

Running head: Pre-exposure along a continuum

**Pre-exposure along a continuum: Differentiation and association**

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### **Abstract**

In five experiments, we assessed the effects of pre-exposure to simple auditory stimuli on subsequent conditioning and discrimination learning. Experiment 1 showed that pre-exposure to a single stimulus retarded acquisition of conditioned responding to that stimulus. The same pre-exposure regimen facilitated the subsequent acquisition of a discrimination between two stimuli that flanked the pre-exposed stimulus along the frequency dimension. Experiment 2 replicated this midpoint pre-exposure effect on discrimination learning but also found that alternating pre-exposure to the discriminative stimuli retarded discrimination learning. Experiments 3 to 5 explored the causes of these effects. These experiments are the first to examine perceptual learning in animals using simple auditory stimuli and their results suggest that in at least some circumstances alternating pre-exposure to auditory stimuli results in an increase in generalization between them.

Keywords: perceptual learning, discrimination, generalization, latent inhibition, auditory

### **Pre-exposure along a continuum: Differentiation and association**

Pre-exposure to two similar stimuli can enhance an animal's ability to discriminate between them. For example, Gibson and Walk (1956) reared two groups of rats in identical home-cages. Black metal shapes – triangles and circles – were attached to the walls of the home cages of the experimental group for a period of approximately 90 days following birth. These shapes were not present during rearing for a control group. All rats were later trained to discriminate between a circle and a triangle where one of the shapes was consistently paired with food and the other shape was paired with nothing. Rats in the experimental group made fewer errors than those in the control group over the course of training, and 15 out of 18 experimental rats learned the discrimination within 15 days whereas only one out of 11 control rats did so.

Several other studies have reported a similar *perceptual learning* effect for geometric shapes in rats (e.g., Channell & Hall, 1981; Gibson, Walk, Pick, & Tighe, 1958; Oswalt, 1972) and chicks (e.g., Honey, Bateson & Horn, 1994), and for complex visual stimuli in chicks (Honey & Bateson, 1996). Over the past 30 years, however, the majority of perceptual learning experiments involving rats have used compound flavours as stimuli and have measured generalization of a conditioned aversion from one flavour to the other. Mackintosh, Kaye and Bennett (1991) gave rats pre-exposure to saline-lemon and sucrose-lemon solutions (compounds AX and BX). Following pre-exposure, one of the compound flavours (AX) was paired with an unpleasant injection of lithium chloride (LiCl). In a later consumption test the rats drank substantially more of solution BX than of solution AX. A control group that was

given just water throughout the pre-exposure phase consumed very little of either solution at test. Pre-exposure to AX and BX reduced generalization between them.

Perceptual learning effects have been interpreted in terms of changes in the associability or effective salience of stimulus features as result of pre-exposure (Hall, 2003; McLaren, Kaye & Mackintosh, 1989; McLaren & Mackintosh, 2000). If AX and BX are both pre-exposed then their common feature, X, will be presented twice as frequently as each of the unique features, A and B. This should result in a greater decrease in the effective salience of X than of A or B. This will have two consequences. First, the unique features should enter into associations with an unconditioned stimulus more readily than the common feature (Lubow, 1973). Second, the relative salience of the unique features compared to the common feature should increase. A consequence of increasing the relative salience of A and B will be to reduce generalization of conditioning between AX and BX, facilitating the acquisition of a discrimination between those stimuli. If differential changes in the salience of common and unique features of stimuli contributes to perceptual learning, then it follows that pre-exposure to the common feature alone will also reduce generalization between two similar stimuli. Indeed, this is the case. In their second experiment Mackintosh et al (1991) found that pre-exposure to the X was sufficient to reduce generalization of a conditioned taste aversion from AX to BX.

In humans, there are numerous demonstrations of perceptual learning involving stimuli that differ along a simple perceptual dimension such as orientation (e.g., Schoups, Vogels & Orban, 1995; Vogels & Orban, 1985), vernier misalignment (e.g., McKee & Westheimer, 1978; Saarinen & Levi, 1995), or motion (e.g., Ball & Sekuler, 1982; Liu, 1999);

or along an artificial dimension (e.g., Dwyer, Mundy & Honey, 2011; Mundy, Downing, Dwyer, Honey & Graham, 2013; Mundy, Honey, Downing, Wise, Graham & Dwyer, 2009; Mundy, Honey & Dwyer, 2007). Using stimuli constructed by digitally morphing between two faces, Mundy et al (2007) assessed participants' ability to discriminate between a pair of faces either following pre-exposure to the test faces, to the mid-point between them, or neither. Consistent with the results of Mackintosh et al (1991), Mundy et al (2007) found that midpoint pre-exposure facilitated later discrimination learning, albeit to a lesser extent than alternating pre-exposure to the discriminative stimuli. Although these stimuli differed along a continuum, this perceptual learning effect can most likely be attributed to a reduction in salience of some features common to both the discriminative stimuli and the midpoint. A related effect was reported by Attneave (1957) who found that pre-exposure to a complex shape facilitated subsequent discrimination between novel forms generated by distorting the pre-exposed prototype.

There are, however, very few published studies of perceptual learning in non-human animals using simple stimuli that differ along a single perceptual dimension. Chamizo and Mackintosh (1989) found that discrimination learning in a maze was facilitated when rats were pre-exposed to the textured floor coverings that later served as discriminative stimuli, but these differed in both material and colour (red sandpaper vs. black rubber). Montuori and Honey (2016), however, conducted a systematic investigation of perceptual learning along a texture continuum using different grades of the same type of sandpaper. They found that alternating pre-exposure to rough and smooth sandpapers facilitated the later acquisition of a discrimination between them relative to a control group given no pre-exposure to sandpaper. They also reported a midpoint pre-exposure effect. Rats pre-exposed to 80 grit

sandpaper learned a discrimination between 40 and 100 grit papers more rapidly than non-pre-exposed controls. Montuori and Honey suggested that even simple stimuli that differ on a single dimension may be represented as collections of notional features, such that the representations of two stimuli may consist of a mixture of common and unique features. Reduction in the effective salience of features as a consequence of pre-exposure is sufficient to explain their results. The purpose of the experiments reported here was to explore the generality of Montuori and Honey's findings for a different perceptual dimension, auditory frequency. Although Mondragón and Murphy (2010; see also Artigas & Prados, 2017) have previously reported a perceptual learning effect using tones that differed in frequency, they presented them in compound with the common feature of white noise. Here we used pure tones or clickers that differed only in frequency which allowed us to explore the effects of pre-exposure to the midpoint between discriminative stimuli as well as pre-exposure to the stimuli themselves.

### **Experiment 1**

Experiment 1 was conducted to determine whether pre-exposure to the midpoint between two auditory stimuli would facilitate the subsequent acquisition of a discrimination between those stimuli. The design of the experiment is shown in the top row of Table 1. Two sets of auditory stimuli were employed: pure tones, separated by steps of one octave (500 Hz, 1 kHz, and 2 kHz); and trains of clicks generated by operating a heavy-duty electromechanical relay at frequencies separated by the same ratio as the tones (5 Hz, 10 Hz, and 20 Hz). Stimuli that differed from each other in intervals of an octave were chosen because perceptual learning effects are typically observed between stimuli that are similar,

rather than different, to each other (e.g., Honey, Bateson & Horn, 1994; Mackintosh et al, 1991; Oswald, 1972) and rats display strong octave generalization (Blackwell & Schlosberg, 1948). Since the stimuli were counterbalanced between subjects, for the sake of clarity we shall refer to these two sets of stimuli as A1, A2, and A3; and B1, B2, and B3.

Two groups of rats received training designed to confirm the efficacy of the pre-exposure regimen in reducing the effective salience of the pre-exposed stimulus and, by extension, those features common to all stimuli in each set. Rats in groups A2:A2+ and B2:A2+ received pre-exposure to the midpoint of one or other of the sets of stimuli; A2 or B2, respectively. All rats then experienced simple conditioning trials in which presentations of A2 were paired with the delivery of food. A third groups of rats, A2:A1+/A3 $\emptyset$ , was pre-exposed to the midpoint of one continuum, A2, before being trained on a discrimination between the end points of that continuum, A1 and A3. Presentations of A1 were consistently followed by the delivery of a food pellet reward, whereas presentations of A3 were not. Rats in a control group, B2:A1+/A3 $\emptyset$ , received exactly the same discrimination training with stimuli A1 and A3 in the second stage of the experiment, but were pre-exposed to the midpoint of the alternative stimulus continuum, B2, during the first stage of the experiment. Hence, rats in the B2: groups received the same amount of exposure to the experimental apparatus as those in A2: groups and were similarly exposed to presentation of a brief auditory stimulus in the absence of food reward. The only difference in the treatment of the two sets of groups was in the similarity of the pre-exposed cue to the conditioning or discriminative cues presented subsequently.

If pre-exposure to the midpoint of a continuum causes a reduction in the salience of features common to stimuli on that continuum, then acquisition of a discrimination between the endpoints should be facilitated following pre-exposure. Hence, rats in group A2:A1+/A3 $\emptyset$  were expected to acquire the stage two discrimination more readily than rats in group B2:A1+/A3 $\emptyset$  which were not pre-exposed to the midpoint.

## Method

**Subjects.** The subjects were 32 experimentally naïve male Lister hooded rats (*Rattus norvegicus*). Prior to the start of the experiment they were placed on a restricted diet and were maintained at 85% of their age-matched ad libitum weights throughout the experiment. The rats had free access to water in their home cages. They were housed in pairs in a light-proof holding room maintained on a 14h light/10h dark cycle (lights on from 6 am to 8 pm). The subjects were tested on successive days, at the same time, during the period that the lights were on in their holding room. Prior to the start of the experiments, the rats were divided into four groups of eight. All procedures complied with the UK Animals (Scientific Procedures) Act 1986 and were subject to Home Office approval.

**Apparatus.** Four standard conditioning chambers were used (Med Associates Inc., St. Albans, VT) each housed within a sound attenuating, ventilated enclosure and arranged in a 2 x 2 array. Each chamber measured 30.5 cm x 24.1cm x 21.0 cm. The left and right walls of the chamber were aluminium, whereas the rear wall, ceiling, and a door which served as the front wall were made of clear Plexiglass. The grid floor of the chamber consisted of 19 steel rods 4.8 mm in diameter, spaced 1.6 cm apart. A recessed 5.1 cm x 5.1 cm food magazine, into which 45 mg food pellets (TestDiet, Richmond, IN) could be delivered, was located in the

middle of the right-hand wall, with its base 0.5 cm above the grid floor. Food reward always consisted of a pair of food pellets, delivery of which was separated by a 200 ms interval. Access to the magazine was recorded by means of infrared detectors mounted across the mouth of the recess. Retractable levers were fitted on either side of the food magazine but remained withdrawn throughout the experiment. Two panel lights (2 W; diameter, 2.5 cm) were located in the right-hand wall above the levers and a houselight (2.8 W; diameter, 1.25 cm) was situated at the top centre of the opposite wall. An 8  $\Omega$  speaker mounted on the rear wall of the chamber delivered 500 Hz, 1 kHz, and 2 kHz tones. A heavy-duty relay, also mounted on the rear wall, was used to generate 5 Hz, 10 Hz, and 20 Hz trains of clicks. All experimental events were controlled by, and responses recorded by, a PC running Med-PC IV software (Med Associates Inc.).

For half of the rats, stimuli identified by the letter 'A' were tones, and for the remaining rats they were clickers. When the 'A' stimuli were tones, for rats in B2: groups the stimuli identified by the letter 'B' were clicks, and vice versa. A2 and B2 were a 1 kHz tone and a 10 Hz train of clicks. For half of the rats in groups A2:A1+/A3 $\emptyset$  and B2:A1+/A3 $\emptyset$ , A1 was either a 500 Hz tone or a 5 Hz train of clicks, whereas A3 was either a 2-Hz tone or a 20-Hz train of clicks. For the remaining rats in these groups the assignment of these stimuli to A1 and A3, and to B1 and B3, was reversed.

### **Procedure**

***Pre-exposure.*** All rats were given five 48-min sessions of pre-exposure with either A2 or B2. Rats in A2: groups received 16 10-sec presentations of A2 in each session, whereas rats in the B2: control groups received 16 10-sec presentations of B2. The mean inter-trial interval

(ITI), measured from the onset of one trial to the onset of the next was 180 sec (range  $\pm 15\%$ ). No food pellets were delivered during pre-exposure.

**Magazine training.** On each of the two days following pre-exposure, all rats received one 15-min session of magazine training in which food pellets were delivered according to a random-time, 60 s schedule.

**Training.** Over the following four sessions, rats in groups A2:A2+ and B2:A2+ received conditioning with stimulus A2. All details of these sessions are the same as for the pre-exposure sessions, with the exception that food pellets were delivered coincident with the termination of the stimulus.

Rats in groups A2:A1+/A3 $\emptyset$  and B2:A1+/A3 $\emptyset$  were trained on a discrimination between A1 and A3 over four sessions. Within a session, A1 and A3 were each presented eight times. Presentations of A1 were followed by the delivery of food, whereas presentations of A3 were not. Trials were presented in a pseudorandom sequence with the constraints that the same stimulus could not be presented more than twice in a row and that each stimulus was presented four times in each half of the session. All other details were the same as for the pre-exposure sessions.

### **Data Analysis**

No data were collected during the pre-exposure phase. During magazine training, the total number of magazine entry responses (interruptions of the infrared beam in the magazine recess) over a session was counted and divided by 15 to give a response rate per minute. For the training phase, magazine responses were recorded during the 10 s

presentation of the stimuli, and during a 10 s pre-stimulus period immediately prior to stimulus presentation. Elevation scores were calculated by taking the difference between these numbers, which were then converted into response rates per minute by multiplying them by six. Scores were averaged over eight blocks of trials, each corresponding to one half of a session of training.

Data were analysed using mixed analyses of variance (ANOVA) and all statistical tests were evaluated against an alpha level of .05. Preliminary analyses were conducted which included counterbalancing conditions (whether stimuli A1-A3 were tones or clicks, and whether A1 or A3 was the high frequency stimulus) as factors. In no case, for this or subsequent experiments, was there a significant main effect of either counterbalancing factor, or a significant interaction involving counterbalancing. Consequently, to simplify the presentation and interpretation of the statistical tests, counterbalancing condition was not included in the analyses reported below.

## Results

**Magazine training.** Over the course of magazine training, the mean number of magazine entry responses made by rats in groups A2:A2+, B2:A2+, A2:A1+/A3 $\emptyset$ , and B2:A1+/A3 $\emptyset$  was 14.0 (standard error of the mean = 1.2), 12.9 (1.6), 14.8 (1.3), and 14.7 (1.0) responses per minute, respectively. Two-sample *t*-tests revealed no difference in the number of magazine entries made by groups A2:A2+ and B2:A2+,  $t < 1$ ; or by groups A2:A1+/A3 $\emptyset$  and B2:A1+/A3 $\emptyset$ ,  $t < 1$ .

**Pre-stimulus response rates.** The rate of responding during the pre-stimulus period declined over the course of training but did not differ between groups. Averaged across all

eight half-session blocks, the rates of pre-stimulus responding for groups A2:A2+, B2:A2+, A2:A1+/A3 $\emptyset$ , and B2:A1+/A3 $\emptyset$  were 4.1 (.6), 5.0 (.8), 3.2 (.8), and 2.6 (.4), respectively. During the first half-session block, rats made an average of 6.4 (.9) responses per minute, and during the final block an average of 1.5 (.3) responses per minute. These data were analysed using two separate two-way ANOVAs, the first comparing groups A2:A2+ and B2:A2+ and the second for groups A2:A1+/A3 $\emptyset$  and B2:A1+/A3 $\emptyset$ . Neither analysis found a significant effect of group,  $F_s < 1$ , or an interaction of group with trial block, largest  $F(7, 98) = 1.51, P = .173$ . In both cases there was a significant effect of trial block, smallest  $F(7, 98) = 2.94, MSE = 9.66, P = .008, \eta^2_p = .173, 90\% CI [.028 .233]$ .

**Conditioning.** Rats that had been pre-exposed to A2 acquired conditioned responding to A2 less rapidly than rats that had been pre-exposed to B2. The top panel of Figure 1 shows the mean elevation scores for the eight (half-session) blocks of conditioning trials. A two-way ANOVA of individual mean elevation scores for rats in each group (A2:A2+, B2:A2+) and for each half-session block (1 to 8) revealed no significant effect of group,  $F < 1$ , but a significant effect of block,  $F(7, 98) = 26.86, MSE = 116.97, P < .001, \eta^2_p = .657, 90\% CI [.539 .702]$ , and a significant Group x Block interaction,  $F(7, 98) = 2.25, MSE = 116.97, P = .037, \eta^2_p = .138, 90\% CI [.005 .191]$ . Subsequent simple effects analyses conducted on the Group x Block interaction revealed a significant effect of group on block 4,  $F(1, 112) = 5.83, MSE = 168.14, P = .017$ . There was no effect of group on any other block (largest  $F(1, 112) = 2.05, P = .156$ ).

<Figure 1 about here>

**Discrimination training.** Rats in group A2:A1+/A3 $\emptyset$  acquired the discrimination more rapidly than those in group B2:A1+/A3 $\emptyset$ . The bottom panel of Figure 1 shows the elevation

scores for rats in each group during presentations of A1 and A3 over the four sessions of training, in half-session blocks. A three-way ANOVA of individual mean elevation scores revealed significant effects of stimulus,  $F(1, 14) = 54.61$ ,  $MSE = 94.93$ ,  $P < .001$ ,  $\eta^2_p = .796$ , 90% CI [.559 .865], and of block,  $F(7, 98) = 19.88$ ,  $MSE = 81.18$ ,  $P < .001$ ,  $\eta^2_p = .587$ , 90% CI [.451 .639]. There was no significant effect of group,  $F < 1$ , and no Group x Block interaction,  $F < 1$ . There were significant interactions of stimulus with group,  $F(1, 14) = 6.65$ ,  $MSE = 94.93$ ,  $P = .022$ ,  $\eta^2_p = .322$ , 90% CI [.029 .544], and with block,  $F(7, 98) = 14.39$ ,  $MSE = 39.67$ ,  $P < .001$ ,  $\eta^2_p = .507$ , 90% CI [.355 .567], as well as a significant three-way interaction,  $F(7, 98) = 3.06$ ,  $MSE = 39.67$ ,  $P = .006$ ,  $\eta^2_p = .179$ , 90% CI [.032 .239].

Simple effects analyses conducted on the Group x Stimulus x Block interaction revealed that rats in group A2:A1+/A3 $\emptyset$  responded more rapidly during the presentation of the reinforced stimulus than animals in group B2:A1+/A3 $\emptyset$ . This difference was significant on trial block 6,  $F(1, 224) = 6.62$ ,  $MSE = 76.47$ ,  $P = .011$ . Furthermore, rats in group A2:A1+/A3 $\emptyset$  showed differential responding to the reinforced and non-reinforced stimuli earlier in training than rats in group B2:A1+/A3 $\emptyset$ . There was a significant difference in the rates of responding to A1 and A3 for group A2:A1+/A3 $\emptyset$  on blocks 4-8, smallest  $F(1, 112) = 13.96$ ,  $MSE = 46.58$ ,  $P < .001$ , and for group B2:A1+/A3 $\emptyset$  only on blocks 7 and 8, smallest  $F(1, 112) = 9.81$ ,  $MSE = 46.58$ ,  $P = .002$ . The effect of stimulus was not significant on blocks 1-3 for the group A2:A1+/A3 $\emptyset$ , all  $F_s < 1$ , or on blocks 1-6 for group B2:A1+/A3 $\emptyset$ , largest  $F(1, 122) = 1.21$ ,  $MSE = 46.58$ ,  $P = .274$ .

## Discussion

The results of Experiment 1 confirm that the pre-exposure regimen was effective in reducing the associability or effective salience of the pre-exposed stimulus. Acquisition of conditioned responding to A2 was slower for rats that had previously been pre-exposed to A2 than for rats that had been pre-exposed to B2. Pre-exposure to the midpoint between two auditory stimuli facilitated the subsequent discrimination between those stimuli. This effect is consistent with the notion that the three stimuli shared certain features in common, and that pre-exposure to A2 reduced the effective salience of some of those features common to A1 and A3, reducing generalization of conditioning between those stimuli. Experiment 2 was conducted to determine whether a conventional perceptual learning effect, as well as this midpoint pre-exposure effect, could be obtained with the same simple auditory cues.

## Experiment 2

Although a reduction in the effective salience of common features has been proposed as one mechanism of perceptual learning, pre-exposure to the common features (or midpoint) alone is not the most commonly used, nor always the most effective, method for producing a perceptual learning effect. Perceptual learning has been found after pre-exposure to the discriminative stimuli themselves in a number of preparations including visual discrimination learning (e.g., Gibson & Walk, 1956), maze learning (e.g., Trobalon, Sansa, Chamizo & Mackintosh, 1991), navigation in a water maze (e.g., Prados, Chamizo & Mackintosh, 1999), conditioned flavour aversion (e.g., Mackintosh, Kaye & Bennett, 1991; Rodríguez, Blair & Hall, 2008; Symmonds & Hall, 1995), texture discrimination learning (Montouri & Honey, 2016), and auditory discrimination learning (Artigas & Prados, 2017;

Mondragón & Murphy, 2010). Indeed, alternating pre-exposure has, on occasion, been found to result in the largest reduction in generalization between two stimuli (e.g., Dwyer, Hodder & Honey, 2004; Honey, Bateson & Horn, 1994; Mundy et al., 2007; Symonds & Hall, 1995). For example, Mundy et al. (2007, Experiment 2), found that alternating pre-exposure to two faces improved subsequent discrimination between those faces more than pre-exposure to the midpoint between them. Montuori and Honey (2016) did not directly compare the effects of midpoint exposure and exposure to the discriminative stimuli in the same experiment, but they did employ the two manipulations in separate experiments involving the same discrimination (their Experiments 1 and 3a). Inspection of their data suggests a similar difference. This effect may be explained by at least two different accounts of perceptual learning (Hall, 2003; McLaren and Mackintosh, 2000), but we shall reserve discussion of these models until later.

The aims of Experiment 2 were to replicate the midpoint pre-exposure effect observed in Experiment 1 and to determine the effect of alternating pre-exposure to A1 and A3 using the same simple auditory stimuli. Consequently, two groups of rats in Experiment 2 received the same pre-exposure and training as rats in the midpoint pre-exposure groups in Experiment 1, A2:A1+/A3 $\emptyset$  and B2:A1+/A3 $\emptyset$ . Two other groups of rats received alternating pre-exposure to two stimuli. Group A1/A3:A1+/A3 $\emptyset$  were pre-exposed to A1 and A3 in an alternating sequence, whereas a group B1/B3:A1+/A3 $\emptyset$  were pre-exposed to B1 and B3. In each case, the rate of learning of a discrimination between A1 and A3 was assessed.

## Method

**Subjects and apparatus.** The subjects were 32 naïve male Lister hooded rats from the same stock and housed in the same manner as those in Experiment 1. At the start of the experiment, the rats were divided into four groups of eight. The apparatus and stimuli were the same as for Experiments 1 and the stimuli were counterbalanced in the same way.

### Procedure

**Pre-exposure.** Rats in groups A2:A1+/A3 $\emptyset$  and B2:A1+/A3 $\emptyset$  received five sessions of pre-exposure to either A2 or B2 in the same manner as described for the groups with the same names in Experiment 1.

Rats in groups A1/A3:A1+/A3 $\emptyset$  and B1/B3:A1+/A3 $\emptyset$  were given five 48-min sessions of pre-exposure with either A1 and A3 or B1 and B3. Rats in the group A1/A3:A1+/A3 $\emptyset$  received eight 10-sec presentations of each of A1 and A3 in every session, whereas rats in group B1/B3:A1+/A3 $\emptyset$  received eight 10-sec presentations of each of B1 and B3. Stimuli were presented in an alternating sequence. For half of the rats in group A1/A3:A1+/A3 $\emptyset$  the first trial of each session was A1, whereas for the remaining rats the first trial of each session was with A3. Similarly, the first trial of each session was with B1 for half of the rats in group B1/B3:A1+/A3 $\emptyset$  and with B3 for the other rats. All other details of the experiment were the same as for Experiment 1.

**Magazine training.** On each of the two days following pre-exposure, all rats received one 15-min session of magazine training in which food-pellets were delivered according to a random-time, 60 s schedule.

**Training.** All rats were trained on a discrimination between A1 and A3 over four sessions. All procedural details were the same as for Experiment 1.

## Results

**Magazine training.** Over the course of magazine training, the mean number of magazine entry responses made by rats in groups A2:A1+/A3 $\emptyset$ , B2:A1+/A3 $\emptyset$ , A1/A3:A1+/A3 $\emptyset$ , and B1/B3:A1+/A3 $\emptyset$  was 11.9 (1.1), 12.9 (1.1), 16.2 (1.0), and 14.2 (1.3) responses per minute, respectively. Two-sample *t*-tests revealed no difference in the number of magazine entries made by groups A2:A1+/A3 $\emptyset$  and B2:A1+/A3 $\emptyset$ ,  $t < 1$ , or by groups A1/A3:A1+/A3 $\emptyset$  and B1/B3:A1+/A3 $\emptyset$ ,  $t(14) = 1.23$ ,  $P = .238$ .

**Pre-stimulus response rates.** The mean rate of responding during the pre-stimulus period was 6.2 (.6) and 6.8 (.5) for groups A2:A1+/A3 $\emptyset$  and B2:A1+/A3 $\emptyset$ , and 5.7 (.8) and 5.5 (1.1) for groups A1/A3:A1+/A3 $\emptyset$  and B1/B3:A1+/A3 $\emptyset$ . Responding declined over the course of discrimination training from 8.1 (.6) responses per minute during the first half-session block to 3.3 (.5) on during the final block. ANOVA conducted on the data for each pair of groups found no effect of group and no Group x Block interaction,  $F_s < 1$ . There were significant effects of trial block in both cases, smallest  $F(7, 98) = 3.00$ ,  $MSE = 11.69$ ,  $P = .007$ ,  $\eta^2_p = .177$ , 90% CI [.030 .236].

**Mid-point pre-exposure.** Acquisition of the discrimination by rats in group A2:A1+/A3 $\emptyset$  was more rapid than for those in group B2:A1+/A3 $\emptyset$ , replicating the results of Experiment 1. Elevation scores for rats in the two groups over eight half-session blocks of training are shown in the top panel of Figure 2. A three-way ANOVA of these elevation scores revealed a significant three-way interaction,  $F(7, 98) = 3.08$ ,  $MSE = 75.56$ ,  $P = .006$ ,  $\eta^2_p = .180$ ,

90% CI [.033 .241]. Simple effects analyses conducted on the three-way interaction found that rats in group A2:A1+/A3 $\emptyset$  responded significantly faster in the presence of A1 than rats in group B2:A1+/A3 $\emptyset$  on blocks 3-5, smallest  $F(1, 224) = 4.37$ ,  $MSE = 140.17$ ,  $P = .038$ , and on block 7,  $F(1, 224) = 4.50$ ,  $MSE = 140.17$ ,  $P = .035$ . Group A2:A1+/A3 $\emptyset$  also acquired the discrimination between A1 and A3 earlier than rats in group B2:A1+/A3 $\emptyset$ ; there was a significant difference in the rates of responding to A1 and A3 for group A2:A1+/A3 $\emptyset$  on blocks 4-8, smallest  $F(1, 112) = 8.89$ ,  $MSE = 111.65$ ,  $P = .004$ , and for group B2:A1+/A3 $\emptyset$  on blocks 6-8, smallest  $F(1, 112) = 9.10$ ,  $MSE = 111.65$ ,  $P < .003$ . The effect of stimulus was not significant on blocks 1-3 for group A2:A1+/A3 $\emptyset$  largest  $F(1, 112) = 6.67$ ,  $P = .058$ , or on blocks 1-5 for group B2:A1+/A3 $\emptyset$ , largest  $F(1, 112) = 2.22$ ,  $P = .139$ .

The ANOVA also revealed significant effects of stimulus,  $F(1, 14) = 24.33$ ,  $MSE = 364.22$ ,  $P < .001$ ,  $\eta^2_p = .635$ , 90% CI [.412 .809], and of block,  $F(7, 98) = 35.01$ ,  $MSE = 147.05$ ,  $P < .001$ ,  $\eta^2_p = .708$ , 90% CI [.605 .747] and a significant interaction of stimulus with block,  $F(7, 98) = 25.38$ ,  $MSE = 75.56$ ,  $P < .001$ ,  $\eta^2_p = .645$ , 90% CI [.523 .690]. There was no effect of group,  $F(1, 14) = 2.50$ ,  $P = .136$ ,  $MSE = 320.16$ , and no Group x Stimulus,  $F(1, 14) = 2.53$ ,  $MSE = 364.22$ ,  $P = .134$ , or Group x Block interactions,  $F(7, 98) = 1.47$ ,  $MSE = 147.05$ ,  $P = .189$ .

<Figure 2 about here>

**Alternating pre-exposure.** The bottom panel of Figure 2 shows elevation scores for rats in each group during presentations of A1 and A3 over the four sessions of training, in half-session blocks. In contrast to the effects of midpoint pre-exposure, rats in the experimental group, A1/A3:A1+/A3 $\emptyset$ , acquired the discrimination less rapidly than those in the control group, B1/B3:A1+/A3 $\emptyset$ . A three-way ANOVA of the elevation scores revealed a significant

interaction of stimulus with group,  $F(1, 14) = 5.27$ ,  $MSE = 233.31$ ,  $P = .038$ ,  $\eta^2_p = .273$ , 90% CI [.009 .506]. Simple effects analyses conducted on this interaction showed significantly faster responding by group B1/B3:A1+/A3 $\emptyset$  than by group A1/A3:A1+/A3 $\emptyset$  during A1,  $F(1, 28) = 5.26$ ,  $MSE = 495.76$ ,  $P = .030$ , but no difference between the groups for responding during A3,  $F < 1$ . There were also significant differences in the rates of responding to A1 and to A3 for both group A1/A3:A1+/A3 $\emptyset$ ,  $F(1, 14) = 14.85$ ,  $MSE = 233.31$ ,  $P = .002$ , and group B1/B3:A1+/A3 $\emptyset$ ,  $F(1, 14) = 50.41$ ,  $MSE = 233.31$ ,  $P < .001$ .

There were also significant effects of stimulus,  $F(1, 14) = 60.00$ ,  $MSE = 233.31$ ,  $P < .001$ ,  $\eta^2_p = .811$ , 90% CI [.587 .875], and of block,  $F(7, 98) = 21.16$ ,  $MSE = 176.71$ ,  $P < .001$ ,  $\eta^2_p = .602$ , 90% CI [.469 .652]. There was a significant interaction of stimulus with block,  $F(7, 98) = 17.28$ ,  $MSE = 98.49$ ,  $P < .001$ ,  $\eta^2_p = .522$ , 90% CI [.409 .608], reflecting acquisition of the discrimination. There was no significant effect of group,  $F(1, 14) = 1.82$ ,  $MSE = 758.21$ ,  $P = .199$ , no Group x Block interaction,  $F < 1$ , and no significant three-way interaction,  $F(7, 98) = 1.47$ ,  $MSE = 98.49$ ,  $P = .186$ .

## Discussion

In this experiment, we replicated the mid-point pre-exposure effect observed in Experiment 1 but failed to find a beneficial effect of pre-exposure to the discriminative cues themselves. Channell and Hall (1981) also found that under some circumstances pre-exposure could retard discrimination learning using a task very similar to Gibson & Walk's (1956). Pre-exposure to horizontally and vertically striped plastic squares in rats' homecages facilitated subsequent discrimination between them in a jumping stand apparatus. If, however, the stimuli were pre-exposed in the jumping stand itself, acquisition of this discrimination was

retarded. One explanation for these results is that the pre-exposure resulted in substantial latent inhibition to both the common and unique features of the two stimuli, and that a context change between pre-exposure and learning caused a release from this latent inhibition, enabling a facilitation of learning to be observed. Hence, the pre-exposure regimen employed in the current experiment might have resulted in a massive reduction in the salience of both the common and unique features of A1 and A3 for group A1/A3:A1+/A3 $\emptyset$ , retarding the acquisition of differential responding to those cues during discrimination training. One purpose of the remaining experiments (3, 4, and 5) was to explore this possibility.

Alternatively, alternating pre-exposure to A1 and A3 may have allowed the development of excitatory associations between the unique and common features of each stimulus, resulting in mediated associations between the unique features of the two. Iordanova and Honey (2012) found evidence for such mediated generalization following pre-exposure to contexts. They gave rats fear conditioning in context B and then recorded freezing responses in contexts A and C. Rats that had received alternating pre-exposure to contexts A and B showed more freezing in context A than in context C. Equivalent levels of freezing to contexts A and C were observed in rats pre-exposed either to context A alone, or to contexts A and D. That is, alternating pre-exposure to contexts A and B resulted in an increase in generalization between the two contexts. Iordanova and Honey suggested that their contexts might be represented as collections of features unique to each ( $a$ ,  $b$ ,  $c$ ,  $d$ ) and features common to all ( $x$ ). Pre-exposure to contexts A and B allowed excitatory associations to form between the features of each ( $a-x$  and  $b-x$ ). Thence, the unique features of context B might

have been associative activated by the common  $x$  features when a rat was placed in context A. This mediated association explanation of our results will be further explored in Experiment 5.

### Experiment 3

The midpoint pre-exposure effect observed in Experiments 1 and 2 suggests that there is significant overlap between the representations of A1, A2, and A3. Hence, if alternating pre-exposure results in a reduction in the effective salience of A1 and A3, one might expect that this treatment will retard the acquisition of conditioned responding to A2 also. The purpose of Experiment 3 was to replicate the retarding effect of pre-exposure to A1 and A3 on the acquisition of a discrimination between those stimuli, and to determine whether the same pre-exposure regimen affected conditioning to A2. Hence, two groups of rats, A1/A3:A1+/A3 $\emptyset$  and A1/A3:A2+, received alternating pre-exposure to A1 and A3, whereas two other groups, B1/B3:A1+/A3 $\emptyset$  and B1/B3:A2+, were pre-exposed to B1 and B3. Subsequently, groups A1/A3:A1+/A3 $\emptyset$  and B1/B3:A1+/A3 $\emptyset$  were trained on a discrimination between A1 and A3, replicating the treatment received by the groups of the same names Experiment 2. The remaining groups, A1/A3:A2+ and B1/B3:A2+, received conditioning trials with A2.

### Method

**Subjects and apparatus.** The subjects were 32 naïve male Lister hooded rats from the same stock and housed in the same manner as those in Experiment 1. At the start of the experiment, the rats were divided into four groups of eight. The stimuli and apparatus were the same as for the previous experiments.

## Procedure

**Pre-exposure.** Rats in Experiment 3 received five sessions of pre-exposure either to A1 and A3 or to B1 and B3 in the same manner as described for groups A1/A3:A1+/A3 $\emptyset$  and B1/B3:A1+/A3 $\emptyset$  in Experiment 2.

**Magazine training.** On each of the two days following pre-exposure, all rats received one 15-min session of magazine training in which food-pellets were delivered according to a random-time, 60 s schedule.

**Training.** After magazine training, rats in groups A1/A3:A1+/A3 $\emptyset$  and B1/B3:A1+/A3 $\emptyset$  were trained on a discrimination between A1 and A3 in the manner described for groups A2:A1+/A3 $\emptyset$  and B2:A1+/A3 $\emptyset$  in Experiment 1. Rats in groups A1/A3:A2+ and B1/B3:A2+ received four sessions of conditioning in which stimulus A2 was paired with the delivery of food in the manner described for groups A2:A2+ and B2:A2+ in Experiment 1.

## Results and discussion

**Magazine training.** Over the course of magazine training, the mean number of magazine entry responses made by rats groups A1/A3:A1+/A3 $\emptyset$ , B1/B3:A1+/A3 $\emptyset$ , A1/A3:A2+, and B1/B3:A2+ was 12.7(1.3), 13.3 (1.1), 13.9 (1.9), and 14.9 (1.4) responses per minute, respectively. Two-sample *t*-tests revealed no difference in the number of magazine entries made by groups A1/A3:A1+/A3 $\emptyset$  and B1/B3:A1+/A3 $\emptyset$ , or by groups A1/A3:A2+ and B1/B3:A2+, *ts* < 1.

**Pre-stimulus response rates.** There was no significant difference in the rate of responding during the pre-stimulus period for groups A1/A3:A1+/A3 $\emptyset$  (7.2 [.9]) and

B1/B3:A1+/A3 $\emptyset$  (6.5 [1.0]), or for groups A1/A3:A2+ (6.0 [1.0]) and B1/B3:A2+ (5.2 [1.2]). Over the course of training, pre-stimulus response rates declined from 9.3 (1.0) to 3.1 (.4) responses per minute. ANOVA conducted on the data from each pair of groups found no effect of group or interaction with trial block,  $F_s < 1$ , but significant effects of block, smallest  $F(7, 98) = 5.24$ ,  $MSE = 17.72$ ,  $P < .001$ ,  $\eta^2_p = .272$ , 90% CI [.108 .340].

**Discrimination learning.** The top panel of Figure 3 shows elevation scores for rats in groups A1/A3:A1+/A3 $\emptyset$  and B1/B3:A1+/A3 $\emptyset$  in the presence of A1 and A3 over the four sessions of training, in half-session blocks. These results replicated the effect seen in Experiment 2: rats that had been pre-exposed to A1 and A3 acquired a discrimination between these stimuli less rapidly than a control group which had been pre-exposed to B1 and B3. A three-way ANOVA revealed a significant interaction of stimulus with group,  $F(1, 14) = 6.87$ ,  $MSE = 204.84$ ,  $P = .020$ ,  $\eta^2_p = .329$ , 90% CI [.032 .549]. Simple effects analyses conducted on this interaction revealed that group B1/B3:A1+/A3 $\emptyset$  responded more in the presence of the cue paired with food, A1, than in the presence of the cue that was not paired with food, A3,  $F(1, 14) = 18.00$ ,  $MSE = 204.84$ ,  $P = .001$ , but that group A1/A3:A1+/A3 $\emptyset$  did not,  $F < 1$ .

The ANOVA also revealed significant effects of stimulus,  $F(1, 14) = 11.42$ ,  $MSE = 204.84$ ,  $P = .004$ ,  $\eta^2_p = .449$ , 90% CI [.107 .635], and of block,  $F(7, 98) = 33.04$ ,  $MSE = 102.93$ ,  $P < .001$ ,  $\eta^2_p = .702$ , 90% CI [.597 .741], and a significant Stimulus x Block interaction,  $F(7, 98) = 4.82$ ,  $MSE = 90.75$ ,  $P < .001$ ,  $\eta^2_p = 0.256$ , 90% CI [.094 .323]. There was no significant effect of group, no Group x Block interaction, and no three-way interaction,  $F_s < 1$ .

<Figure 3 about here>

**Conditioning.** The results for groups A1/A3:A2+ and B1/B3:A2+ are shown in the bottom panel of Figure 3. Rats in group A1/A3:A2+ which had experienced presentations of stimuli A1 and A3 in the absence of food reward, and those in group B1/B3:A2+ which had similar experience of B1 and B3 acquired conditioned responding to stimulus A2 at the same rate when it was paired with food.

This observation was confirmed by a two-way ANOVA of individual mean elevation scores for rats in each group (A1/A3:A2+, B1/B3:A2+) for each session of training (1 to 8) which found no effect of group, and no Group x Block interaction,  $F_s < 1$ . Furthermore, on no individual trial block was there a difference between the two groups even approaching significance, largest  $F(1, 112) = 1.12$ ,  $MSE = 183.85$ ,  $P = .293$ . The effect of block was significant,  $F(7, 98) = 22.52$ ,  $MSE = 118.38$ ,  $P < .001$ ,  $\eta^2_p = .617$ , 90% CI [.488 .666].

Experiment 3 confirmed the results of Experiment 2; pre-exposure to A1 and A3 retarded acquisition of a discrimination between those cues. There was, however, no evidence that this same schedule of pre-exposure had any influence on the rate of conditioning to A2.

#### Experiment 4

Although there was no evidence that alternating pre-exposure to A1 and A3 retarded conditioning to A2 in Experiment 3, it is possible that our testing procedure was not sufficiently sensitive to detect an effect, and null results should be interpreted with caution. Experiment 4 was conducted to determine whether the absence of the effect could be replicated, while at the same time confirming that our procedures were sensitive enough to detect difference in the rate of conditioning following pre-exposure to stimulus A2.

Two groups of rats, A2:A2+ and B2:A2+, received the same training as the corresponding groups in Experiment 1; they were pre-exposed to either A2 or to B2 and then received conditioning trials in which A2 was paired with food. Another two groups of rats, A1/A3:A2+ and B1/B3:A2+, were treated in the same way as the corresponding groups in Experiment 3. Conditioning trials with A2 followed pre-exposure to either A1 and A3 or to B1 and B3.

## Method

**Subjects and apparatus.** The subjects were 32 naïve male Lister hooded rats from the same stock and housed in the same manner as those in Experiment 1. At the start of the experiment, the rats were divided into four groups of eight. The stimuli and apparatus were the same as for the previous experiments.

### Procedure

**Pre-exposure.** Rats in groups A2:A2+ and B2:A2+ received five sessions of pre-exposure to either A2 or B2 in the same manner as described for Experiments 1 and 2.

Rats in groups A1/A3:A2+ and B1/B3:A2+ were given five sessions of pre-exposure with either A1 and A3, or B1 and B3 in the same manner as described for Experiments 2 and 3.

**Magazine training.** On each of the two days following pre-exposure, all rats received one 15-min session of magazine training in which food-pellets were delivered according to a random-time, 60 s schedule.

**Training.** After magazine training, all rats received four sessions of conditioning in which stimulus A2 was paired with the delivery of food in the manner described for groups A2:A2+ and B2:A2+ in Experiment 1.

## Results and discussion

**Magazine training.** Over the course of magazine training, the mean number of magazine entry responses made by rats groups A2:A2+, B2:A2+, A1/A3:A2+, and B1/B3:A2+ was 7.9 (.9), 7.6 (.7), 9.9 (1.2), and 9.5 (1.0) responses per minute, respectively. Two-sample *t*-tests revealed no difference in the number of magazine entries made by groups A2:A2+ and B2:A2+, or by groups A1/A3:A2+ and B1/B3:A2+,  $t_s < 1$ .

**Pre-stimulus response rates.** The average rate of pre-stimulus responding was 5.6 (.8) responses per minute during the first half-session block, and 2.4 (.5) during the final block. The average rate of responding across all blocks of training was 4.4 (1.2) for group A2:A2+ and 4.0 (.5) for group B2:A2+. Corresponding rates for groups A1/A3:A2+ and B1/B3:A2+ were 4.8 (.8) and 3.8 (.7). ANOVAs conducted on response rates for each pair of groups found no significant effect of group,  $F_s < 1$ , or trial block, largest  $F(7, 98) = 1.85, P = .086$ , and no Group x Block interaction, largest  $F(7, 98) = 1.12, P = .360$ .

**Mid-point pre-exposure.** The top panel of Figure 4 shows the mean elevation scores for rats in groups A2:A2+ and B2:A2+ in the presence of A2 over the four sessions of conditioning, in half-session blocks. These results replicated the effect seen in Experiment 1: rats that had been pre-exposed to A2 acquired conditioned responding to that stimulus less rapidly than rats that had been pre-exposed to B2. A two-way ANOVA revealed a significant effect of group,  $F(1, 14) = 6.37, MSE = 521.20, P = .024, \eta^2_p = .313, 90\% CI [.025 .536]$ . There

was also a significant effect of block,  $F(7, 98) = 28.21$ ,  $MSE = 82.41$ ,  $P < .001$ ,  $\eta^2_p = .668$ , 90% CI [.553 .711], but no interaction of group and block,  $F(7, 98) = 1.18$ ,  $MSE = 82.41$ ,  $P = .320$ .

<Figure 4 about here>

**Alternating pre-exposure.** The results for groups A1/A3:A2+ and B1/B3:A2+ are shown in the bottom panel of Figure 4. The two groups of rats acquired conditioned responding to A2 at equivalent rates, replicating the results of Experiment 3.

This observation was confirmed by a two-way ANOVA of individual mean elevation scores for rats in each group (A1/A3:A2+, B1/B3:A2+) for each session of training (1 to 8) which found no effect of group, and no Group x Block interaction,  $F_s < 1$ . On no individual trial block did the difference between the two groups approach significance, all  $F_s < 1$ . The effect of block was significant,  $F(7, 98) = 17.17$ ,  $MSE = 161.10$ ,  $P < .001$ ,  $\eta^2_p = .551$ , 90% CI [.407 .607].

Experiment 4 confirmed the results of Experiments 1 and 3; pre-exposure to A2 retarded conditioning to A2. Alternating pre-exposure to A1 and A3 had no effect on the rate of conditioning to A2.

### Experiment 5

We found no evidence in either Experiment 3 or Experiment 4 that alternating pre-exposure to A1 and A3 affected conditioning to A2, but it is still possible that this pre-exposure resulted in changes in the effective salience of the unique features of A1 and A3. Hence, we cannot discount changes in the salience of the unique features as an explanation for the retardation of discrimination learning observed in Experiments 2 and 3. It is also the case that

in the experiments reported here we have employed a different assay of perceptual learning to that used in a large proportion of published studies. In many cases, particularly those using conditioned taste aversion procedures, perceptual learning has been assessed by measuring generalization of conditioned responding from one stimulus to another. It may well be that discriminative performance is linked to generalization, but it is possible that this difference in methodology might still account for our results.

Experiment 5 was conducted to determine whether the effects observed in Experiment 2 could be replicated using a test of generalization rather than one of discrimination learning. The pre-exposure regimens were the same as for Experiment 2. Rats in groups A2:A1+ and A1/A3:A1+ were pre-exposed to A2 or to A1 and A3, respectively. Those animals in groups B2:A1+ and B1/B3:A1+ were pre-exposed to B2 or to B1 and B3, respectively. There then followed a conditioning phase where all rats received pairing of A1 and food. Finally, generalization of conditioned responding from A1 to A3 was assessed over a series of test trials. As well as providing a different measure of perceptual learning to that used in the previous experiments, the conditioning phase also allowed us to determine whether the alternating pre-exposure to A1 and A3 experienced by group A1/A3:A1+ resulted in a reduction in effective salience of A1. Furthermore, it provides a test of the mediated association explanation of the results of Experiment 2 and 3. If alternating pre-exposure to two stimuli results in the development of excitatory associations between the unique and common features of each, then we should observe an increase in generalization between A1 and A3.

Because of some expected differences in the rates at which rats acquired conditioned responding to A1, the conditioning phase was extended to eight sessions. This ensured that all groups were responding at the same rate in the presence of stimulus A1 before the generalization test with A3. For the sake of consistency and to allow comparison with the previous experiments, data from the first eight half-sessions of conditioning were analysed separately.

## **Method**

**Subjects and apparatus.** The subjects were 32 naïve male Lister hooded rats from the same stock and housed in the same manner as those in Experiment 1. At the start of the experiment, the rats were divided into four groups of eight. The stimuli and apparatus were the same as for the previous experiments.

### **Procedure**

**Pre-exposure.** Rats in groups A2:A1+ and B2:A1+ received five sessions of pre-exposure to either A2 or B2 in the same manner as described for Experiments 1 and 2.

Rats in groups A1/A3:A1+ and B1/B3:A1+ were given five sessions of pre-exposure with either A1 and A3, or B1 and B3 in the same manner as described for Experiment 2.

**Magazine training.** On each of the two days following pre-exposure, all rats received one 15-min session of magazine training in which food-pellets were delivered according to a random-time, 60 s schedule.

**Training.** After magazine training, all rats underwent eight consecutive sessions of conditioning to stimulus A1 alone. With the exception that training was conducted with stimulus A1 rather than A2, all procedural details were the same as for Experiment 1.

**Generalization Test.** On the day after the final training session, a generalization test was performed with stimulus A3. In a single 12-min session, rats received four 10-sec presentations of stimulus A3 separated by a 180-sec ITI (range  $\pm 15\%$ ). No food pellets were delivered during the session.

## Results

**Magazine training.** Over the course of magazine training, the mean number of magazine entry responses made by rats in groups A2:A1+, B2:A1+, A1/A3:A1+, and B1/B3:A1+ was 10.3 (.6), 9.4 (1.1), 10.9 (1.6), and 10.6 (.5) responses per minute, respectively. Two-sample *t*-tests revealed no difference in the number of magazine entries made by groups A2:A1+ and B2:A1+, or by groups A1/A3:A1+ and B1/B3:A1+,  $t_s < 1$ .

**Pre-stimulus response rates.** The average rate of pre-stimulus magazine entry responding was 9.4 (.7) responses per minute during the first half-session block and 2.9 (.8) during the final half-session block of training. Rats in groups A2:A1+ and B2:A1+ responded at an average rate of 6.1 (.7) and 8.4 (2.1) across the 16 blocks of training. The corresponding figures for groups A1/A3:A1+ and B1/B3:A1+ were 6.7 (.7) and 5.5 (.8). Two-way ANOVAs revealed no effect of group, largest  $F(1, 14) = 1.06$ ,  $P = .322$ , and no Group x Block interaction, largest  $F(7, 98) = 1.05$ ,  $P = .406$ , but significant effects of block, smallest  $F(7, 98) = 3.35$ ,  $MSE = 21.07$ ,  $P < .001$ ,  $\eta^2_p = .193$ , 90% CI [.042 .255].

**Mid-point pre-exposure.** Pre-exposure to A2 resulted in retarded conditioning to A1, but no evidence of a change in generalization between A1 and A3. The results of the training and test sessions are shown in the upper panel of Figure 5. Rats in groups A2:A1+ and B2:A1+ learned to respond in the presence of stimulus A1 over the sixteen half-session blocks of training. During the first eight blocks of conditioning, rats in group B2:A1+ responded at a higher rate than rats in group A2:A1+; pre-exposure to A2 retarded conditioning to A1 in the latter group. By the end of conditioning, both groups attained the same level of conditioned responding to A1. At test, rats in the two groups responded to stimulus A3 at the same rate.

For the sake of consistency with the previous four experiments, data from the first four and the last four sessions of conditioning were analysed separately. A two-way ANOVA of elevation scores for rats in each group (A2:A1+, B2:A1+) for each of the first eight half-session blocks of training (1 to 8) confirmed that rats in the pre-exposure group acquired conditioned responding less rapidly than those in the control group. There was no significant effect of group,  $F(1, 14) = 2.02$ ,  $MSE = 489.67$ ,  $P = .177$ . The effect of block was significant,  $F(7, 98) = 42.01$ ,  $MSE = 81.47$ ,  $P < .001$ ,  $\eta^2_p = .750$ , 90% CI [.659 .783], and so was the Group x Session interaction,  $F(7, 98) = 2.29$ ,  $MSE = 81.47$ ,  $P = .033$ ,  $\eta^2_p = .141$ , 90% CI [.006 .194]. Simple effects analysis revealed that group B2:A2+ responded more rapidly than group A2:A2+ on block 4,  $F(1, 112) = 10.30$ ,  $MSE = 132.49$ ,  $P = .002$ .

A corresponding ANOVA of the data from the final eight blocks of conditioning found no effect of group,  $F(1, 14) = 2.61$ ,  $MSE = 657.98$ ,  $P = .129$ , or of block,  $F < 1$ , and no Group x Block interaction,  $F < 1$ .

There was no difference in the rates of responding to A1 by rats in the two groups on the final block of conditioning,  $t < 1$ , or in the rates of responding to A3 on the test trials. A two-way ANOVA conducted on the test data found no effect of group,  $F < 1$ , or of trial (1 to 4),  $F(3, 42) = 1.03$ ,  $MSE = 78.91$ ,  $P = .391$ , and no Group x Trial interaction,  $F < 1$ .

<Figure 5 about here>

**Alternating pre-exposure.** Pre-exposure to A1 and A3 had no effect on the rate of acquisition of conditioned responding to A1 but did cause a large increase in generalization of responding to A3. The lower panel of Figure 4 shows elevation scores for groups A1/A3:A1+ and B1/B3:A1+ for each of the 16 half-session blocks of training and for the four trials in the test session. During training, the two groups of rats learned to respond to stimulus A1 at the same rate. On the test session, however, rats in group A1/A3:A1+ responded more rapidly in the presence of stimulus A3 than rats in group B1/B3:A1+.

A two-way ANOVA of individual mean elevation scores for rats in each group (A1/A3:A1+, B1/B3:A1+) for each of the first eight half-session blocks of conditioning (1 to 8) confirmed that there was no effect of group,  $F < 1$ , and no Group x Block interaction,  $F(7, 98) = 1.87$ ,  $MSE = 117.22$ ,  $P = .083$ . The effect of block was significant, reflecting the acquisition of responding across sessions,  $F(7, 98) = 30.80$ ,  $MSE = 117.22$ ,  $P < .001$ ,  $\eta^2_p = .687$ , 90% CI [.578 .728]. A corresponding ANOVA for the final eight half-session blocks similarly found no effect of blocks, or of group and no interaction of group with block,  $F_s < 1$ .

On the final block of conditioning, the two groups responded to A1 at the same rate,  $t < 1$ . A two-way ANOVA of the generalization test data confirmed that group A1/A3:A1+ responded more rapidly in the presence of A3 than group B1/B3:A1+ did. There was a

significant effect of group,  $F(1, 14) = 12.24$ ,  $MSE = 265.50$ ,  $P = .004$ ,  $\eta^2_p = .466$ , 90% CI [.121 .647]. There was no effect of trial,  $F < 1$ , and no Group x Trial interaction,  $F(3, 42) = 1.59$ ,  $MSE = 262.71$ ,  $P = .205$ .

## Discussion

Experiment 5 showed that pre-exposure to A2 retarded conditioning to A1. This may have been due to a reduction in the effective salience of features common to A1 and A2. There was no effect of pre-exposure to A2 on the generalization of conditioning responding from A1 to A3, as one might expect on the basis of this analysis and the results of Experiments 1 and 2. The amount of generalized responding to A3 shown by rats in group B2:A1+ was, however, minimal and left little room for further reduction. The failure to observe an effect at test in this experiment might, therefore, simply be due to a floor effect.

Conditioning to A1 proceeded at the same rate in rats that had been pre-exposed to A1 and A3 or to B1 and B3. These results suggest that alternating pre-exposure to two auditory cues did not affect the salience of their features. Following conditioning to A1, however, generalization of responding to A3 was much greater in rats pre-exposed to A1 and A3. These results are consistent with those of Experiment 2 where a discrimination between A1 and A3 was learned less rapidly following the same pre-exposure schedule. Together, the results of these two experiments suggest that alternating pre-exposure can produce an increase in generalization between the stimuli. The results are consistent with those reported by Iordanova and Honey (2012) who observed greater generalization between two contexts when rats had been pre-exposed to both.

### General discussion

Two key results are reported here. First, pre-exposure to the mid-point between two simple auditory stimuli facilitated later discrimination learning involving those stimuli. In Experiments 1 and 2, rats that were pre-exposed to A2 showed faster acquisition of a discrimination between A1 and A3 than rats that had been pre-exposed to B2. Second, alternating pre-exposure to two simple auditory stimuli retarded, rather than facilitated, discrimination learning involving those stimuli. In Experiments 2 and 3, rats that were pre-exposed to the A1 and A3 were slower to learn a subsequent discrimination between those stimuli compared with rats that had been pre-exposed to B1 and B3. There was no strong evidence that the effect of alternating pre-exposure on subsequent discrimination learning was due to changes in the associability or effective salience of either the common or the unique features of the pre-exposed stimuli. Alternating pre-exposure to A1 and A3 increased generalization between those stimuli (Experiment 5) but had no impact on the rate of conditioning to either A1 (Experiment 5) or to A2 (Experiments 3 and 4).

Mackintosh et al. (1991) found that pre-exposure to the common cue X reduced generalization between flavour compounds AX and BX. The effects of mid-point pre-exposure observed in Experiments 1 and 2 are novel because they did not involve training with stimulus compounds with an explicit common element, but rather used simple auditory stimuli. Nevertheless, facilitation of discrimination learning involving A1 and A3 was observed following pre-exposure to A2. One explanation for this effect is that stimuli A1, A2, and A3 share some common features and that pre-exposure to A2 reduced the effective salience of these common features. A selective reduction in the salience of the common features should

reduce generalization between A1 and A3. Experiment 5 failed to confirm this hypothesis using a test of generalization, but this failure is difficult to interpret due to the extremely low level of generalization between A1 and A3 in the control group. There is evidence that gradients of generalization may sharpen over the course of extended conditioning (Bellingham & Gillette, 1981; Hoffeld, 1962; see also Hall, 1991, pp. 63-66.). Given that the conditioning phase of Experiment 5 consisted of a large number of trials and that there was little change in the rate of responding by either group over the latter half of training, it is possible that any differences in gradients of generalization between A1 and A3 for groups pre-exposed to A2 and B2 were eliminated by this extended conditioning phase. Experiment 5 did, however, provide evidence that changes in stimulus salience might play a role in the effects of mid-point pre-exposure on discrimination learning observed in Experiments 1 and 2. The retardation of conditioning to A1 following pre-exposure to A2 was consistent with a reduction in the salience of features common to A1 and A2.

Although there is some similarity between the mid-point pre-exposure effects reported here and by Mundy et al. (2007), there may also be differences. While the effects seen in Experiments 1 and 2, and those observed by Montuori and Honey (2016), persisted over several conditioning sessions, there is preliminary, unpublished evidence that Mundy et al's effect was transient. When the same task was used but a 24 hour interval was inserted between pre-exposure and learning, the beneficial effects of mid-point pre-exposure was abolished (R.C. Honey, personal communication, July 9, 2020). The same interval did not affect the beneficial influence of either alternating or blocked pre-exposure to the discriminative stimuli. This suggests that in people the mechanisms responsible for the mid-

point pre-exposure effect may not be the same as those engaged by more traditional perceptual learning treatments.

It is commonly reported that alternating pre-exposure to two similar stimuli reduces generalization between those stimuli (e.g., Dwyer, Hodder & Honey, 2004; Honey, Bateson & Horn, 1994; Mundy et al., 2007; Symonds & Hall, 1995). One explanation for this effect is that such pre-exposure reduces the effective salience of features common to both stimuli. On this basis, it was expected that such pre-exposure should also facilitate the acquisition of discrimination learning. In Experiments 2 and 3 the opposite effect was observed: pre-exposure to two stimuli retarded subsequent discrimination learning. Although this was not the expected result, it is also not without precedent. Using visual stimuli similar to those employed by Gibson and Walk (1956), Channell and Hall (1981) found that pre-exposure to the discriminative stimuli retarded later discrimination learning if the pre-exposure was conducted in the experimental apparatus. A context change between pre-exposure and training was required to observe a facilitation of discrimination learning. Channell and Hall's results were not, however, replicated by Winefield, Green and Metzger (2001) who found that perceptual learning was not dependent upon a change in context. Furthermore, the vast majority of perceptual learning experiments involving a conditioned taste aversion do not rely on changes in context (e.g., Bennett & Mackintosh, 1999; Dwyer & Mackintosh, 2002; Symonds & Hall, 1995), and neither did Mondragon & Murphy's (2010; see also Artigas & Prados, 2017) using appetitive conditioning with discrete auditory stimuli.

The impairment of discrimination learning following pre-exposure to A1 and A3 observed in Experiments 2 and 3 can be explained in terms of changes in stimulus salience in

several ways. First, these effects of alternating pre-exposure may be consistent with the predictions of Rescorla and Wagner's (1972) model of Pavlovian conditioning. According to this model, addition of common features can facilitate discrimination learning. The removal of (or a reduction in the salience of) common features should therefore retard discrimination learning. Although this prediction appears counter-intuitive, the Rescorla-Wagner model could reconcile the current results regarding discrimination learning and previous findings concerning generalization. Unfortunately, there is little empirical evidence that the addition of common features facilitates discrimination learning, even in situations where the predictions of the Rescorla-Wagner model are much less equivocal (e.g., Rescorla, 1972; Pearce & George, 2002; cf. Myers, Vogel, Shin & Wagner, 2001). In any case, no evidence was found in Experiments 3 or 4 that pre-exposure to A1 and A3 affected the salience of A2. Furthermore, in Experiment 5 alternating pre-exposure was shown to increase, rather than decrease, generalization between A1 and A3.

Second, the effects of alternating pre-exposure will depend upon the amount of pre-exposure given. If the initial salience of common and unique features is approximately equal (or the unique features are of greater salience than the common features), then the effect of alternating pre-exposure should be to increase the relative salience of the unique features. At some point, however, the effective salience of the common features will reach a minimum level after which any further pre-exposure would serve only to reduce the salience of the unique features. Prolonged pre-exposure might therefore retard discrimination learning simply by reducing the salience of all features to the same, low, level. The absence of any negative effect of alternating pre-exposure on conditioning to either A1 (Experiment 5) or A2 (Experiments 3 and 4) suggests that this was not the case here.

A third possibility is that the discrimination between A1 and A3 was an easy one. In a maze learning task, Rodrigo, Chamizo, McLaren and Mackintosh (1994) observed a similar pattern of results to those that we found in Experiments 1 and 2. In an eight-arm radial maze they trained their rats on a discrimination between a fixed positive goal arm and one of two negative goal-arms each separated from the positive arm by 90°. A group of rats that had been pre-exposed to the arms located between the three goal arms learned the discrimination more rapidly than a control group who had received no pre-exposure to the extra-maze cues. A third group of rats that had been pre-exposed to the goal arms themselves learned even less rapidly than the control group. Although there were substantial differences in the design and procedure of Rodrigo et al's experiment and ours, parallels may be drawn if the array of extra-maze cues observed from different locations within the maze formed a continuum of sorts. Using a similar procedure, Trobalon, Sansa, Chamizo and Mackintosh (1991) found that a discrimination between goal arms separated by 45° was facilitated by pre-exposure, whereas when the goal arms were separated by 135° pre-exposure retarded learning. Oswalt (1972) also found that pre-exposure facilitated discrimination learning between difficult visual patterns (circle vs. square) but not between easy patterns (horizontal vs. vertical lines). Despite some evidence that rats display octave generalization (Blackwell & Schlosberg, 1948), it is possible that our stimuli were quite different to each other. Indeed, we found little evidence of generalization between A1 and A3 in Experiment 5 for rats that had not been pre-exposed to those stimuli. Two very dissimilar stimuli will share very few features in common and the effect of pre-exposure would primarily be to reduce the effective salience of their unique features. Consistent with this analysis, we observed retardation of discrimination learning following alternating pre-exposure to A1 and A3 in Experiments 2 and

3. The same pre-exposure regimen, however, had no effect on acquisition of conditioned responding to A1 in Experiment 5 suggesting that the unique features of A1 had not in fact undergone a substantial reduction in salience.

Stimulus pre-exposure may, however, have consequences other than simply reducing stimulus salience. An associative model of perceptual learning was proposed by McLaren and Mackintosh (2000) in which a stimulus is represented by a distributed pattern of activity across a population of representational elements. Each time a stimulus is presented, a sample of these elements is activated, but different elements might be sampled on different trials. Excitatory associations develop between elements that are concurrently active, and so after pre-exposure the subset of elements sampled when a stimulus is presented may associatively activate the remaining elements. If two stimuli are pre-exposed on an alternating schedule, associations will develop between the unique features of each and the features common to both. Iordanova and Honey (2012) suggested that such within-compound associations might explain the increase in generalization between contexts that they observed following pre-exposure. Some of our results are also consistent with this proposal. Mediated associations between the unique features of A1 and A3 would be expected to impair the acquisition of a discrimination between the two stimuli (Experiments 2 and 3) and increase generalization between them (Experiment 5).

McLaren and Mackintosh (2000) suggested that within-stimulus associations also contribute to three mechanisms of perceptual learning. First, the salience of elements is determined by how well they are predicted; as associations between elements develop, their effective salience declines. If two stimuli, AX and BX, are pre-exposed in alternation, common

X elements should undergo a greater reduction in salience than unique A and B elements because the common elements are present and available for learning about on every trial. Second, McLaren and Mackintosh (2000) suggest that sampling of unique elements is initially more variable than that of common elements. The A elements sampled on a trial may associatively activate other A elements, meaning that they are available to be learned about. Because X elements are sampled more reliably, they will not benefit from this process of unitization in the same way. Third, the negative contingency between the unique features of two stimuli pre-exposed in alternation will lead to the development of inhibitory associations between them. Hence, pre-exposure to AX and BX, will result in excitatory  $a-x$  and  $b-x$  associations and also inhibitory  $a-b$  associations.

Opposing influences of unitization and salience reduction might explain why we did not observe an effect of alternating pre-exposure on conditioning to A1 in Experiment 5. Elements unique to A1 may have undergone some reduction in salience, but because they were sampled more reliably following the pre-exposure phase, more elements would have been available on each trial to accrue and express associations during conditioning. In Experiments 3 and 4, the same pre-exposure regimen had no effect on conditioning to A2. These results may be explained in the same way if we assume that A1 and A3 each had elements in common with A2 which they did not share with each other. Unitization of these  $a_{12}$  and  $a_{23}$  elements might have counteracted the effect of any reduction in their salience, and that of elements common to all three stimuli ( $a_{123}$ ).

Contrary to the predictions of McLaren and Mackintosh (2000), however, our experiments revealed no evidence for inhibitory associations between the distinctive features

of A1 and A3 following alternating pre-exposure. Using discrete auditory and visual cues, Polack and Miller (2018) reported results consistent with the development of excitatory within-compound associations following limited pre-exposure to AX and BX (4 presentations of each compound). But after more extensive alternating pre-exposure (64 presentations each), they found that inhibitory associations had also developed between the unique features A and B (see also Polack & Miller 2019). In our experiments, A1 and A3 received similar extensive pre-exposure – each was presented 40 times over five sessions – but the retardation of discrimination learning (Experiments 2 and 3) and increase in generalization (Experiment 5) following pre-exposure to A1 and A3 suggests their unique features were not mutually inhibitory.

Finally, we shall consider the account of perceptual learning proposed by Hall (2003). Like McLaren and Mackintosh (2000), he suggested that alternating pre-exposure to stimulus compounds will result in the development of excitatory within-compound associations and that repeated presentation of a stimulus will result in a reduction in its effective salience. Critically, however, Hall argued that when the representation of a stimulus is associatively activated in its absence, its effective salience will *increase* – reducing or even reversing the decreases resulting from the stimulus' direct presentation. Hence, while alternating pre-exposure of AX and BX will result in a decrease in the effectiveness of X, the effectiveness of A and B should be maintained.

This maintenance of the effective salience of the unique features of stimuli allows Hall's (2003) account of perceptual learning to explain our results in much the same way as unitization does for McLaren and Mackintosh's (2000) model. Alternating pre-exposure to A1

and A3 will result in a decrease in the salience of the features they have in common ( $a_{123}$ ), but not their distinctive features ( $a_1$ ,  $a_{12}$ ,  $a_3$ ,  $a_{23}$ ), or the unique features of A2. The reduction in salience of the common features  $a_{123}$  might be expected to influence the rate of conditioning to stimulus A1 (Experiment 5) or A2 (Experiments 3 and 4), but there are two reasons why any effect might be small or non-existent. First, if A1 and A3 share relatively few features with each other, then a reduction in the salience of those common features will have minimal impact. Second, Hall allows for the possibility that associative activation of stimuli might increase their salience above initial levels; that is, any effect of the reduction in salience of  $a_{123}$  might be counteracted by an increase in the salience of features  $a_1$  and  $a_{12}$  (in the case of conditioning with A1) or features  $a_{12}$ , and  $a_{23}$  (in the case of A2) even if A1 and A3 do share a substantial number of features.

The impairment of the discrimination between A1 and A3 following alternating pre-exposure (Experiments 2 and 3) and the increase in generalization between A1 and A3 (Experiment 5) are challenges for Hall's (2003) account. They may be explained by the development of excitatory associations between the unique features of each stimulus and their common features, but like McLaren and Mackintosh (2000), Hall proposed that alternating pre-exposure should lead to the development of inhibitory associations between the stimuli's unique features.

In summary and conclusion, the mid-point pre-exposure effects reported here are relatively novel. This collection of experiments is only the second to explore the effect of mid-point pre-exposure on discrimination learning in non-human animals, and the first to use auditory stimuli. These effects are readily explained by assuming that similar stimuli are

represented as collections of features, some unique to each stimulus, and others common to two or more stimuli, and that pre-exposure to a stimulus results in a reduction in the associability or perceptual effectiveness of its features. Hence, pre-exposure to A2 resulted in retardation of subsequent conditioning to A2 (Experiment 1), and of a similar stimulus, A1 (Experiment 5). This same pre-exposure facilitated discrimination between the end-points of the continuum, A1 and A3, by increasing the relative salience of their unique features (Experiments 1 and 2). It is difficult to explain the effects of alternating pre-exposure to the endpoints of a continuum in the same terms (Experiments 2-5). Furthermore, mechanisms of perceptual learning proposed by McLaren and Mackintosh (2000) and Hall (2003) can *only* explain these results if one ignores the role of inhibitory associations between the unique features of the pre-exposed stimuli.

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**Figure captions**

*Figure 1.* Mean elevation scores for conditioning with A2 (top panel) and discrimination training with A1+ and A3 $\emptyset$  (bottom panel) in Experiment 1. Prior to this training phase, rats in the A2: groups had been pre-exposed to A2; rats in the B2: groups had been pre-exposed to B2.

*Figure 2.* Mean elevation scores for discrimination training with A1+ and A3 $\emptyset$  in Experiment 2. Rats in groups A2:A1+/A3 $\emptyset$  and B2:A1+/A3 $\emptyset$  (top panel) had previously been pre-exposed to A2 or B2, respectively. Rats in group A1/A3:A1+/A3 $\emptyset$  had been pre-exposed to A1 and A3; and those in group B1/B3:A1+/A3 $\emptyset$  had been pre-exposed to B1 and B3 (bottom panel).

*Figure 3.* Mean elevation scores for discrimination training with A1+ and A3 $\emptyset$  (top panel) and conditioning with A2 (bottom panel) in Experiment 3. Rats in groups A1/A3:A1+/A3 $\emptyset$  and A1/A3:A2+ had previously been pre-exposed to A1 and A3; rats in groups B1/B3:A1+/A3 $\emptyset$  and B1/B3:A2+ had been pre-exposed to B1 and B3.

*Figure 4.* Mean elevation scores for conditioning with A2 in Experiment 4. Rats in groups A2:A2+ and B2:A2+ (top panel) had previously been pre-exposed to A2 or B2, respectively. Rats in group A1/A3:A2+ had been pre-exposed to A1 and A3; and those in group B1/B3:A2+ had been pre-exposed to B1 and B3 (bottom panel).

*Figure 5.* Mean elevation scores for conditioning to A1 and a subsequent generalization test with A3 in Experiment 5. Rats in group A2:A1+ had previously been pre-exposed to A2; and those in group B2A1+: had been pre-exposed to B2 (top panel). Group A1/A3:A1+ had previously been pre-exposed to A1 and A3, and group B1/B3:A1+ to B1 and B3 (bottom panel).

## Tables

*Table 1.* Design of Experiments 1 to 5. Stimuli A1 to A3 and B1 to B3 were 500-Hz, 1-kHz, and 2-kHz tones, and 5-Hz, 10-Hz, and 20-Hz clickers. + denotes that a stimulus signalled the delivery of food,  $\emptyset$  denotes that it did not.

<i>Experiment</i>	<i>Group</i>	<i>Pre-exposure</i>	<i>Training</i>	<i>Test</i>
1	A2:A2+	A2...A2...	A2+	
	B2:A2+	B2...B2...		
	A2:A1+/A3 $\emptyset$	A2...A2...	A1+ A3 $\emptyset$	
	B2:A1+/A3 $\emptyset$	B2...B2...		
2	A2:A1+/A3 $\emptyset$	A2...A2...	A1+ A3 $\emptyset$	
	B2:A1+/A3 $\emptyset$	B2...B2...		
	A1/A3:A1+/A3 $\emptyset$	A1...A3...A1...A3...		
	B1/B3:A1+/A3 $\emptyset$	B1...B3...B1...B3...		
3	A1/A3:A1+/A3 $\emptyset$	A1...A3...A1...A3...	A1+ A3 $\emptyset$	
	B1/B3:A1+/A3 $\emptyset$	B1...B3...B1...B3...		
	A1/A3:A2+	A1...A3...A1...A3...	A2+	
	B1/B3:A2+	B1...B3...B1...B3...		
4	A2:A2+	A2...A2...	A2+	
	B2:A2+	B2...B2...		
	A1/A3:A2+	A1...A3...A1...A3...		
	B1/B3:A2+	B1...B3...B1...B3...		
5	A2:A1+	A2...A2...	A1+	A3
	B2:A1+	B2...B2...		
	A1/A3:A1+	A1...A3...A1...A3...		
	B1/B3:A1+	B1...B3...B1...B3...		

Figures

Figure 1

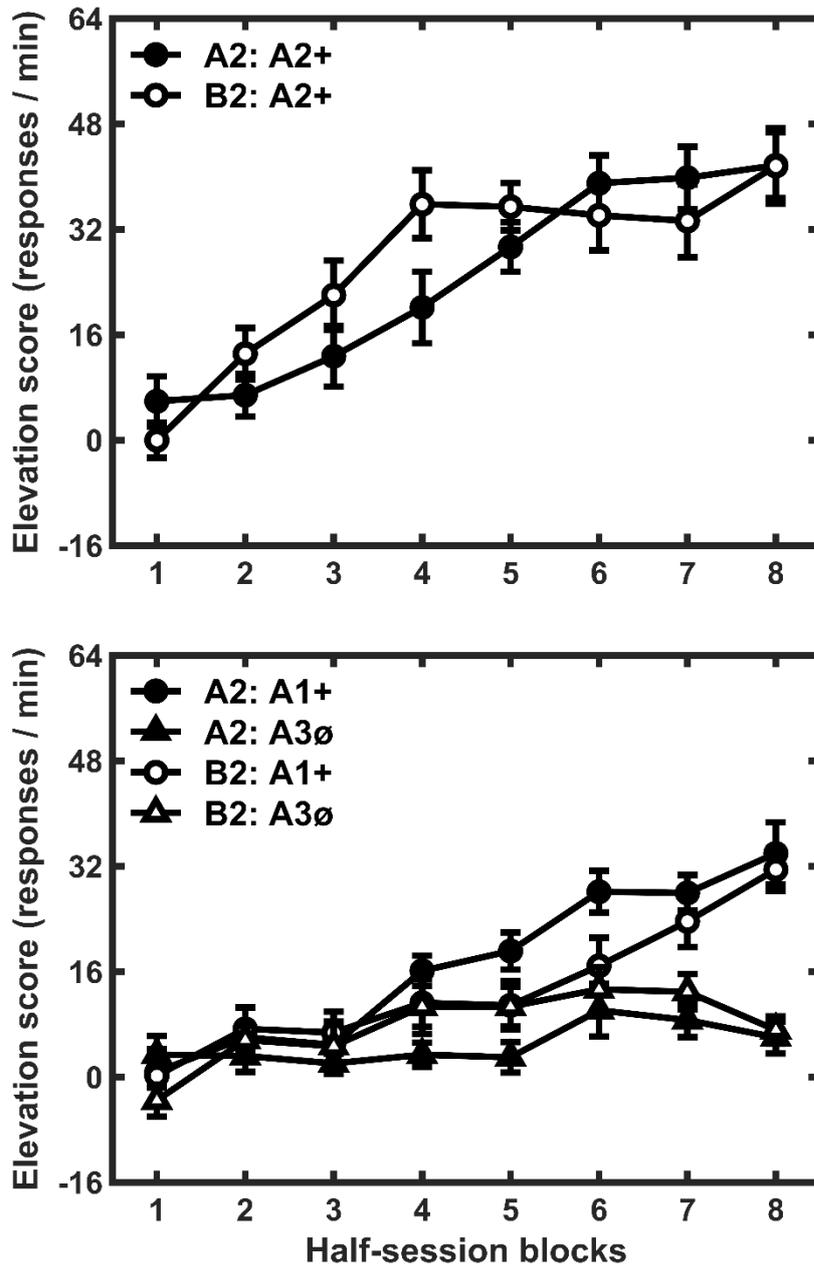


Figure 2

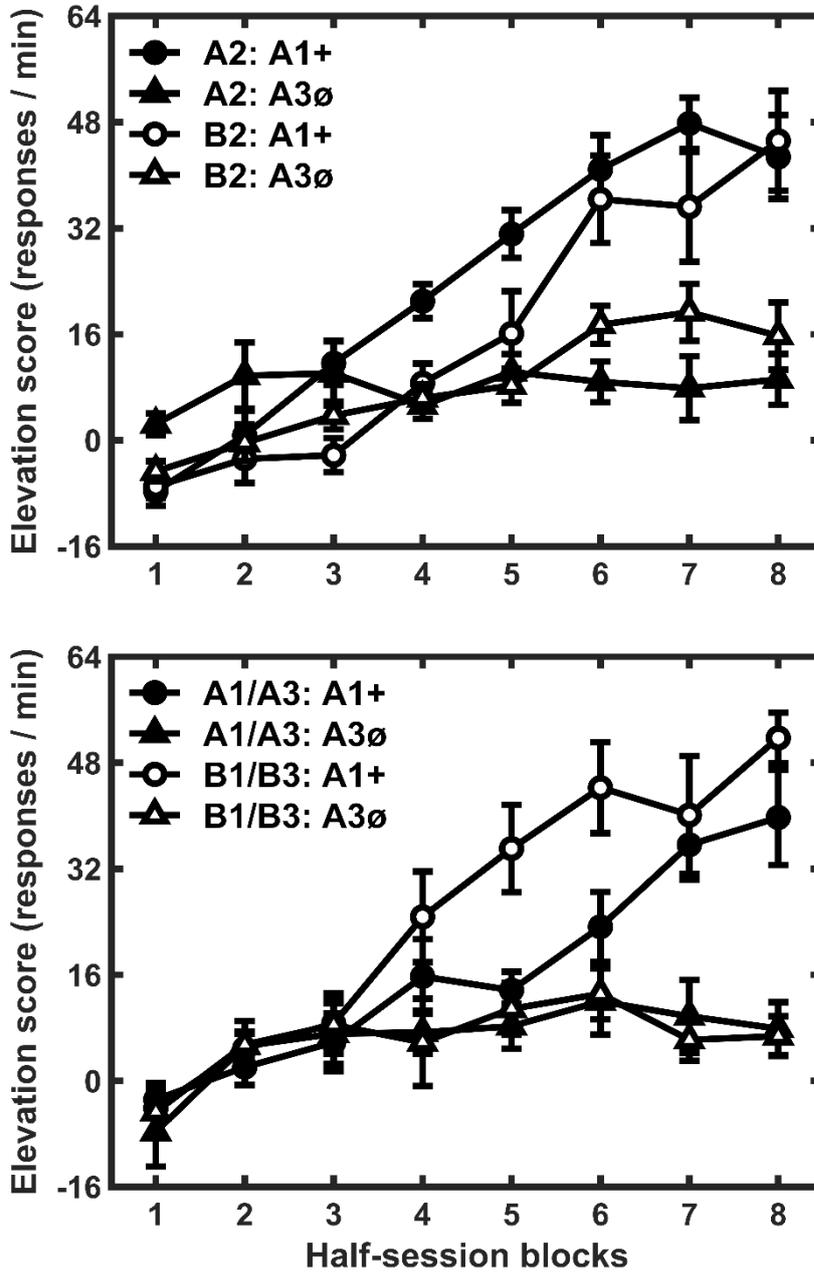


Figure 3

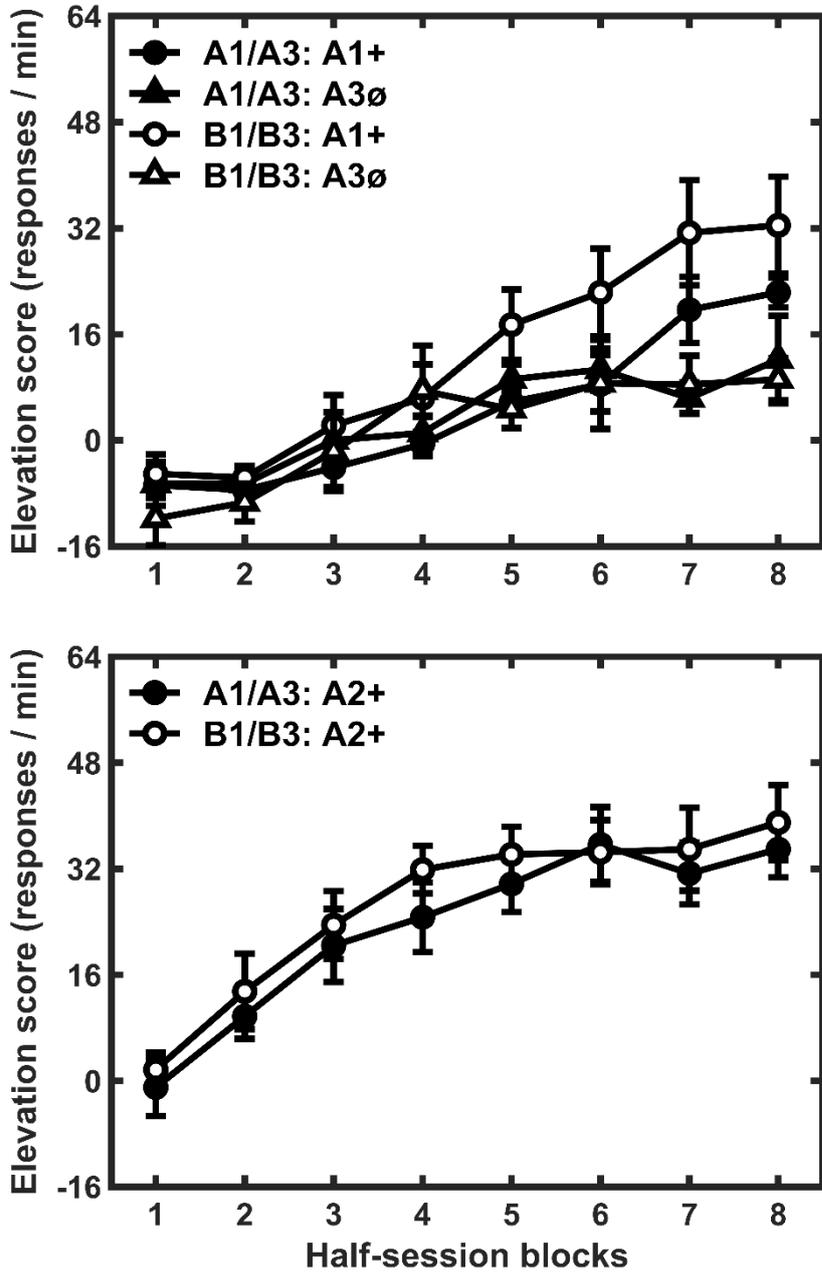


Figure 4

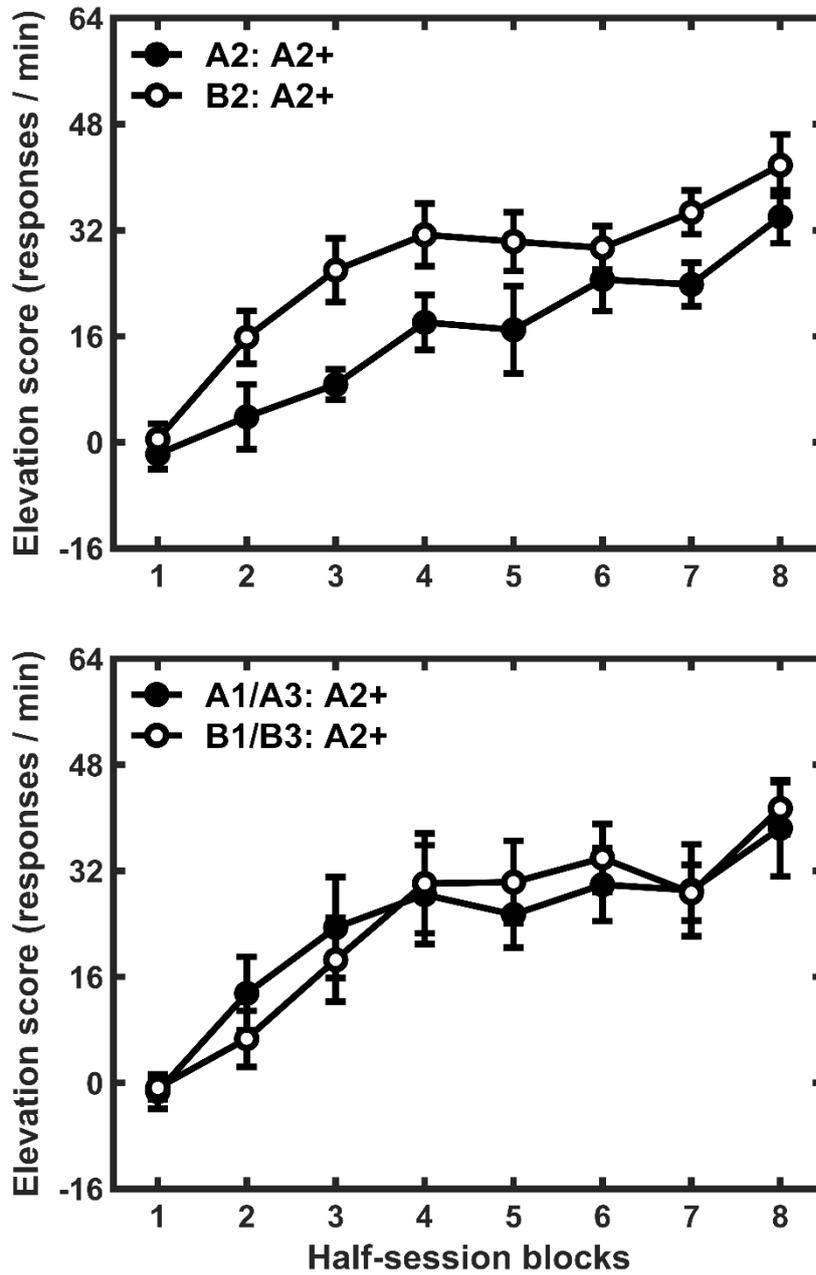


Figure 5

