by an assistant facing the screen, behind which was the array and the experimenter. The containers were fitted with opaque laminated covers and so bait hidden inside was not visible except from directly above. Behind the screen, and with blind lowered, the bait was positioned inside one container and the two containers were placed on the spatial array at two particular locations, as determined by the spatial problem (see below). The curtain was raised and the dog was released and allowed to search. Once the dog had made a choice the other container was picked up so it could not be explored. The outcome of the trial was recorded by the experimenter, then the dog was guided back to the starting position.

The position of the containers on the search array was determined by the spatial problem, which was chosen at random before the session (see Experiment 4). The possible locations A-D remained constant over the spatial problem but on any given trial the containers were placed on only two locations. In the prereversal phase only locations A and B were used, and A was always baited (A+B-). In the reversal phase the three conditions included all four locations with reward contingency opposite to the prereversal phase (A-B+, A-C+, D-B+).

In the prereversal phase the proportion of correct responses was monitored. Once the dogs obtained the bait in 9 out of 10 consecutive trials the prereversal phase ended and the laminated container covers were removed.

The three reversal conditions A-B+, A-C+, and D-B+ were presented. As in previous experiments, one trial of each condition was presented in a random order, then the proceeding trials were six trials of each condition, with no more than two consecutive trials of the same condition. The first three reversal trials of each session were excluded from the main analysis as in previous studies (these trials acted to inform the dog that the reward contingency had changed).

All tests featured two opaque containers in the prereversal phase and two transparent containers in the reversal phase. There were three types of test sessions based on the level to which the bait was enclosed within the transparent container during the reversal phase. Sessions were either 1) Fully Enclosed, with bait positioned inside the transparent container; 2) Partially Enclosed, in which bait was positioned on a ledge so that it protruded out of the top of the container; and c) Not Enclosed, in which bait was positioned *outside* the container leaning against the

front side of the container nearest the dog. Each dog was presented with three sessions for each enclosure condition in a random order (nine tests altogether).

Data Analysis

In previous experiments, the data in the prereversal phase was not normally distributed (see Appendix 2), therefore, Freidman's test was used to compare the TTC across the three sessions. In the reversal phase, a one-way ANOVA was used to assess for differences in the PCR between the reversal conditions. The use of simple strategy 'follow the experimenter's hand' did not apply in this experiment, as baiting was not visible prior to search. The change in PCR from session 1 to session 3 in the reversal phase was assessed using a paired samples t-test. Finally, the initial reversal performance was assessed by comparing the initial PCR with Experiment 4 and 5 (which had the same spatial search problem arrangements) using a one-way ANOVA.

Results

Prereversal Phase

The mean number of trials to reach criterion (TTC) in Experiment 7 for each enclosure conditions were as follows: Fully Enclosed=14.27 (95% CI=9.97, 18.56), Partially Enclosed=13.20 (95% CI=8.91, 17.49), Not Enclosed=12.63 (95% CI=1.65, 14.62). K-S tests demonstrated that the data for the prereversal phase was not normally distributed (see Appendix 2), therefore, non-parametric tests were used.

To assess whether there was any learning from sessions 1-3, Friedman's test was carried out on the TTC in each condition. In all conditions, there were no changes in performance (Fully Enclosed $\chi^2(2, N=3)=1.53, ns$; Partially Enclosed $\chi^2(2, N=3)=.15, ns$; Not Enclosed $\chi^2(2, N=3)=4.13, ns$).

Reversal phase

The mean proportion of correct responses for trials in all reversal condition and enclosure condition was .84 (95% CI = .82, .86). For the Fully Enclosed condition, the mean PCR in all conditions was .84 (95% CI = .80, .87); for Partially Enclosed condition it was .83 (95% CI = .79, .87); and for the Not Enclosed condition it was .84 (95% CI = .81, .88). The PCR in each reversal condition of all bait enclosure conditions is presented in Figure 11.

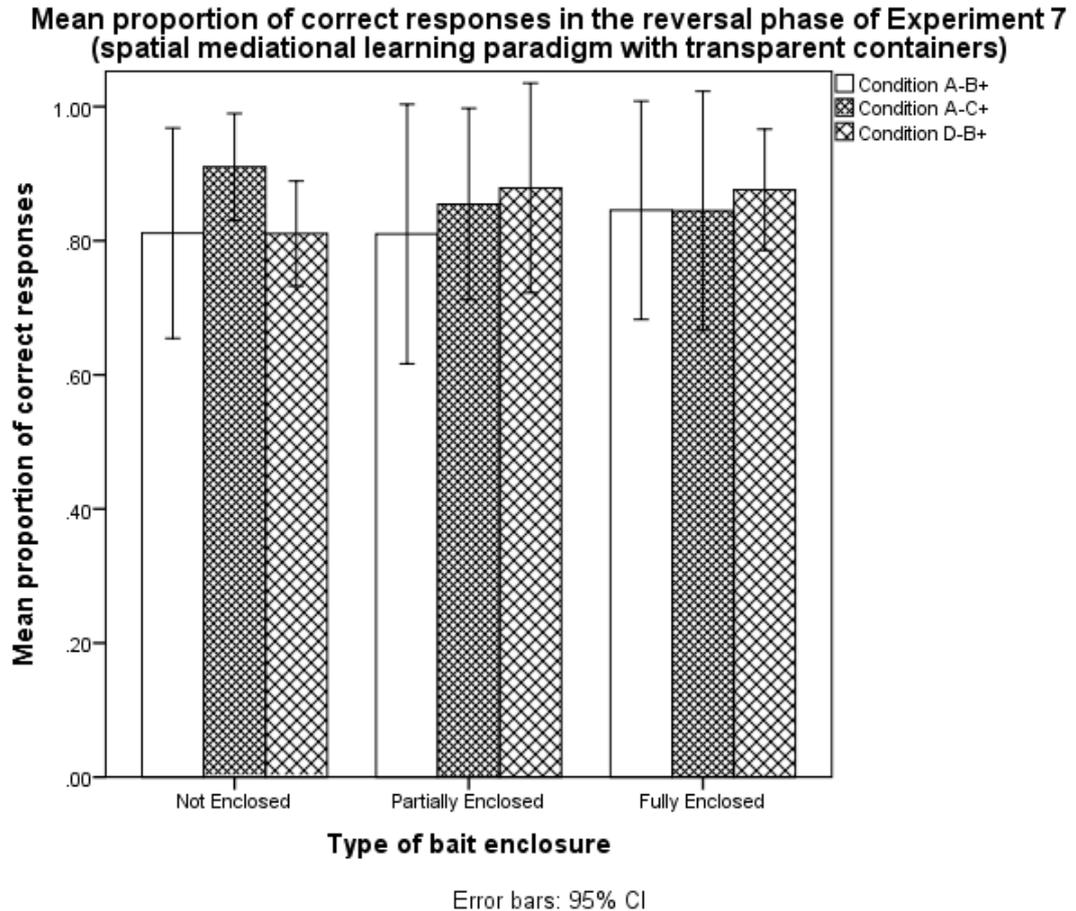


Figure 11 PCR in the reversal phase of Experiment 7, in which transparent containers were presented in the spatial Mediational Learning Paradigm. The groups of bars represent the bait enclosure condition, and the different colours indicate the reversal condition.

There were two hypotheses tested in this experiment. The first was that if dogs were able to use the visible bait (through transparent barriers) to correctly search for the bait and override associative learning in the reversal phase, then the performance across the reversal conditions would be equal. However, if they continued to rely on associative learning to guide search, they would make more errors in the control condition A-B+. This would be indicated by a significant difference between the performance in the reversal conditions. Secondly, in previous experiments, dogs benefitted from the additional information provided by the communicative cues presented in the reversal phase. If this same effect of

salient cues extends also to the non-social physical cues, then performance would be highest in the conditions in which the food was most obvious and not enclosed inside the container. Therefore, if dogs were able to use the more salient physical cues to increase their chances of searching correctly, then performance in the Not Enclosed condition would be significantly higher than the other conditions.

The effect of reversal condition and bait enclosure condition on the proportion of trials correct was assessed using a repeated measures ANOVA with a 3 reversal condition x 3 bait enclosure, within-subjects model. There was no significant effect of reversal condition ($F(2,16)=1.64, ns$), of bait enclosure condition ($F(2,16)=1.28, ns$) nor was there a significant interaction of reversal condition and bait enclosure condition ($F(4,16)=.47, ns$). Based on these results, dogs were able to override associative learning when the containers were transparent and they could see the bait. However, the salience of the physical cues had no effect on the dogs, as the performance in all the enclosure conditions was equal.

Learning in the reversal phase

To assess whether there was any increase in performance over the three test sessions, the proportion of correct responses in the first session was compared to the last session. In the first test session of Experiment 7, the proportion of correct responses observed in the reversal trials was .80 (95% CI=.67, .95). This rose to .85 in the third session (95% CI=.71, .98). A paired samples t-test was carried out to assess whether there was an increase in search performance from the beginning to the end of the experiment, which would indicate that some learning had taken place. The test was not significant ($t(14)=-1.76, ns, 95\% CI=-.12, .01$). This sample was very small, but we may suppose that no learning took place across the sessions.

Immediate performance following reward reversal

As in previous experiments, the first three trials of the reversal phase were excluded from the main analysis, as they acted to inform the dogs that the reward contingency had changed. This data is useful in assessing whether the dogs used the visible bait to override prior learning from the very beginning, or if they began to use this physical cue only after associative learning had proven ineffective. If the performance in the initial trials was significantly different to chance (.5), the dogs were using associative processes to guide search and were committing a large number of errors. The proportion of correct responses in the first three trials in all enclosure conditions was .58 (95% CI=.48, .68). In the Not Enclosed condition the PCR was .60 (95% CI=.49,.71), Partially Enclosed .58 (95% CI=.46,.70) and Fully Enclosed .56 (95% CI=.46,.66).

In order to compare performance immediately following reward reversal, PCR in the initial reversal trials was compared with Experiment 4b, in which an object hiding cue was presented. This Experiment also featured the same spatial problem as Experiment 7. A one-way ANOVA was carried out on the PCR in the initial trials by Experiment and it found that there was a significant difference between Experiments ($F(3,24)=4.92, p<.05$, partial $\eta^2=.02$). Post-hoc LSD tests showed that Experiment 4b was significantly lower than all conditions in Experiment 7 (Not Enclosed mean difference=.30, $p<.016$; Partially Enclosed mean difference=.28 $p<.016$; Fully Enclosed mean difference=.26, $p<.016$). The three conditions within Experiment 7 did not differ significantly from one another. This meant that upon witnessing any of the cues presented in Experiment, dogs were more likely to correctly search for the food, than when they saw the object hiding cue in Experiment 4b.

Conclusion

Experiment 7 was designed to assess whether dogs used the visibility of bait to override prior learning in the spatial Mediation Learning Paradigm. In Experiment 2, an object cue showing the bait being hidden inside the correct container was not sufficient for dogs to override prior learning. When communicative cues were presented to dogs, they were able to override prior learning. In Experiment 5, a non-communicative object cue of a longer duration also allowed dogs to override learning. This suggests that increasing the salience of cues conveyed increases the chances of overriding associative processes as a search strategy. The results of Experiment 7 support the notion that dogs are able to override spatial associations with non-social physical cues. The dogs all achieved a learning criterion in the prereversal phase without any kind of cues (the containers were opaque at this stage). When the dogs saw the bait hidden inside transparent containers in the reversal phase, they were able to avoid making errors in the reversal phase. The performance across all three reversal conditions was equal.

Experiment 7 was designed to assess whether dogs could override spatial associations using cues which had no social characteristics. To determine whether the ability of dogs to override spatial learning was limited to following social cues, dogs were presented with a non-social, non-communicative cue in the reversal phase of the Mediation Learning Paradigm. The physical cues took the form of visible bait inside transparent containers, and they varied in their explicitness in that the food was either enclosed inside the transparent container, partially enclosed, or not enclosed placed in-front of the container.

The second aim of Experiment 7 was to assess whether or not the salience of the physical cues had an effect on the proportion of correct responses in the reversal phase. In the 'Not Enclosed' condition, which featured the most salient cue to the bait location, reversal performance was the same as 'Fully Enclosed' and 'Partially Enclosed' conditions. The dogs used the not enclosed, partially enclosed and fully enclosed physical cues equally in the reversal phase to override learned associations. If dogs struggled to use the sight of bait in the less conspicuous 'Fully Enclosed' condition to search for the food, we may have seen a drop in the most difficult condition, A-B+, when the least salient physical cue, the 'Fully Enclosed' condition was presented. Yet performance across all reversal conditions and all enclosure conditions was equal. It is worth noting that the small sample size of this experiment may be the cause of this negative result, but in general, the results of Experiment 7 indicate that dogs are able to override spatial associations when provided with cues about the physical organisation of objects.

Dogs could override learning when they could see the bait inside transparent containers. Were the dogs able to infer that the sight of bait inside a transparent container indicated the food location had changed? The performance in the initial reversal trials of Experiment 7 was equal to that of Experiment 5, when a communicative cue was presented in the reversal phase. In all other experiments, performance in these initial trials had been very low. This suggests that the communicative cues and the bait visible inside transparent containers had similar effects on dogs' search. It is perhaps useful to further understand the level to which dogs processed the physical cues presented in Experiment 7. In the next experiment, the ability of dogs to utilise the sight of bait inside transparent containers in a non-reversal discrimination was be assessed.

Experiment 8: Can dogs find bait hidden in plain sight?

In this final experiment, the tendency of dogs to utilise the sight of bait inside transparent containers to search correctly in a spatial discrimination was assessed. Dogs show a strong inclination to form spatial associations (Elgier et al., 2009) and may use these as a means to guide search (Shapiro, Janik, and Slater, 2003). Dogs also commit errors in search that would imply that they are using associative learning during object permanence tasks (Collier-Baker, Davis and Suddendorf, 2004), however, some researchers have noted the negative effects that social cues can have on dogs' ability to inhibit perseverative errors (Topál et al., 2009). Additionally, infants that previously were not able to pass certain object permanence tasks were able to perform much better when transparent barriers were used (Bower and Wishart, 1972). Given that dogs were not able to pass higher-level object permanence tasks, they may perform much better searching behind transparent barriers.

In Experiment 7, dogs were able to override associative learning searching for food hidden inside transparent containers. However, they had formed spatial associations in the absence of any cues (as the containers were opaque in the pre-reversal phase), and this task was a reversal paradigm. To carry out a clearer assessment of dogs' ability to pass object permanence tasks with transparent barriers, a non-reversal discrimination was carried out.

In Experiment 8, the position of the bait hidden inside transparent containers was constantly changed so it was never in the same location more than two consecutive trials. The ability of dogs to search for food hidden inside transparent containers was assessed by presenting a discrimination search task with transparent

containers. Dogs did not see the human place food inside the correct container and so no human interaction with the equipment took place. The correct hiding place alternated between the containers to reduce that chance that dogs did not make any associations between a particular location and reward. Three conditions were presented which varied the salience of the cues: the bait was placed either inside the container, partially inside the container or outside the container.

Methods

Subjects

Five dogs with mean age 4.20 years (range 4.00 years, 95% CI=2.36, 6.04) took part in Experiment 8. There were four males and one female. There was one boxer, two Dalmatians, one Great Dane, and one Collie.

Apparatus

The dogs' starting position and semi-circular array were marked on the rubber mat. The screen and horizontal blind were positioned in-between the starting position and the array. Two large transparent containers as described in Experiment 7 were used. In addition, in certain conditions, a clear laminated circle the same diameter of the interior space of the containers was attached horizontally in the middle of the space inside the containers. It was secured with clear tape in several places and acted as a shelf to hold the bait protruding out of the top of the container.

All types of containers featured a white opaque laminated circular sheet inside the base, secured with tape, to create an inaccessible space in which bait was hidden to provide scent cues at both containers.

Procedure

There were three different enclosure conditions: Enclosed, Partially Enclosed and Not Enclosed. In the Enclosed condition, the bait was placed inside the container leaning against the side nearest the dog. In the Partially Enclosed condition the container featured a transparent laminated circular sheet attached horizontally inside, creating a shelf on which the bait rested. The bait was placed inside the container on the shelf leaning against the side nearest the dog, so that approximately half of the bait was visible directly over the top of the container, and the other half was visible through the side of the container. In the Not Enclosed condition the bait was positioned outside the container, resting on the floor and leaning against the outer side nearest the dog.

At the beginning of the first session the dog was released and allowed to explore the testing room and the apparatus, without the containers, for three minutes. After this time, a lead was attached to the collar and the dog was guided to the starting position facing the screen.

With the horizontal blind lowered, the containers were placed centrally on the array 60cm apart. Bait was placed inside one and a similar sound of the bait meeting the container was produced at the other container. The baited container was chosen at random but was never placed in the same location for more than two consecutive trials. The curtain was raised and the dog was released and allowed to search. A choice was scored if the dog positioned its head above the container so that the bait could be directly seen, in the case of Partially Enclosed and Enclosed conditions. For the Not Enclosed condition, a choice was taken as the positioning of the paws within 30cm of the container location. As soon as a choice had been made, the other container was removed. The dog was given time to fully explore

the chosen container, and eat the bait, if present. The dog was then guided to the starting position by the lead.

There were 10 trials in one session and each session featured trials of one condition. The dogs were presented with six sessions, two of each of the three conditions in a random order. Between the sessions, there was a break of approximately 30 minutes and all sessions were completed within two days.

In Experiment 8, dogs were presented with a two choice discrimination task with transparent containers as in the Experiment 7. Bait was hidden in either the left or right hand container, with the chosen location never occurring more than two times in the same place. In three conditions, the bait was either placed a) inside the container (Fully Enclosed) b) on a transparent shelf inside the container so it was partly visible over the top of the container (Partly Enclosed) or c) on the mat immediately in front of the container (Not Enclosed). All dogs were presented with a session (10 trials) of one condition, followed by 1 session for the other two conditions, with a short break in between.

Data analysis

The data were analysed for a change in performance between the three conditions Fully Enclosed, Partly Enclosed and Non Enclosed. The data were analysed using non-parametric Binomial test to assess whether the dogs had a preference to choose a certain location, compared to the null hypothesis which stated that the probability of one of the two locations being chosen was .50. Using K-S test the data were found to be not normally distributed ($D(270)=.49, p<.05$), therefore non-parametric binomial tests were used in the main analysis. The tests

were carried out in order to test the hypothesis that the dogs had a preference to choose the correct location.

Results

The proportion of correct responses for all dogs across all conditions was .55 (95% CI=.51, .66). The proportions of correct responses for each condition are presented in Figure 12.

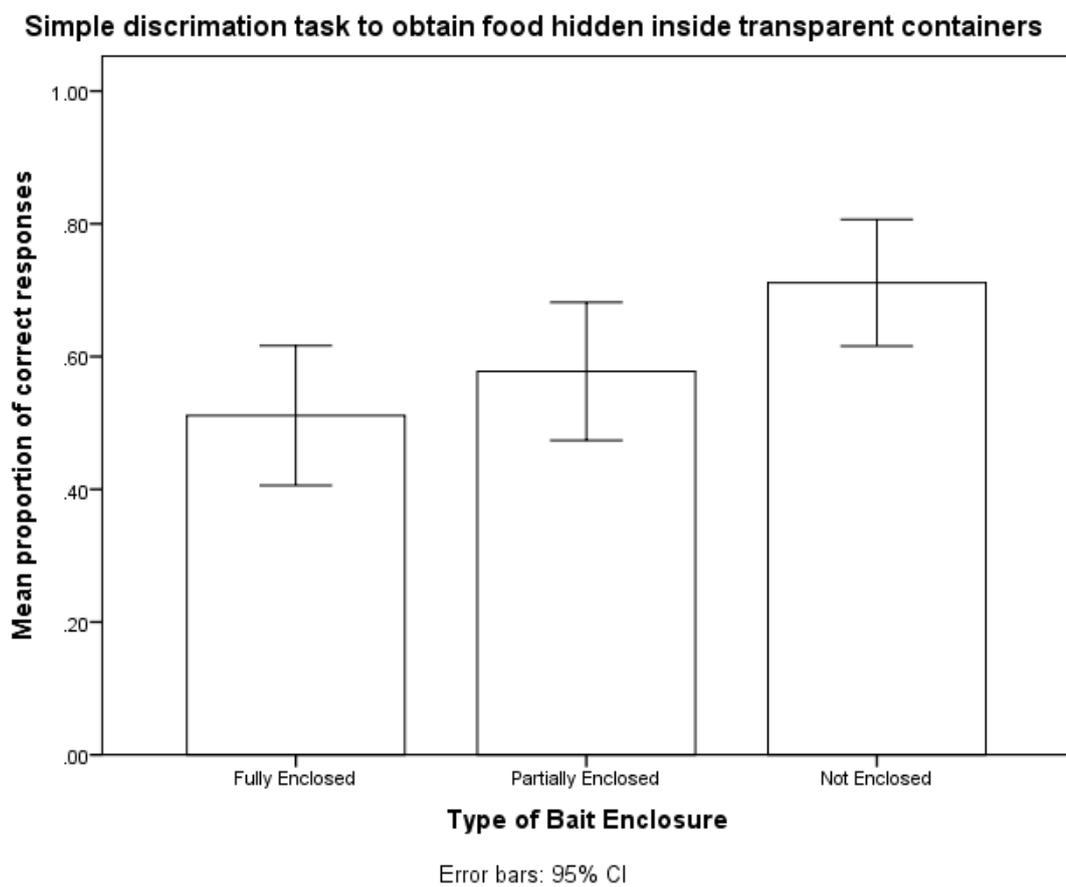


Figure 12 Proportion of correct trials during search for bait fully enclosed, partially enclosed, or not enclosed within one of two identical transparent containers. Error bars 95% CI. Data weighted to match number of left versus right baited trials.

The tendency to choose the correct container in each condition was assessed using binomial tests with test proportion of .50. If the dogs had no preference for choosing the correct container, it would be not significantly different to .50. There was no preference in the Fully Enclosed condition (ns). There was a significant tendency to choose the correct container in the Partially Enclosed ($p < .05$) and the Not Enclosed condition ($p < .05$). Dogs could only follow the sight of bait to choose the baited container when the bait was not enclosed inside the container.

Discussion

In this final experiment, the ability of dogs to utilise the sight of bait inside transparent containers to search correctly for hidden food was assessed. In Experiment 7, dogs had demonstrated that they were able to use this same cue to override prior learning, and they avoided errors in search when the location of hidden food changed. However, the reward was associated with location in the prereversal and reversal phases of this experiment. It was unclear whether dogs were able to discriminate the location of food based on this cue alone, when the location did not remain the same.

In this Experiment, when the bait was placed inside the transparent container in the Fully Enclosed condition, dogs were not able to find the bait in any more trials than predicted by a random search. However, when the bait was only partly inside the container, or completely outside of the container in the Partially Enclosed and Not Enclosed condition, dogs were more likely to obtain the bait. This strongly suggests that dogs are not able to determine the location of hidden food through transparent barriers alone. When the location of food remains consistent, as it did in Experiment 7, they are able to use the visibility of food to

search correctly. A strong tendency to search where dogs have previously found food has a stronger influence on dogs' search than these visible bait cues.

In Experiment 7, following the prereversal phase, dogs had learned the location of the bait as they obtained the criterion performance of 90% correct. When the reversal phase began, they were able to interpret the sight of the bait inside or outside of the transparent containers to adjust their search. However, when the location of the bait changed in Experiment 8, they were not able to ignore the tendency to consistently search in one place. The sight of the bait inside the transparent containers was not sufficient for them to override this tendency to persevere.

This experiment demonstrated that little or no learning took place over the small number of trials, as there was no change in the proportion of correct responses across the two sessions. This suggests that the dogs were not associating the sight of the bait inside the transparent container with the reward, and were not able to form learned associations as rapidly as they may have for other types of cues.

Chapter 6: Conclusions

There has been great interest in comparative cognition research in recent years regarding the skills of dogs in following communicative cues conveyed by humans. In object search tasks, a human experimenter performed a pointing gesture towards one of two containers in which an object was hidden. Dogs were very successful in selecting the correct container in the majority of cases, by following pointing, eye gaze, and head nodding (e.g. Lakatos et al., 2011; Cooper et al., 2003; Miklósi, Topál, and Csányi, 2004). Apes performed poorly and only began to select the correct container when they had been presented with the social cues many times (e.g. Anderson, Sallaberry, and Babier, 1995; Call, Agnetta and Tomasello, 2000). However, dogs may have been using alternative methods to search for the food other than following the point cues.

These procedures were based on the assumption that those animals that correctly search for food understood the referential nature of pointing. The ability to understand the referential nature of pointing is related to the tendency to generalise to novel situations (Herman et al., 1999). Dogs have demonstrated that they are able to use different types of pointing, but they are limited when it comes to more advanced point gestures. When novel types of pointing were presented to the dogs, for instance the experimenter pointed to the target with her leg and pointed with the opposite hand across the body, the dogs were successful in searching for the hidden object. However, more advanced types of pointing involving a chain of two or more point gestures were too complex for the dogs to follow and they failed to find the hidden item (Lakatos et al., 2011). They also tended to search the location closest to the point gesture. Therefore, the authors

interpreted that dogs were using simple strategies to follow the pointing gestures and that this led to errors in circumstances in which more advanced gestures were presented. If dogs use associative processes to follow human point gestures, these processes are not effective enough to follow pointing gestures, which are slightly different from those, which they would encounter every day (Hare et al. 2002; Soproni et al., 2002; Lakatos et al., 2011).

So the problem stands that dogs may be using associative learning or simple strategies to follow human communicative gestures, rather than utilising the numerous cognitive processes such as understanding referential information in the point cues, and generalising novel situations. In addition, it is also unclear the extent to which dogs rely on association in Object Permanence (OP, Collier-Baker, Davis and Suddendorf, 2004). OP has been used widely to evaluate animal cognition in relation to humans (Doré and Dumas, 1987; Pepperberg and Funk, 1990; Pepperberg, 2002) and was originally used to assess the development of sensorimotor development in infants (Piaget and Cook, 1954). Early studies carried out on dogs demonstrated that they could pass advanced OP tasks (Gagnon and Doré, 1992, 1993; Triana and Pasmak, 1981), matching the abilities of great apes and some monkey species (Natale et al., 1986; de Blois and Novak, 1994; Call, 2001; Barth and Call, 2006; Collier-Baker and Suddendorf, 2006). However, suggestions were made that dogs were using simple strategies to solve the tasks, rather than object concept, which the tasks were designed to assess for (Collier-Baker, Davis and Suddendorf, 2004). They may have been making associations between events in the tasks (Fiset and LeBlanc, 2007; Bräuer et al., 2006), using a heightened sensitivity towards human gestures (Collier-Baker, Davis and Suddendorf, 2004) to pass the high level OP tasks.

Accordingly, the specific aims of this thesis were to find out if dogs use associative learning to process object cues as those presented in OP tasks, and also if they use associative learning in following human communicative cues. The Mediation Learning Paradigm (MLP) was modified to a spatial task and was an ideal tool for addressing this aim. The MLP (Rumbaugh, 1971) was originally designed to compare directly the use of associative processes with other types of learning. Associative learning refers to the connection between specific stimuli to predict the outcome of favourable or unfavourable events. When these predictions no longer match the favourable or unfavourable events, or the stimuli change, this type of search strategy can lead to many errors. Mediation learning considers relations between stimuli and in many cases leads animals succeed in selecting the correct stimulus in a discrimination in a few trials, even when the stimuli pairs are changed, through the use of rules such as 'win-stay, lose-shift' (Levine, 1959). The occurrence of mediation learning as a search strategy is prevalent in primates, and has been linked with the emergence of advanced cognition such as that found in humans (Rumbaugh and Pate, 1984).

The spatial Mediation Learning Paradigm, as appropriately modified for this study, represents a novel approach to assessing how dogs process different types of cues in search tasks. It directly assesses whether animals are using associative learning as a search strategy, compared with alternatives, such as object cues typically assessed in object permanence (OP) tasks, and human communicative signals such as point and gaze cues. In Experiment 1, a modified version of the MLP was presented to the dogs to assess the type of learning they used. In the absence of any cues, Experiment 1 was designed to first assess whether dogs used associative learning, or mediation learning. The learning mode of dogs

has not been assessed in this way before. Food was always hidden in one of two locations, the other location was always empty (A+B-). Once a criterion performance was reached, (9 out of 10 consecutive trials correct), the reversal phase began. Now the food location was switched to the B location. There were three test conditions, which featured either the original stimuli locations from the prereversal phase (A-B+), or one of these locations substituted for a novel stimulus location (A-C+, B+D-). Specific patterns of differences between test conditions indicate dogs were using either associative learning or direct use of cues to search in the test phase. If the dogs were using associative learning, the condition featuring the original stimuli locations would be most difficult. To successfully find the food in condition A-B+, dogs had to simultaneously override both the tendency to approach A and avoid B. In the other two conditions the novel locations had no pre-existing tendency for approach or avoidance and so to successfully search dogs only had to override one of these tendencies (either override approach A in A-C+, or override avoid B in B+D-). As a result, conditions A-C+ and B+D- were easier if the dogs were using associative processes to guide search. The proportion of correct responses in these conditions would be significantly higher than A-B+ if dogs were using associative learning in the prereversal phase.

However, if dogs used mediational learning as a search strategy in the prereversal phase, the difficulty of all conditions should have been similar. This is because choice on any particular trial is determined by the outcome of the previous trial, for instance in the use of the rule 'win-stay, lose-shift'. There are no tendencies to approach or avoid a particular location so that in the reversal phase, the animal is as likely to approach or avoid any of the locations. Subsequently, after

the first few trials, the proportion of correct responses in the reversal conditions would be equal.

It was determined that dogs use associative learning and not mediational learning as a strategy to search for food in the absence of any cues. This was clear from the results of Experiment 1, as there was a difference between the proportion of correct responses in the reversal conditions. When the reversal phase began, and dogs' searches at the A location were now incorrect, they were not able to modify their search behaviour based on this feedback. They might have switched to the other alternative location in as little as 1 trial, as some of the species which are capable of mediational learning do (Rumbaugh and Pate, 1984). In other words, dogs demonstrated an inability to inhibit their previous success.

Dogs have been found to rely on associative learning in preference of other search strategies in other spatial tasks. Watson et al. (2001) used an invisible displacement task to test whether they are able to infer the location of the hidden objects. The authors designed the task to compare the rate at which dogs search successively, predicting that inference by negation, as a search strategy would produce more rapid search times with each incorrect choice, as greater certainty was placed on the presence of food at the remaining unsearched locations. Conversely, associative learning would lead to a slower rate of search following an incorrect search, as general commitment to search decreased with each no-reward outcome (see Chapter 1 for more details). Although there are a few issues that may impact on this interpretation, which are outlined in Chapter 1, the conclusions we can reach broadly from this experiment is that dogs refer to associative processes to guide search, as opposed to another strategy (in the case of Watson et al., 2001, reasoning by exclusion). The Mediational Learning Paradigm here is slightly

different to that of Watson et al.'s (2001) search task; namely, that dogs all acquire learned spatial associations before the test phase began. Despite this difference, Experiment 1 of this thesis reached the same conclusion that dogs rely on associative processes as a search strategy.

Following the first experiment, the proceeding experiments investigated the focus of this thesis, which was to assess the extent to which dogs rely on associative processes in following object cues and human communicative cues. We predicted that if dogs were not using associative learning to follow object cues and human communicative cues, they could follow the cues provided, and override associations made between location and reward in the first phase. However, if dogs use associative learning to follow object cues and communicative cues, they would not be able to override the spatial associations about the location of food when these cues were presented.

In Experiment 2, the prereversal phase mirrored that of the first phase in Experiment 1. Dogs formed association between location and reward until a search criterion was met. Then when the reversal phase began, the dogs witnessed object cues such as those presented in object permanence (OP) tasks. With the curtain raised, the experimenter placed bait inside the baited container. Dogs had all the means necessary to find the hidden food, but they would have to override associative learning from the prereversal phase in order to search correctly. If they did not override associative learning, then this would be apparent as they would make most errors in condition A-B+, and the proportion of correct responses across the conditions would be significantly different. It was clear in Experiment 2 that the dogs found condition A-B+ more difficult, and so were not able to override associative learning with the object cues.

We may have predicted that dogs' performance in Experiment 2 would have been different if we consider dogs' abilities in Object Permanence tasks. Triana and Pasnak (1981) determined that dogs were able to pass very high object permanence tasks, in which dogs were required to follow multiple invisible transpositions of hidden objects. In their tasks, the dogs would have had to overcome a tendency to simply search the last location they saw the object, at the very beginning before the invisible transpositions took place. From the results of Experiment 2, it seems unlikely that the dogs would have been able to inhibit this tendency to search where it was last seen. Dogs committed many errors in the A-B+ condition, which was a reversal of the initial learning task, despite being able to see the hiding process.

Furthermore, failures in earlier tests in the Object Permanence framework, such as the 'A-not-B' error in stage IV tasks bear resemblance to the search behaviours of the dogs in Experiment 2. In this error, the animals watch an object being hidden consistently at the same location for a series of trials, followed by a search (similar to the prereversal phase of Experiment 2). In the proceeding trial, the object is hidden at a new location, in clear view of the animal (as in the reversal phase of Experiment 2). Animals that are able to pass stage IV Object Permanence tests search correctly at the new location. However, an inability to ignore previous success leads stage IV animals to the previously correct location. Based on the results of Experiment 2, it would appear that dogs are not able to pass these 'A-not-B' error tasks.

Even when hiding cues were presented from the beginning of the experiment, search performance remained the same. Dogs continued to make errors in the reversal phase of Experiment 3, particularly in control condition A-B+, indicating that they could use the cues to override the spatial associations they had

learned in the first phase of the experiment. The dogs definitely noticed the object cues in Experiment 3, as they learned the associations more rapidly when this information was provided from the beginning of the experiment. Experiment 4 replicated these findings with different spatial stimuli arrangements and determined that the distance between the stimuli does not influence the type of search strategy used.

One of the main arguments presented by Gagnon and Doré (1992) that dogs were not utilising simple strategies to solve the object permanence task was that their performance was high from the very beginning of the experiment. The authors state that if dogs were opportunistically using human cues in the object permanence task, they may follow many types of cues conveyed by the human experimenter before they successfully found one that predicted the location of the object. Post-hoc analysis presented on the few trials in which the task was repeated offered support that there was no change in performance across trials. When presented with the Mediation Learning Paradigm, the dogs produced results contradicting this. In particular, Experiments 2 and 4b, in which a non-social cue was presented, are comparable to the procedure of Gagnon and Doré (1992) because they present visible displacement of a reward without any communicative cues. In the case of the Mediation Learning Paradigm, the dogs' performance in the initial trials was very low, and it increased over the course of the experiment. Both these features were described by Gagnon and Doré (1992) as indicative that simple rules were in use during the task. This notion is also supported by further analysis carried out to assess whether the rule 'search where the experimenter's hand last visited'. In trials in which the experimenter visited the correct container just prior to search, the dogs were more likely to search correctly than if the experimenter performed the sham

baiting procedure on the empty container. The results of these experiments suggest that in the absence of communicative cues, dogs shift their search strategy and use other apparent stimuli to predict the location of hidden food.

From the literature review, it was unclear the extent to which dogs comprehended human pointing, and what role associative learning played in socio-communication with humans. Having determined that dogs do not use hiding cues conveyed by humans to override prior learning, the aim of Experiment 5 was to investigate whether the communicative content of the cues influenced dogs' ability to override prior learning. When communicative cues were conveyed at the point of reversal, dogs were able to override spatial associations. They avoided making errors in the reversal phase even though the reward was hidden in a location that was different from that where they had previously found the reward. Importantly their performance was similar in the three reversal conditions. It appeared that the key factor allowing dogs to override associative learning was the communicative nature of the cue conveyed by a human.

Experiment 5 supports what has consistently been found in previous research: that dogs are able to follow human points, and use them flexibly when the task changes (Miklósi et al., 1998, Miklósi, Topál and Csányi, 2004, Cooper et al., 2003). However, these previous studies only assessed whether dogs could generalise the ability to follow human points to more novel types, such as leg pointing and doll pointing (Udell, Giglio and Wynne, 2008), but Experiment 5 used the novel approach to contrast the ability to follow points with pre-existing associative learning. In this experiment, dogs demonstrated comprehension of pointing by overriding learned associations and following the point and gaze cues. This offers alternate support for the theory that dogs understand messages inherent

in human pointing, and that they do not simply form associations between stimulus and reward.

In fitting with other research, the results of these experiments also support the idea that comprehension of point gestures is not a learned process over the course of the experiment. The idea that a consistent performance in search tasks involving pointing indicates that dogs do not use the repetitive nature of the task to gain experience in this ability was supported by many studies (Agnetta, Hare, and Tomasello, 2000; Miklósi et al., 1998; Riedel, Schumann, Kaminski et al., 2008; Soproni, Miklósi, Topál, et al., 2001). This thesis certainly collaborates this notion, as the dogs' performance in the reversal phase of Experiment 5 following a point gesture did not change over the course of the sessions. This was not the case when other, non-communicative cues were presented, such as in Experiment 1-4. Here, the performance rose from the first to the last session, demonstrating that there was task learning taking place.

The dogs' performance was also already relatively high from the start of the reversal phase when point gestures were introduced in Experiment 5. In comparison, in Experiment 4b, in which a non-communicative cue was presented, the performance in the initial reversal trials was significantly lower. In these same trials when pointing cues were presented, the performance rose to .59. The purpose of these initial reversal trials is to indicate to the animals that the reward contingencies have changed. Following a non-communicative cue in Experiment 4b, the dogs continued to search in the previously rewarded location, leading to a very low performance in the initial reversal trials. Introducing the pointing cue effectively wiped the influence of the previous trials out.

However, there was a potential confound in the communicative cues experiment. The communicative cue used in Experiment 5 was longer in duration than the non-communicative cue in Experiments 1-4. The shorter duration of the cue in Experiments 2-4 could have been the reason why dogs could not override associative learning there. We tested this possibility by presenting a cue in Experiment 6, which was similar in duration to the pointing cue used in Experiment 5, but did not feature any explicitly communicative characteristics. In Experiment 6 dogs achieved an equal performance in all three reversal conditions again. This indicated they had overridden spatial associations without the communicative component of the hiding cue. Nevertheless, the dogs showed a lower overall performance in the reversal phase of Experiment 6 compared to that of Experiment 5 suggesting that the communicative cues had a beneficial effect in the reversal phase.

It is unclear whether dogs interpreted the object cues in Experiments 2, 3, 4 and 6 as any different from the communicative point and gaze cue in Experiment 5. The early experiments, which presented object cues, were designed to be separate from the communicative cues in Experiment 5, yet the dogs may have not considered them as different types of cues. Research comparing dogs' ability to follow communicative and object cues seem to indicate that dogs cannot tell the difference. In Brauer et al. (2006), dogs were presented with a search task with communicative and behavioural cues. They performed equally when following both types of cues, yet Chimpanzees were compared and were able to use the communicative cues to better effect. Brauer et al. (2006) suggested that the dogs could not detect when cues are communicative. If the dogs had considered both the object and communicative cues both as communicative, this may have affected

their performance in the spatial MLP. For instance, overtly ostensive communicative messages from humans can adversely affect the ability of dogs to follow the actions of humans (Kupan, Miklósi, Gergely, and Topál, 2011; Szeteci, Miklósi, Topál & Csányi, 2003).

The results up to this point suggested that, although they are beneficial, explicitly communicative cues might not be necessary for dogs to overcome the effects of associative learning in the spatial ML paradigm. However, it is possible that dogs interpreted the object cue performed by humans in Experiments 1-4 as a communicative gesture, so it was important to assess the effects of cues where any possible social component was removed. Experiments 7 and 8 continued this investigation of communicative cues by presenting non-social, non-communicative physical cues to assess whether dogs could override prior learning. Unlike the previous experiments, the human experimenter did not convey any cues. Instead, the bait was visible through transparent barriers at the time of reversal. Very little research has been conducted on the ability of dogs to search for food hidden inside transparent containers. Some researchers adopted this approach to circumvent limitations in memory, which may have lead some infants fail in object permanence tasks (Shinsky and Munakata, 2001). It also is a useful methodology here because completely non-social cues can be conveyed to the dogs about the location of food without any interaction from the human experimenter.

In Experiment 7, the Mediation Learning Paradigm was presented to dogs with no cues visible in the prereversal phase – the containers were wrapped in covers so they were opaque. Once dogs had formed association in the absence of any cues, the covers were removed in the reversal phase. In most trials, dogs were able to use the sight of bait inside transparent containers to override pre-existing

spatial associations. They were also as likely to search for food hidden inside transparent containers, as they were if the food was placed directly in front of the container. This suggests that whether food was enclosed inside a container presented little difficulty to the dogs.

For this reason, Experiment 8 was conducted to complement the findings of Experiment 7. The task used in Experiment 8 was not a reversal discrimination task but involved simply the presentation of two transparent containers in a discrimination task. Unlike the spatial Mediation Learning Paradigm, the location of the hidden food always changed so that it was not in the same place for more than two trials. When the location of the bait consistently changed, the dogs were not able to locate successfully bait visible inside the transparent containers. Dogs have a strong tendency to form spatial associations as they rapidly form a preference for searching in a particular location (Nitzschner, Kaminski, Melis, and Tomasello, 2014). This suggests that dogs cannot reliably use the visibility of bait as a means to guide search, and that they have a strong tendency to persist in searching where they have previously found the bait. In the spatial Mediation Learning Paradigm with transparent containers, they may have followed the visibility of bait to supplement their search, and because the location of the bait remained constant, they were able to search correctly in the majority of trials.

Wobber and Hare (2009) assessed whether dogs can detect the difference between social and non-social cues and presented a social and non-social reversal task to dogs. They reasoned that if dogs' cognitive skills extend beyond the social context, they should be able to perform better in a reversal task when the discriminating cues are social than when they are non-social. The dogs performed equally in the social and non-social reversal task, therefore, dogs did not benefit

from the additional social information provided in the social condition. In fact, it shows perhaps that the dogs were not able to tell the difference between the social and the non-social task. In the spatial Mediation Learning Paradigm, it was clear that dogs were able to override previously learned responses in conditions in which communicative cues were presented. However, the results of Experiment 7 perhaps support the overall observation of Wobber and Hare (2009) that dogs do not distinguish between social and non-social cues in reversal tasks.

It is worth noting the differentiation that Wobber and Hare (2009) make between 'social' and 'non-social'. In both types of task used by these authors, the procedures featured human experimenters directly handling the containers in which the bait was hidden. In the social task, the containers were identical and the identity of the human experimenters was the discriminating stimulus: in the non-social task, the identity of the experimenter was not related to the location of food, but the containers were marked differently. Although both tasks featured humans, dogs only considered one of the tasks social, based on the kinds of discriminating stimuli. In the spatial Mediation Learning Paradigm, a clear distinction was made between social and non-social stimuli. The social cues were conveyed by the experimenter, and the non-social cues did not involve the experimenter interacting with the containers in any way. It is perhaps more accurate to state in this case that dogs are equally able to inhibit prior responses with both social and non-social types of cues.

A second analysis of Wobber and Hare's (2009) results featured the analysis of the change in performance over the course of the reversal phase. The dogs were more likely to search correctly in the final stages of the test than they were in the first stage. This indicates that learning took place in both social and non-social

tasks. In the present series of experiments, the instance of learning across the reversal phase was only recorded when a non-communicative social cue was presented. In Experiments 2 and 3 (and then mirrored in Experiment 4), the dogs witnessed the human experimenter's hand placing the bait inside the correct container. Performance increased in the reversal phase from the first to the third test. Yet when presented with communicative and explicit social cues, and non-social physical cue, no learning took place. The instance of learning only occurred when dogs *were not* able to override prior learning in the reversal phase.

An overarching theme in the results of the experiments in this thesis is that in order to override learning, dogs require specific and explicit visual cues. These types of cues might include communicative cues, but dogs may also be able to overcome what they have previously learnt if non-communicative cues are salient enough. This conclusion may be valuable in an applied setting in working dogs. For example, in scent detection dogs, when human handlers interact with one particular location this can lead to dogs making more false-positive alerts (Lit, Schweitzer, and Oberbauer, 2011). In this way, handlers may inadvertently cause dogs to alert presence of an illicit scent when there was none by using overtly communicative cues, but the results of these experiments lead to the recommendation that trainers can attract attention to potential targets by using non-communicative cues, or by reducing the amount of overtly ostensive cues they provide.

Conversely, scent dogs trained to signal for the presence of contraband may fail to signal a positive when they have repeatedly searched the location without previously encountering any targets (Porrit, Shapiro, Waggoner, Mitchell, Thomson, Nicklin and Kacelnik, 2015). The same applies for explosive detection dogs, as Gazit, Goldblatt and Terkel (2005) found that the number of targets

previously detected in an area directly influences the length of time the dogs spend searching in that area in the future. The findings of this thesis suggest that handlers and trainers should increase the use of communicative cues to engage dogs to search in cases where persistent search takes place. In this way, the cues will increase the likelihood that the dogs will override their previous learnt associations (that no target was found at this location), and signal the presence of a target in a well-searched location.

Similarly, the cost associated with training individual assistance dogs can be incredibly expensive. Training methods are continually being refined to reduce the numbers of non-successful dogs, and the length of time taken to train assistance dogs (Coppinger, Coppinger, and Skillings, 1998). This research has shown that the use of specific explicit cues decreases the number of errors in dogs when circumstances change. Additionally, in cases where training contradicts what has previously been learnt, or the assistance dog is required to undermine the handler in critical circumstances (e.g. the handler is in danger when crossing the road), more overt cues may be needed to override what has previously been learnt. In these cases, increasing the use of communicative cues in training for contradicting behaviours may reduce the need for negative reinforcement, and may decrease the length of training needed.

A clear outcome we can take from the results of this thesis is that dogs have a comprehension of pointing which negates the involvement of learning in adulthood. Dogs were able to override a previously learned response and avoid making errors in search by following a pointing gesture. When we take into consideration the theory that through domestication, dogs have developed a predisposition to inhibit independent behaviours in order to benefit from human

direction (Gacsi, McGreevy, Kara and Miklósi, 2009c), it is clear to see that this series of experiments illustrates this theory. In the absence of a communicative human cue, the dogs relied on their own associative learning in experiments 1-4. Once a communicative cue was introduced, they immediately began inhibiting this associative learning, and followed the human directive gesture to search correctly.

In addition, this thesis has shown that dogs cannot override learning with object cues such as those presented in object permanence tasks. The early assessments in object permanence made by Triana and Pasnak (1981), and Gagnon and Doré (1992; 1993) are considered an overestimation according to the results of this study. If dogs are not able to override learning with object cues, then they most likely cannot pass level V and VI tests, which require tracking multiple displacements that occur out of sight. Although these two tasks are slightly different, for instance, the Mediational Learning Paradigm encourages learning before the object cues are presented; both tasks involve multiple taxing processes such as memory and flexibility in learning.

A second discovery following experiments presented in Chapter 2 is that dogs do not use mediational learning when presented with a series of reversal discrimination problems. This further supports the notion that dogs cannot pass late stage object permanence tasks. Chimpanzees for instance, have passed stage V and VI object permanence (Spinozzi and Potí, 1993), and show evidence of using mediational learning in the Mediational Learning Paradigm (Rumbaugh and Pate, 1984). We can further conclude that if dogs do not use mediational learning, it is unlikely that they can pass stage V and VI object permanence. It is worth noting that the spatial Mediational Learning Paradigm presented here was a modified version of the original paradigm described in (Rumbaugh and Pate, 1984). As such,

for an accurate assessment of whether dogs can use mediational learning, it may be practical to present the original non-spatial paradigm to dogs.

Finally, the conclusion of this study is that dogs do not necessarily require social cues in order to override learning. The review by Bräuer et al. (2006), that dogs' unique skills in following informative cues are limited to the social domain, was contradicted here. Dogs were able to overcome the negative effects of spatial learning with only the physical cues presented in Experiment 7 (transparent barriers). It is important to emphasise that dogs have a strong tendency to form associations between location and reward, and thus quickly develop location preference in a search task. This was clear from the results of Experiment 8, in which dogs were not able to find food when it was hidden inside transparent containers, when the correct location persistently changed. A further study might replicate this small experiment to assess whether dogs could override learning following a physical cue when the food was not consistently in the same location.

The relative importance of different types of cues in dogs' search was assessed in this thesis. A new paradigm was created to test whether dogs could use various types of cues to enable them to override associative learning. In past research, dogs were found to be utilising simple strategies in object permanence tasks. This theory was confirmed, as dogs were not able to override associative learning by following object cues. In addition, dogs' apparent ability to follow human pointing may be explained by associative learning. Unlike the object cues, dogs were able to override learning in the Mediational Learning Paradigm with point cues. Finally, as a further assessment into the level of understanding dogs have of object cues, bait was visible through transparent barriers, and dogs used these cues to override associative learning. Dogs are able to detect body cues from

humans to increase the likelihood of finding food; however, they have a strong tendency to search where they have previously found food, despite cues from humans signalling the location of food elsewhere. They do rapidly form associations relating to search for food and maximise the likelihood of success in search.

Appendices

Appendix 1. An overview of the procedures of the experiments reported in this thesis.

Experiment	Cues presented in		Notes
	Prereversal Phase	Reversal Phase	
1	No cues	No cues	Baseline experiment
2	No cues	Object cues	
3	Object cues	Object cues	
4a	No cues	No cues	Container locations controlled from this point on
4b	No cues	Object cues	
5	No cues	Communicative cues	
6	No cues	Explicit Object cues	Replicated Exp 2 with longer duration cue
7	No cues	Transparent containers	
8	Transparent container discrimination (no reversal)		

Appendix 2. Tests for normality of all data in this thesis using Kolmogorov-Smirnov test. In the prereversal phase, data from all experiments (apart from session 3 of experiment 1 and 3) were not normal, and consequently, this data was analysed using non-parametric tests for the main analysis.

Experiment	n	D	p	D	p	D	p
Prereversal phase, df = 2		Session 1		Session 2		Session 3	
1	9	.22	ns	.32	ns	.47	p<.05
2	10	.23	ns	.23	ns	.34	ns
3	10	.30	ns	.43	ns	.52	p<.05
4a	10	.23	ns	.15	ns	.35	ns
4b	10	.24	ns	.29	ns	.19	ns
5	10	.27	ns	.22	ns	.26	ns
6	10	.25	ns	.31	ns	.19	ns
7a	5	.27	ns	.35	ns	.24	ns
7b	5	.47	ns	.22	ns	.34	ns
7c	5	.36	ns	.22	ns	.32	ns
	n	D	p	D	p	D	p
Reversal phase, df = 2		Condition A-B+		Condition A-C+		Condition B+D-	
1	9	.17	ns	.18	ns	.21	ns
2	10	.15	ns	.35	ns	.20	ns
3	10	.18	ns	.38	ns	.19	ns
4a	10	.14	ns	.13	ns	.23	ns
4b	10	.11	ns	.23	ns	.16	ns
5	10	.27	ns	.33	ns	.21	ns
6	10	.14	ns	.19	ns	.17	ns
7a	5	.20	ns	.22	ns	.16	ns
7b	5	.29	ns	.19	ns	.23	ns
7c	5	.17	ns	.22	ns	.22	ns

Appendix 3 A description of all human cues presented in the Experiments of this thesis. In all cues, the Experimenter stood centrally between the two containers. The order of baiting and sham baiting actions was specifically controlled, as described on page 62.

Type of Cue	Description	Parts of Experimenter visible	Presented in Experiment
Object hiding cue	The bait was held in one hand between finger and thumb and placed inside the container. With the other hand, the empty container is lifted 2cm off the ground and replaced again.	Screen obscures body above the knee	Experiment 2 Experiment 3 Experiment 4b
Communicative cue	The object hiding cue is performed. In addition, a point cue is made for 3 seconds with hand nearest the container, towards the container. The experimenter also moves head and looks towards the container.	All of body is visible	Experiment 5
Explicit hiding cue	The bait is held approximately 15cm above the correct container for 3 seconds. The empty container is lifted and then replaced.	Screen obscures body above the knee	Experiment 6

Appendix 4. Experiments 1-4 published in Journal of Comparative Psychology, 2011.

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Glossary of Terms and Acronyms

Enclosure condition: A condition of the spatial Mediation Learning Paradigm with transparent containers, which determines whether the bait was placed inside, outside or partially inside the containers.

Invisible Displacement: Moving an object to a hiding place with a transporting device. The target object remains out of direct sight of the subject during the transposition. (See visible displacement)

Mediation learning: A type of learning which takes into consideration relations between stimuli, rather than the identity of the stimuli themselves. For example, animals may form rules for maximising the chance of choosing the correct stimulus: ‘if A is empty, then choose B’, also termed ‘win-stay, lose shift’.

Mediation learning paradigm: An experimental procedure to assess whether animals use associative learning or mediation learning to discriminate which of two stimuli is rewarded. There is an initial discrimination of two stimuli, for example two identical containers at different locations on a spatial array. Once the dogs obtain the reward in 84% trials, the rewarded stimulus is switched and three different conditions are presented. The relative performance in these three reversal conditions indicates whether they used associative learning to choose the correct location. (Related: spatial problem)

Object concept: The ability to conceive that objects continue to exist when they are out of sight; can exist inside other objects, and that two objects seen at different times in different places are the same object.

Object permanence: A theoretical framework for the cognitive development of object concept in human children and animals first presented by Jean Piaget. Early stages describe the behaviours of children, which fail to search for hidden objects, to late stages that describe children that are able to search for objects that have undergone invisible displacements.

Ostensive: The directive component of a communicative message or gesture by example.

PCR, Proportion of correct responses: The proportion of trials presented in the spatial Mediation Learning Paradigm in which the dog chose the correct container and obtained the reward.

Perseveration: Also referred to as 'A-not-B' error'. A search error typical of infants and animals at stage III object permanence. When an object is found repeatedly at one location and then is seen hidden at a second location, children at this stage persist in searching at the first location. This is so even when they have seen the object being hidden at the correct location.

Prereversal phase: The first phase of the Mediation Learning Paradigm, in which containers are placed at the A and B location. Location A is consistently rewarded. The length of the prereversal phase is determined by how many trials it takes for the dogs to reach the performance criterion (9 out of 10 correct trials in 10 consecutive trials).

Reversal condition: Test conditions in which containers are presented at different locations on the spatial array to assess the type of learning that occurred in the prereversal phase. The three reversal conditions have a reward contingency opposite to that of the prereversal phase, and feature either: both locations from the prereversal phase, A and B, or one of these locations together with a new unfamiliar location (A-B+, A-C+, and B+D-).

Reward contingency: The current reward or non-reward status of the stimuli or locations presented to the dog.

Spatial problem: Each spatial problem comprised of a prereversal or training condition, followed by the three reversal conditions. The locations on the spatial array at which the containers were placed were changed in each spatial problem.

TTC, Trials to criterion: The number of trials required in order for a performance criterion of 9 out of 10 consecutive trials to be reached in the spatial Mediation Learning Paradigm. Once this criterion was reached, the reversal phase of the Mediation Learning Paradigm would begin.

Transportation device: Used in some object permanence tasks to obscure objects that are to be hidden, during the hiding process. They typically take the form of a small box

on the end of a pole. The transportation device highlights whether animal are searching the last location they have seen the object.

Visible Displacement: A type of object permanence task in which a target object is hidden behind a screen or inside a container. Unlike invisible displacement, the target object is visible to the subject up until the point that it is hidden inside the container.