

Perceptual Learning Transfer in an Appetitive Pavlovian Task

Antonio A. Artigas

Universitat de Barcelona

Jose Prados

University of Leicester

Author Note:

Antonio A. Artigas, *Departament de Psicologia Bàsica and Institut de Recerca en Cervell, Conducta i Cognició (IR3C), Universitat de Barcelona, Spain*; Jose Prados, Department of Neuroscience Psychology and Behaviour, University of Leicester, United Kingdom.

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Correspondence concerning this article should be addressed to Jose Prados, Department of Neuroscience Psychology and Behaviour, University of Leicester, Lancaster Road, Leicester LE1 9HN, United Kingdom; jpg19@le.ac.uk

Abstract

In two experiments, rats were given intermixed or blocked pre-exposure to two similar compound stimuli, AX and BX. Following pre-exposure, conditioning trials took place in which AX (Experiment 1) or a novel compound stimulus NX (Experiment 2) was paired with a food-unconditioned stimulus in an appetitive Pavlovian preparation. Animals that were given alternated pre-exposure showed lower generalization from AX to BX (Experiment 1) and from NX to a new compound ZX (Experiment 2) than animals that were given blocked pre-exposure, a perceptual learning and a perceptual learning transfer effect respectively.

Keywords: perceptual learning; elemental learning; configural learning; stimulus sampling theory; selective attention.

A conditioned response developed to one conditioned stimulus (CS) is likely to generalize to a novel stimulus to the extent that they share some common elements. Any two stimuli can be conceptualized as AX and BX, where A and B are the unique elements that would help discrimination, and X correspond to the common elements that contribute to the ambiguity of the situation. To successfully discriminate between AX and BX the animal would need to attend, for example, to the unique distinctive features and ignore the common elements. Interestingly, learning processes are engaged which direct the attention of the animals to the unique elements and away from the common elements in situations in which the animals are simply exposed to the compound stimuli in the absence of any reward. We refer to these learning processes as perceptual learning (e.g., Gibson, 1969; Hall, 2003; McLaren & Mackintosh, 2000; see Mitchell & Hall, 2014, for a full review).

Perceptual learning processes are more likely to affect stimuli that are presented intermixed (AX, BX, AX, BX) than stimuli presented in separate blocks of trials (AX, AX... BX, BX). This intermixed/blocked effect, an instance of perceptual learning, has been widely researched in a variety of species and procedures: in domestic chicks using visual discriminations (Honey, Bateson, & Horn, 1994); in humans using visual (Lavis & Mitchell, 2006) and flavor (Dwyer, Hodder, & Honey, 2004) discriminations; and in rats using flavor (e.g., Artigas, Sansa, & Prados, 2006; Blair & Hall, 2003; Prados, Hall, & Leonard, 2004), spatial (e.g., Prados, Artigas, & Sansa, 2007) and acoustic discriminations (Mondragon & Murphy, 2010). Mondragon and Murphy (2010), for example, using a standard appetitive Pavlovian preparation, exposed two groups of rats to AX and BX according to an intermixed or a blocked schedule. Following conditioning with the compound AX, animals were tested in the presence of the compound BX, a generalization test. Animals given intermixed pre-exposure showed

better discrimination between AX and BX than animals in the blocked condition. The experiment by Mondragon and Murphy (2010) remains the only instance of perceptual learning reported using a standard appetitive Pavlovian conditioning technique in rats.

Enhanced discrimination between AX and BX could be the consequence of the action of a number of processes. On the one hand, modern theories of perceptual learning suggest that intermixed, but not blocked, pre-exposure increases the salience of the unique features A and B; these theories tend to assume no differences in the salience of the common element X in the two pre-exposure schedules (e.g., Hall, 2003). However, earlier theories of perceptual learning suggested a second mechanism that might affect the discriminability of AX and BX, namely the reduced attention paid to the irrelevant common feature, X (e.g., Gibson, 1969).

There is evidence that intermixed pre-exposure tends to maintain high the salience of A and B compared to the blocked pre-exposure procedure (e.g., Artigas, Sansa, Blair, Hall, & Prados, 2006; Blair & Hall, 2003; Contel, Sansa, Artigas, & Prados, 2011; Hall, Blair, & Artigas, 2006). Furthermore, Mondragon and Murphy (2010; see also Mondragon & Hall, 2002), have reported evidence that support the notion that the common element X is less salient after intermixed than blocked pre-exposure. Using a standard appetitive conditioning task, Mondragon and Murphy observed that animals that were given intermixed pre-exposure to AX and BX showed less conditioning to the common element X than those given blocked pre-exposure. According to standard associative learning theory (e.g., Mackintosh, 1975; Pearce & Hall, 1980; Rescorla & Wagner, 1972), a low in salience X element would be less likely to associate with the unconditioned stimulus (US) during the conditioning phase of a typical perceptual learning experiment (in which the AX compound is paired with the US), reducing mediated generalization to the BX element during the generalization test. Also, lack of

attention to the common element X would also enhance the discrimination between similar compounds (as anticipated by Gibson, 1969) in experiments in which the generalization test is not used. For example, studies in which human participants were required to discriminate between different versions of the same photograph of a face created with a morphing procedure, showed that pre-exposure to the common element X alone could enhance discrimination between compound stimuli with novel unique characteristics (AX and BX). However, alternated pre-exposure to the two compound stimuli, AX and BX, was found to be a more effective procedure to enhance their discriminability (e.g., Mundy, Honey & Dwyer, 2007). These results suggest the existence of two mechanisms contributing to the perceptual learning effect, one based upon the increased salience or effectiveness of A and B, and another based upon the reduced salience of X.

Increased salience of A and B in the intermixed schedule would result in enhanced discriminability of the pre-exposed compound stimuli AX and BX exclusively. However, assuming the existence of a second mechanism, reduced salience of X in the intermixed procedure, would extend the facilitatory effect of pre-exposure to similar compound stimuli containing new unique features (like NX and ZX, for example). Artigas and Prados (2014) recently reported some evidence for such a perceptual learning transfer effect using a flavor discrimination task. After receiving intermixed or blocked pre-exposure to AX and BX, rats were given conditioning trials with a novel compound stimulus, NX. It was expected that a less salient X element in the intermixed group should acquire less control over the conditioned response during conditioning with NX than in the blocked group, reducing the generalization (mediated by the common element) to novel compound stimuli containing the X element. In agreement with this hypothesis, animals that were given intermixed pre-exposure to AX and BX

showed lower generalization of the aversive response conditioned to NX to a new compound, ZX, than animals that were given blocked pre-exposure.

As pointed out above, the Mondragon and Murphy (2010) study reports the only instance of a perceptual learning effect using a standard appetitive Pavlovian conditioning task. The aim of Experiment 1 was to obtain a double replica of this result by using a set of stimuli which intended to be identical to those used by Mondragon and Murphy, as well as with a new set of stimuli. These two sets of stimuli were then used to explore the perceptual learning transfer effect reported by Artigas and Prados (2014) in a flavour aversion procedure using a more orthodox appetitive procedure.

Experiment 1

Mondragon and Murphy (2010) suggested that one reason for the lack of evidence of perceptual learning with standard Pavlovian procedures could be the fact that perceptual learning might be evident only when the stimuli are initially rather difficult to discriminate. In previous unsuccessful attempts (for example, Honey, 1990) animals were required to discriminate between relatively distinctive stimuli, tones and clicks, arguably an easy task. Pre-exposure has been shown to benefit subsequent discrimination only when the to-be-discriminated stimuli share a high proportion of common elements. It has often been shown, for example, that adding explicit common features facilitates discrimination after intermixed (but not blocked) pre-exposure (e.g., Mackintosh, Kaye, & Bennett, 1991; Prados, Chamizo, & Mackintosh, 1999). In their experiments, Mondragon and Murphy (2010) observed perceptual learning in a relatively difficult task that made use of two similar compound stimuli formed by two pure tones (which differed in their frequency; the unique features A and B) and a white noise delivered through an additional speaker (the explicit common element X).

In the present Experiment 1 we sought to replicate this experiment using exactly the same stimuli used by Mondragon and Murphy (Experiment 1A). In Experiment 1B we aimed to replicate the effect using two additional compound stimuli in which the elements A and B were two discontinued tones presented at different rates of intermittence. The reason why we wanted to replicate the effect with a new set of stimuli is our interest in the perceptual learning transfer effect, which is the objective of Experiment 2: to assess the transfer of perceptual learning we would need two sets of stimuli (AX and BX; NX and ZX) that can be reliably used to demonstrate the perceptual learning effect.

In both experiments 1A and 1B, animals in the Group Intermixed were given presentations of AX and BX in an alternated schedule (AX, BX, AX, BX...) whereas animals in the Group Blocked were exposed to the same stimuli in two separate blocks of identical trials (AX, AX... BX, BX). All the animals were then given conditioning trials in which the AX compound was paired with the presentation of a food unconditioned stimulus (US). Differences in discrimination were assessed by comparing responding during a generalization test to BX (see experimental designs in Table 1). If intermixed pre-exposure is more effective in engaging perceptual learning processes that increase the discriminability of the AX and BX compounds, less responding to the BX compound could be expected after intermixed than blocked pre-exposure.

Table 1 around here

Method

Subjects.

The subjects of Experiment 1A were 16 experimentally naïve male hooded Long Evans rats (ad lib body weight range 345:437 g); the subjects of Experiment 1B were 16 naïve male hooded Long Evans rats (ad lib body weight range 329:438 g). They were

housed, in standard transparent plastic cages 24 x 50 x 14.5 cm, in groups of two or three animals in a colony room that was artificially lit from 9:00 a.m. to 9:00 p.m. daily with free access to water. The animals were handled, weighed and fed a restricted amount of food at the end of each session to keep them at 85% of their ad lib body weight for the course of the experiment.

Apparatus.

Four identical Modular Operant Box chambers (25.0cm×25.0cm×25.0 cm) from Panlab (Model LE1005, Panlab/Harvard Apparatus) were used. The chambers were inserted in sound and light attenuating boxes (Model LE26, Panlab/Harvard Apparatus) with background noise produced by ventilation fans (≈ 70 dB). Each chamber was dimly illuminated by a shielded houselight operating at 20 V located on the wall opposite to the food tray. The floor of each chamber consisted of 20 tubular stainless steel bars; these bars were perpendicular to the wall where the food tray was located (Model LE100501, Panlab/Harvard Apparatus). This wall and the opposite one were made of aluminum; the ceiling and remaining walls were of clear methacrylate. A magazine pellet dispenser (Model LE100550, Panlab/Harvard Apparatus) delivered 45-mg Dustless Precision Pellets (Bio Serv; Rodent Purified Diet) into the food tray. A head entry into the food tray was recorded by interruption of a LED photocell (Model LE105-51, Panlab/Harvard Apparatus). Two speakers (Model LE100543, Panlab/Harvard Apparatus) were attached to the top sides of the front wall. The left speaker could deliver four different 15 s tones. In Experiment 1A, a 3.2 kHz (80dB) and a 9.5 kHz (80 dB) were used as the elements A and B of the experimental design. In Experiment 1B, two 5 kHz (80 dB) discontinuous tones that could be presented at two different rates of intermittency were used as the elements A and B of the experimental design. One of the tones was presented at a low rate of intermittency (200 ms period of the tone alternated

with 200 ms of silence) whereas the other was presented at a high rate of intermittency (200 / 100 ms). The right speaker delivered a 75 dB white noise, the X element of the experimental design in both experiments. A computer running the Packwin software platform 2.0 for Windows XP controlled experimental events.

Procedure.

There were three phases in the experiment: pre-exposure, conditioning and test. Throughout the experiment rats were presented with trials separated by a variable ITI with a mean of 240 s. During the first two days of the experiment, animals were exposed to the compound stimuli AX and BX (5 presentations of each compound every day). The initial order (counterbalanced) in which the stimuli were exposed in day 1 was reversed on day 2 and the identity of the first stimulus was also counterbalanced. In Group Intermixed the stimuli were exposed in an alternated fashion (e.g., AX, BX, AX, BX...). In Group Blocked the stimuli were presented in separate blocks of identical trials (e.g., AX, AX... BX, BX). Two sessions of conditioning followed, each of which comprised 10 presentations of AX followed by 2 pellets of food. During the final day of the experiment, the animals were given a test in which the compound BX was presented six times in extinction. The amount of time the animals kept their head in the food tray was recorded during the stimulus presentation (CS period) and during the 15 s that preceded it (the Pre-CS period). A difference score in which time responding during the Pre-CS was subtracted from that recorded during the CS was computed and used as a response measure.

Data Analysis.

The analysis of this measure of performance was conducted with analyses of variance (ANOVA) using a rejection criterion of $p < .05$. The reported effect size for ANOVA with more than one factor is partial eta squared (η_p^2), while for comparisons

between two means it is eta squared (η^2). For both measures of effect size, 95% confidence intervals (CIs) were computed using the method reported by Steiger (2004).

Results and discussion

Experiments 1A and 1B produced the same pattern of results. Figure 1 shows the group means for the magazine approach response calculated from difference scores (CS-PreCS) during the conditioning trials with the AX compound (in blocks of 5 conditioning trials) for the two replicas. ANOVAs with Pre-exposure (Intermixed vs. Blocked) and Blocks of Trials as factors showed a significant effect of Blocks of Trials for Experiment 1A, $F(3,42)=7.66$, $p=.00$, $\eta_p^2=.35$, 95% CI [.09, .50], and for Experiment 1B, $F(3,42)=4.64$, $p=.00$, $\eta_p^2=.24$, 95% CI [.02, .40]. The remaining factors and interactions were all non-significant in both replicas, maximum $F(3,42)=1.22$.

Figure 1 around here

The same analyses were carried out on the Pre-CS levels of responding during the conditioning phase of Experiments 1A and 1B. In Experiment 1A, the mean Pre-CS scores for the four blocks of conditioning trials were 1.67 (± 0.66 SEM), 1.50 (± 0.59), 1.90 (± 0.51) and 2.27 (± 0.43) for group Intermixed; and 1.42 (± 0.32), 1.80 (± 0.36), 1.86 (± 0.53) and 2.19 (± 0.30) for group Blocked. In Experiment 1B, the mean Pre-CS scores for the four blocks of conditioning trials were 1.37 (± 0.39), 1.30 (± 0.66), 2.03 (± 0.65) and 1.59 (± 0.56) for group Intermixed; and 1.43 (± 0.34), 1.84 (± 0.63), 1.72 (± 0.48) and 1.86 (± 0.48), for group Blocked. ANOVAs with Pre-exposure (Intermixed vs. Blocked) and Blocks of Trials as factors showed no significant effects, $F_s < 1$.

Figure 2 shows the group means for the magazine approach response during three blocks of two test trials with the BX compound for experiments 1A and 1B. ANOVAs with Pre-exposure (Intermixed vs. Blocked) and Blocks of Test Trials as the factors showed a significant effect of Pre-exposure for Experiment 1A, $F(1,14)=5.03$,

$p=.04$, $\eta_p^2=.26$, 95% CI [.00, .54], and for Experiment 1B, $F(1,14)=5.30$, $p=.03$, $\eta_p^2=.27$, 95% CI [.00, .55]. The factor Blocks of Test Trials was also significant in Experiment 1B, $F(3,42)=4.29$, $p=.02$, $\eta_p^2=.23$, 95% CI [.00, .39]. The remaining main factors and interactions were all non-significant in both replicas, maximum $F(3,42)=1.36$.

Figure 2 around here

The same analyses were carried out on the Pre-CS scores during the test phase of Experiments 1A and 1B. In Experiment 1A, the mean Pre-CS scores for the three blocks of test trials were 1.68 (± 0.66), 2.18 (± 1.03) and 1.98 (± 1.05) for group Intermixed; and 1.30 (± 0.63), 2.40 (± 0.75) and 1.39 (± 0.93) for group Blocked. In Experiment 1B, the mean Pre-CS scores for the three blocks of conditioning trials were 0.63 (± 0.63), 1.11 (± 0.52) and 1.22 (± 0.43) for group Intermixed; and 0.82 (± 0.34), 1.49 (± 0.67), and 0.65 (± 0.34), for group Blocked. ANOVAs with Pre-exposure (Intermixed vs. Blocked) and Blocks of Test Trials as factors showed no significant effects, $F_s < 1$.

Experiment 1A fully replicates the perceptual learning effect observed by Mondragon and Murphy (2010) using a standard appetitive Pavlovian conditioning task: intermixed pre-exposure to AX and BX significantly reduced the generalization between these compound stimuli, comparison made with the blocked pre-exposure condition. Experiment 1B stands as a second replica of the effect using an alternative set of stimuli (with discontinuous tones as the unique elements A and B).

Most of current theories of perceptual learning assume pre-exposure to alter the perceptual characteristics of complex stimuli through intermixed pre-exposure by increasing, on the one hand, the perceptual effectiveness of the distinctive characteristics A and B (e.g., Hall, 2003; Honey & Bateson, 1996; McLaren & Mackintosh, 2000; Mitchell, Nash, & Hall, 2008), and reducing, on the other hand, the effectiveness of the common elements, X (e.g., Gibson, 1969). Increased attention paid

to the unique features A and B could perfectly well account for the intermixed/blocked effect observed in the present experiment without having to assume any role for the common element X.

Artigas & Prados (2014) hypothesized that a common element X with a reduced salience would acquire less predictive value during the conditioning phase with AX, lowering the generalization (mediated by the common element) of the conditioned response to the BX element. Unfortunately, the contribution of the X element to the standard perceptual learning effect would be masked by the well-established contribution of the increased in salience unique elements A and B: on the one hand, A can be expected to acquire most of the predictive value during conditioning, overshadowing X; and on the other hand, the presence of a salient B element would interfere with the retrieval of the conditioned response controlled by the X element at the time of the generalization test with BX (e.g., Artigas, Sansa, Blair, Hall, & Prados, 2006).

To go round this problem and assess the contribution of the X element to the perceptual learning effect, Artigas & Prados (2014) assessed the transfer of perceptual learning to novel compound stimuli sharing the X element in the absence of A and B. As already described above, they found, using a flavor aversion preparation, that intermixed pre-exposure to AX and BX increased the discriminability of two novel compound stimuli, NX and ZX. Experiment 2 was designed to replicate this perceptual learning transfer using a standard appetitive Pavlovian procedure.

Experiment 2

Animals were pre-exposed to AX and BX according to an intermixed or a blocked schedule. Following pre-exposure, all animals were given conditioning trials with a new compound stimulus, NX, followed by a generalization test with yet another new

compound, ZX. For the present experiment, four stimuli were needed as the elements A, B, N and Z. The two sets of tones used in Experiment 1 were used: two tones of different frequency, the set 1; and two discontinuous tones presented at different rates of intermittence, the set 2. Half of the subjects were pre-exposed to the set 1, and conditioned and tested with the set 2. For the remaining animals this arrangement was reversed. The actual stimuli that played the role of A and B, or N and Z were, therefore, fully counterbalanced across animals.

Method

Subjects and apparatus.

The subjects were 16 experimentally naïve male hooded Long Evans rats (ad lib body weight range 240:393 g). The animals' maintenance and the apparatus were the same as that used in the previous experiment.

Procedure.

The procedure of Experiment 2 replicates the procedural details described for Experiment 1. However, during the pre-exposure phase, the animals were pre-exposed to two of the four compound tones, AX and BX, and were subsequently conditioned with a different compound (NX) and tested in the presence of a fourth compound (ZX). The four tones described for Experiment 1 were used in the way described above.

Results and discussion

Figure 3 shows the group means for the magazine approach response during the conditioning trials with the NX compound. An ANOVA with Pre-exposure (Intermixed vs. Blocked) and Blocks of Trials as factors showed a significant effect of Blocks of Trials, $F(3,42)=22.31$, $p=.00$, $\eta_p^2=.61$, 95% CI [.38, .71]. Neither the Pre-exposure factor nor the Pre-exposure x Blocks of Trials interaction was significant, $F_s < 1$.

Figure 3 around here

The same analysis was carried out on the Pre-CS levels of responding during the conditioning phase. The mean Pre-CS scores for the four blocks of conditioning trials were 1.58 (± 0.51 SEM), 1.57 (± 0.47), 1.65 (± 0.44) and 1.95 (± 0.55) for group Intermixed; and 1.45 (± 0.41), 1.58 (± 0.40), 1.66 (± 0.66) and 1.97 (± 0.92) for group Blocked. An ANOVA with Pre-exposure (Intermixed vs. Blocked) and Blocks of Trials as factors showed no significant effects, $F_s < 1$.

Figure 4 shows the group means for the magazine approach response during the test trials with the ZX compound. An ANOVA with Pre-exposure (Intermixed vs. Blocked) and Blocks of Test Trials as factors showed a significant effect of Pre-exposure, $F(1,14)=6.14$, $p=.02$, $\eta_p^2=.30$, 95% CI [.00, .56]. Neither the factor Blocks of Test Trials nor the interaction was significant, $F_s < 1$.

Figure 4 around here

The same analysis was carried out on the Pre-CS scores during the test phase of the experiment. The mean Pre-CS scores for the three blocks of test trials were 1.27 (± 0.62), 1.62 (± 0.93) and 1.10 (± 0.69) for group Intermixed; and 0.64 (± 0.33), 1.65 (± 0.84) and 0.77 (± 0.75) for group Blocked. An ANOVA with Pre-exposure (Intermixed vs. Blocked) and Blocks of Test Trials as factors showed no significant effects, $F_s < 1$.

Experiment 2 fully replicates the perceptual learning transfer effect observed by Artigas and Prados (2014) using a standard appetitive Pavlovian conditioning task instead of a flavour aversion discrimination task: Intermixed pre-exposure to AX and BX significantly reduced the generalization between two novel compound stimuli, NX and ZX. Given that N and Z are novel stimuli, we can assume that they would have a similar salience or effectiveness for the animals in the Intermixed and Blocked groups.

One possibility that we need to discuss is the possible generalisation of the effects of pre-exposure from A and B to the N and Z elements used during the generalisation test of the experiment. Some perceptual learning theories (e.g., Hall, 2003) suggest that intermixed pre-exposure maintains high the salience or effectiveness of A and B whereas blocked pre-exposure reduces it. Transfer of low salience from AB to NZ would result in less interference with the acquisition and expression of predictive value by the common element X in the blocked condition. This would be, in principle, consistent with the perceptual learning transfer observed in the present experiment. However, the use of very distinctive stimuli as AB and NZ (continuous and discontinuous tones) would have limited or prevented this generalisation. Furthermore, Mondragon & Murphy (2010; see also Mondragon & Hall, 2002) have shown that the X element is certainly less salient in the intermixed than in the blocked condition. All in all, the perceptual learning transfer seems to be better explained in terms of differential perceptual effectiveness of the common element X than as a result of differential generalization from AB to NZ. The reason why the common element X is more susceptible to the effects of pre-exposure in the intermixed arrangement would be the focus of the General Discussion.

General Discussion

The present research was designed to address the mechanisms of perceptual learning assessed through generalization tests in a standard Pavlovian conditioning task. In spite of the fact that perceptual learning is supposed to depend upon associative learning and has been reported in different species using a variety of discrimination tasks and sensory modalities, its generality had not been extended to standard appetitive Pavlovian preparations until recently. Only one study reported by Mondragon & Murphy (2010) had been able to demonstrate perceptual learning in an appetitive Pavlovian task.

Experiment 1 replicated the basic effect reported by Mondragon and Murphy using the same stimuli they used in their experiments (tones of different frequencies, Experiment 1A) as well as with a new set of stimuli (discontinuous tones presented at different rates of intermittency, Experiment 1B). These two sets of stimuli were then used in Experiment 2 to explore whether the perceptual learning transfer effect observed by Artigas & Prados (2014) using a flavour discrimination task could also be observed using a more orthodox appetitive preparation. In Experiment 2, animals given intermixed pre-exposure to AX and BX showed improved discrimination of two novel compounds, NX and ZX, in comparison with animals given blocked pre-exposure. In the perceptual learning transfer test, N and Z are novel stimuli identical for all the animals; therefore, the differences observed between the groups given intermixed and blocked pre-exposure should be attributed to the differential salience of the common element, X.

Artigas and Prados (2014) suggested that the best way to account for the perceptual learning transfer, on the one hand, and the reduced conditioning of the X element observed by Mondragon and Murphy (2010; Mondragon & Hall, 2002) on the other, is by reference to the different representations that might arise from intermixed and blocked pre-exposure to AX and BX: elemental in the case of intermixed and configural in the case of blocked pre-exposure. The hypothesis is based upon the principles of the stimulus sample theory (Atkinson & Estes, 1963; Estes, 1959; McLaren & Mackintosh, 2000), which presume stimuli to be formed by elements that are sampled in every presentation. During blocked pre-exposure to AX, for example, the elements of A and X can confidently be expected to be sampled at the same rate—A and X can be assumed to be equally salient¹. Co-activation of the elements of A and X in

¹ Our analysis develops the argument put forward by McLaren and Mackintosh (2000, p. 226) about the sampling process in the perceptual learning effect reported by Gibson and Walk (1956). In this study, rats showed enhanced discrimination learning between black geometrical figures (circle and triangle) that had been continuously exposed in the home cage of the animals. According to McLaren and Mackintosh, even

each pre-exposure trial would lead to the establishment of associations among them ($x-a$ associations), as well as associations between the elements of X ($x-x$) and A ($a-a$).

The existence of strong $x-a$ associations would contribute to the establishment of a unique configural-like representation of AX.

In the intermixed pre-exposure procedure, alternation of AX and BX would result in a different sampling rate for the unique and the common elements: the X elements would be sampled in every trial whereas the A (and B) elements would be sampled only every two trials. In the first AX trial, for example, we can expect the establishment of associations between the X elements ($x-x$), the A elements ($a-a$) and the X and A elements ($x-a$); however, the $x-a$ associations can be expected to weaken in the absence of A during the subsequent BX trials, in which new links will be established between $x-x$, $b-b$ and $x-b$ (which will be weakened in the following AX trials). In the long term we can expect the development of strong $x-x$, $a-a$, and $b-b$ associations, and relatively weak $x-a$ and $x-b$ associations. The final outcome of intermixed pre-exposure would therefore tend to be elemental representations of the elements X, A and B rather than configural-like AX and BX representations (which would require strong $x-a$ and $x-b$ associations).

All the representations that arise from intermixed and blocked pre-exposure would be subject to the effects of pre-exposure: loss of salience and associability. How this pre-exposure effects affect the conditioning of the X element presented by itself (as in the experiments by Mondragon & Murphy, 2010) or in compound with a novel element (NX, as in the present experiment) can be expected to be different in the intermixed and

when exposed to one such stimulus (rather than both of them simultaneously) the animals would be more likely to process the obvious common elements (black colour) than the less salient distinctive geometric features (only evident from particular perspectives), leading to differential sampling of the common and the unique elements. In the present experiments, using very different pre-exposure procedures, only Intermixed pre-exposure would be likely to result in differential sampling; in the blocked condition, equal salience of A and X (a white noise and a tone) would result in equivalent sampling of their elements.

blocked conditions. It is worth noting that in these experiments the element X was presented in different contexts: in the presence of A and B during pre-exposure, and in the presence of N and Z during discrimination training (present Experiment 2) or by itself (in the experiment by Mondragon & Murphy, 2010). We can refer to the common element during pre-exposure, where it is always presented with A or B, as X_P , and during the conditioning or discrimination training, where it is presented either by itself or in the company of N or Z, as X_T . The effects of pre-exposure (habituation and latent inhibition) upon X_P would generalize to X_T only if they are perceived as similar stimuli by the individuals. It is reasonable to assume that there would be more similarity between the elemental representation X_P and X_T in the intermixed condition than between the configural representation AX_P and X_T in the blocked condition. As a result, high habituation and latent inhibition of X_T in the intermixed condition would limit the capacity of the common element to enter into association with the US, reducing its conditioning (as observed by Mondragon & Murphy, 2010), and limiting the generalization of conditioning from NX to ZX (as observed in Experiment 2).

As an alternative, Mondragon and Murphy (2010) suggested that differential changes in the salience of the X element in the intermixed and blocked schedules of pre-exposure could be due to the influence of a selective attention mechanism “in the spirit” of that proposed by Mackintosh (1975). According to Mackintosh, stimuli perceived as good predictors of their outcomes would be preferentially attended whereas those which are poor predictors would be ignored. During blocked pre-exposure, X is paired with A for a number of trials (and then with B in a separate block of trials). In this way, X could be said to be a good predictor of the unique elements A and B, and its salience should increase. In the intermixed pre-exposure schedule, however, X is paired with A and B in alternating trials and would therefore be perceived as a poor predictor of the

unique features A and B; as a consequence, the salience of X could be expected to decline. Artigas and Prados (2014) pointed out that the opposite prediction could be made, however, from other selective attention models. According to Pearce and Hall (1980), stimuli perceived as good predictors of their consequences would be ignored whereas stimuli whose consequences are not certain would be preferentially attended. In the absence of a clear criterion to select one attentional mechanism or the other, selective attention models would remain ambiguous.

A different approach would be to assume that selective attention depends upon different attentional mechanisms which refer to different aspects of the stimulus. The hybrid model proposed by Le Pelley (2004) and Pearce and Mackintosh (2010) assumes the existence of two different parameters that modulate how a stimulus would be processed: *attentional associability*, which determines which stimuli would have access to the learning process; and *salience associability*, which controls the rate at which each stimulus will be learnt. The former would vary according to the principles put forward by Mackintosh (1975), and can be identified as α ; the latter would vary according to the principles advocated by Pearce and Hall (1980), and can be identified as σ . Le Pelley (2004) has argued for the convenience in a hybrid model that the value of α varies between 0.05 and 1 whereas σ should adopt values between 0.5 and 1. The net associability of a stimulus would depend upon the interaction between these two parameters. In the blocked pre-exposure condition, where X is a good predictor of the unique elements A and B, the attentional associability would be high ($\alpha \approx 1$) whereas the salience associability would be relatively low ($\sigma \approx 0.5$). The net associability of the X element would therefore be relatively high ($\alpha \cdot \sigma \approx 0.5$). In the intermixed condition, however, where X is a poor predictor of A and B, attentional salience would tend to be low ($\alpha \approx 0.05$) whereas the salience associability would be high ($\sigma \approx 1$). The net

associability would therefore be lower than in the blocked condition ($\alpha \cdot \sigma \approx 0.05$). This would account for the lower conditioning of X after intermixed than blocked pre-exposure in the experiments reported by Mondragon and Murphy (2010) as well as for the perceptual learning transfer reported in the present Experiment 2.

To conclude, the present research adds to the previous report by Mondragon and Murphy (2010) in showing that the generality of the perceptual learning effect extends to standard appetitive Pavlovian tasks (Experiment 1). Furthermore, the present research confirms that pre-exposure to AX and BX improves the discriminability of two novel compound stimuli, NX and ZX, a perceptual learning transfer effect (Experiment 2). A way to account for the differential effectiveness of the common element X after intermixed and blocked pre-exposure is by reference to the way in which the compound stimuli AX and BX are processed: elemental in the case of intermixed pre-exposure, and configural in the case of the blocked pre-exposure. An elemental representation of the X element after intermixed pre-exposure would facilitate the generalization of the effects of pre-exposure (latent inhibition, habituation) to the element X when it is encountered in a novel context during the discrimination phase of the experiment. This generalization can be expected to be lower between the configural cues established during blocked pre-exposure (AX and BX) and the X element encountered during the discrimination task. As an alternative, a hybrid selective attentional model (Le Pelley, 2004; Pearce & Mackintosh, 2010) could provide a good explanation for the differences observed in the associability of X in the intermixed and blocked conditions.

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Table 1. Experimental Designs

	Group	Pre-exposure	Conditioning	Test
Experiment 1	Intermixed	AX / BX	AX +	BX
	Blocked	AX – BX	AX +	BX
Experiment 2	Intermixed	AX / BX	NX +	ZX
	Blocked	AX – BX	NX +	ZX

Note: A, B, N, Z and X represent different acoustic stimuli. Stimuli separated by a forward slash (/) in the Pre-exposure phase were presented on alternate trials; stimuli separated by a dash (–) were presented in separate blocks of trials. + represents the delivery of a food-US (two food pellets).

Figure 1

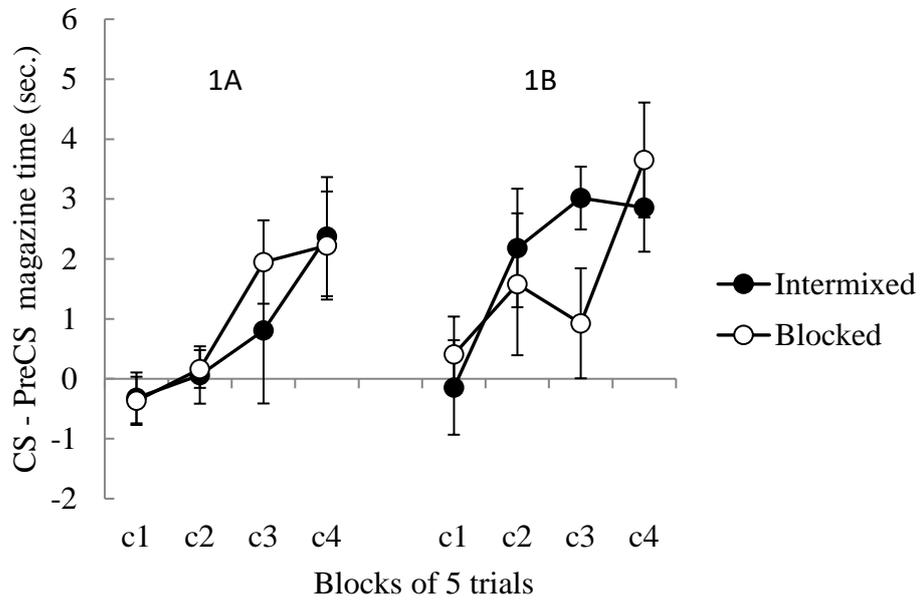


Figure 1. Mean time ($\pm SEM$) of magazine approach response calculated from difference scores (CS - PreCS) during the four blocks of conditioning trials with the compound AX for Groups Intermixed and Blocked in Experiment 1 (Experiment 1A, left hand panel; Experiment 1B, right hand panel).

Figure 2

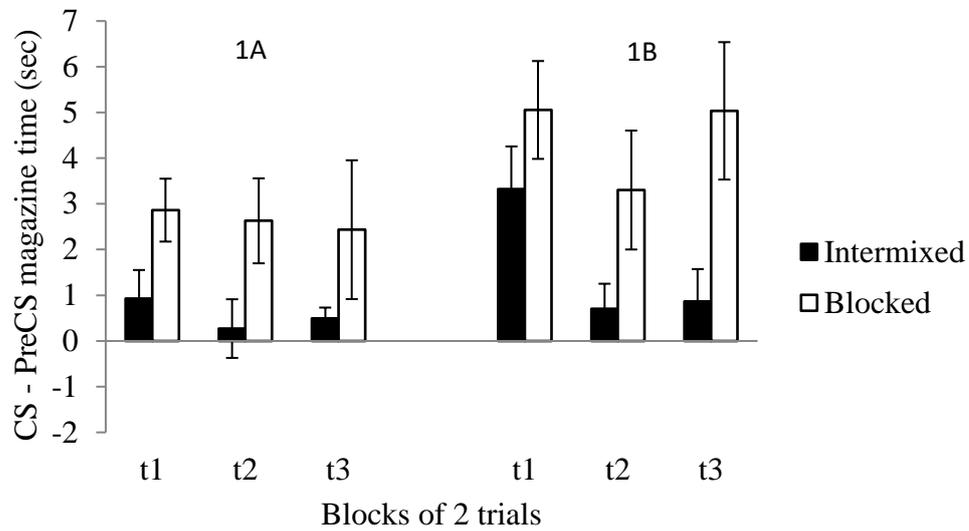


Figure 2. Mean time ($\pm SEM$) of magazine approach response calculated from difference scores (CS - PreCS) during the three blocks of test trials with the compound BX for Groups Intermixed and Blocked in Experiment 1 (Experiment 1A, left hand panel; Experiment 1B, right hand panel).

Figure 3

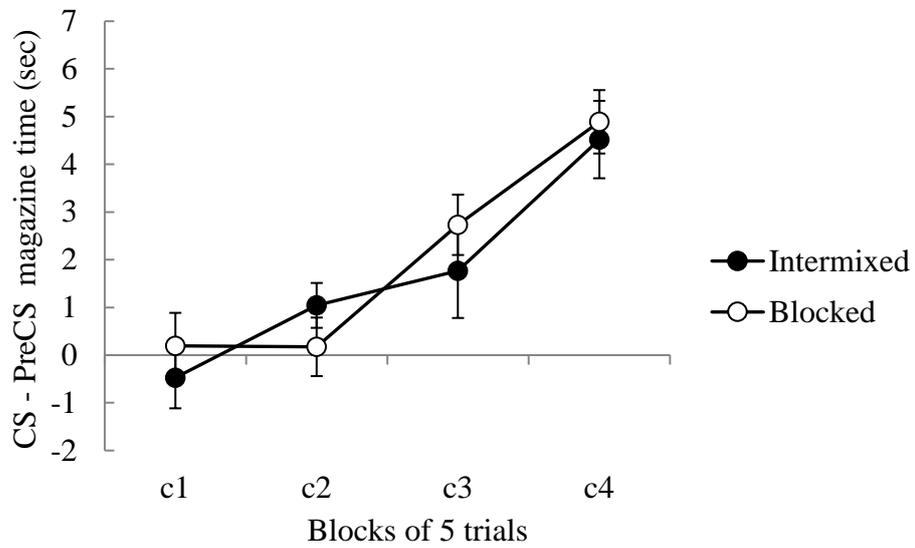


Figure 3. Mean time ($\pm SEM$) of magazine approach response calculated from difference scores (CS - PreCS) during the four blocks of conditioning trials with the compound NX for Groups Intermixed and Blocked in Experiment 2.

Figure 4

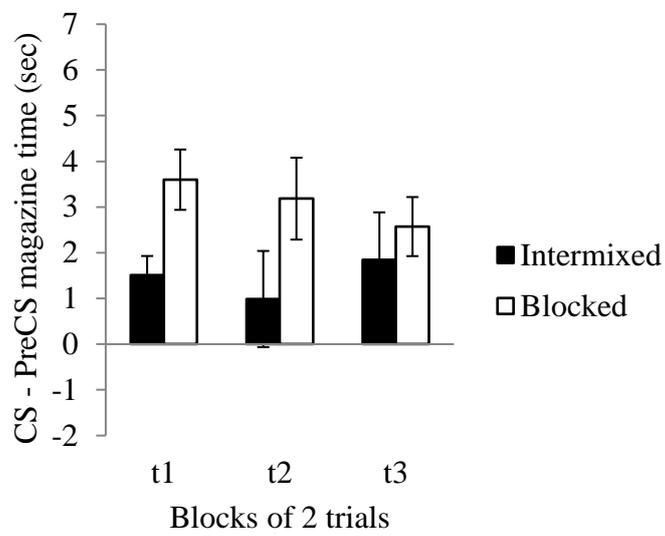


Figure 4. Mean time ($\pm SEM$) of magazine approach response calculated from difference scores (CS - PreCS) during the three blocks of test trials with the compound ZX for Groups Intermixed and Blocked in Experiment 2.