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Perceptual learning in an appetitive Pavlovian procedure: Analysis of the effectiveness of the common element

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Nonreinforced preexposure to two stimuli often enhances discrimination between them. Analyses of this perceptual learning phenomenon have mainly focused on the role played by the distinctive stimulus features; this study examined the contribution of the non distinctive common elements. A standard appetitive Pavlovian procedure was used. Rats received two different schedules of exposure –alternated or blocked– to two compound auditory stimuli, *AX* and *BX*. In Experiment 1 a generalization test to *BX* that followed conditioning to *AX* showed that animals responded less, and hence discriminated better, following alternated exposure, thus extending the generality of this perceptual learning effect to standard appetitive Pavlovian procedures. The degree to which the common element *X* was mediating this effect was explored in the next three experiments. Experiment 2 assessed the effectiveness of *X* following conditioning to *AX*. Experiment 3 explored *X*'s effectiveness throughout extensive conditioning to *X*. Experiment 4 tested the ability of *X* to overshadow a novel stimulus *Y*. The results were consistent with the suggestion that alternated preexposure can reduce the relative effectiveness of the common element.

Keywords: associability; classical conditioning; common feature; perceptual learning; salience

1. Introduction

Nonreinforced exposure to a stimulus has at least two relatively well known effects. Firstly, it retards conditioning when the exposed stimulus is subsequently paired with a reinforcer. This phenomenon, labeled latent inhibition, has been extensively studied in a wide range of procedures (for a review, Hall, 1991; Lubow, 1989). Secondly, exposure to a pair of stimuli has been found to enhance discrimination between them. Discrimination is commonly assessed by establishing a conditioned response (CR) to one of the stimuli, the conditioned stimulus (CS), and measuring generalization to the other stimulus. A discrimination enhancement –or, alternatively, a generalization reduction– of this sort is what is known in associative learning terms as a perceptual learning effect. Although perceptual learning was originally considered to be of non associative nature (Gibson and Gibson, 1955; Gibson, 1969; but see, Postman, 1955), from the perspective of animal learning literature the phenomenon is regarded as associative based. Current perceptual learning models in animal research are all associative based.

Perceptual learning has been found in several training procedures such as simultaneous visual discrimination learning in rats (e.g., Gibson and Walk, 1956; Hall, 1979, 1980), spatial learning discriminations in a radial maze with visual and tactile cues (e.g., Chamizo and Mackintosh, 1989; Trobalon, Sansa, Chamizo and Mackintosh, 1991), visual discriminations in navigation tasks in a swimming pool (e.g., Prados, Chamizo and Mackintosh, 1999), visual discrimination in domestic chicks (e.g., Honey and Bateson, 1996; Honey, Bateson and Horn, 1994), generalization after flavor-aversion conditioning in rats (e.g., Honey and Hall, 1989; Mackintosh, Kaye and Bennett, 1991; Symonds and Hall, 1995), a same/different learning task in humans (Dwyer, Hodder and Honey, 2004);

and human generalization tasks (Lavis and Mitchell, 2006). However, and even though perceptual learning is supposed to be an associative based phenomenon (Hall, 2003; McLaren and Mackintosh, 2000) and it has been demonstrated in many preparations and species, it has never been reported in a standard appetitive Pavlovian preparation with rats.

Since Gibson's early studies (e.g., Gibson, 1969), perceptual learning investigation has changed significantly. Far from the original developmental perspective or from other modern cognitive approaches (e.g., Goldstone, 1998) associative learning research has stressed the need for identifying the learning mechanisms that, under certain conditions, boost discrimination performance. Generalization from *A* to *B*, for example, is assumed to be determined primarily by the associative strength acquired by the features that the stimuli hold in common. Discrimination therefore depends on the number and strength of the common features: The fewer or weaker these are, the better the discriminative performance is. To enhance similarity and, more importantly, to facilitate the manipulation of common elements, an explicit common stimulus *X* added to *A* and *B* is used in many studies (e.g., Mackintosh *et al*., 1991; Symonds and Hall, 1995).

McLaren and Mackintosh (2000) proposed an associative model, outlined first in McLaren, Kaye and Mackintosh (1989), in which three mechanisms were considered to account for perceptual learning effects. First, the reduction in generalization that follows preexposure could emerge as a result of latent inhibition. During exposure the common features undergo more latent inhibition than the unique stimulus elements –the former appearing twice as often as the latter. Hence, the relative effective salience of the common features is reduced and overshadowed by the unique elements which acquire most of the associative strength when subsequently conditioned. Thus, when compared with a non-exposed control the common elements will be less able to mediate generalization of responding to the test stimulus. A second mechanism called unitization was proposed that could enhance discrimination between two similar stimuli. According to this mechanism, repeated presentations of a stimulus engender a number of associations between its constituent elements. Since the unique elements lose salience less readily than the common elements, associations between them are formed preferentially compared to associations between common and unique elements. As a result, when a set of unique elements is activated other non-active unique elements are associatively activated and become available for acquiring or expressing learning.

McLaren and Mackintosh's first mechanism certainly accounts for some instances of perceptual learning but seems insufficient to explain the effect when latent inhibition is controlled. Honey *et al*. (1994) and Symonds and Hall (1995) developed a technique for controlling the contribution of differential latent inhibition to the perceptual learning effect by equating the amount of stimulus exposure. Their results showed that an exposure regime in which two stimuli are presented in alternation is more effective at reducing generalization between them than a schedule in which the stimuli are presented equally often but in separate blocks of trials. A process of unitization, the proposed second mechanism, might be expected to facilitate learning in explicit discrimination training but it is not obvious how the mechanism would apply to these generalization tasks. As a result of simple stimulus exposure unitization might facilitate the acquisition of positive and negative associative strength by associatively activating more non-sampled unique elements than common elements during subsequent discrimination training trials (*AX*+, *BX*-), therefore enhancing discrimination. In order to explain how unitization could reduce generalization in a generalization task, it must be assumed that there is no random sample of elements but instead common elements are preferentially sampled: "Unitization will reduce generalization only if the initial sampling of a complex CS is biased toward those elements it shares in common with the stimulus to which generalization is being measured" (McLaren and Mackintosh, 2000, p.233). If during exposure a process of unitization occurs, it might reduce generalization by counteracting the otherwise normal bias. More unique elements will be associatively retrieved during conditioning that will therefore acquire most of the available associative strength in detriment of the common elements. A process of unitization might be therefore thought to reduce generalization between two similar compounds that have been preexposed. However there is no reason why this process should produce differential discrimination depending on the preexposure regime the stimulus compounds have undergone unless it is also assumed that alternated preexposure does result in an increased tendency to favour the oversampling of common elements.

Although there is general agreement on the role played by the common elements as the main source of generalization (see, Mackintosh, 1974; Rescorla, 1976) the differential effect of the above regimes of exposure in which both conditions allegedly share the same elements has yielded to different sort of interpretations. Thus, the attention of modern theoretical accounts has been displaced towards the function of the unique features in generating the effect somehow neglecting as a result the analysis of the common elements' involvement.

McLaren and Mackintosh's third mechanism assumes that during alternated exposure of two compound stimuli, (e.g., *AX* and *BX*) excitatory within-compound associations (e.g., between *X* and *A*, and between *X* and *B*) will be established. These associations ensure that on each trial (e.g., *BX*) the representation of the other unique stimulus (e.g., *A*) is associatively activated. According to McLaren and collaborators, under these circumstances a mutually inhibitory link between the unique stimuli (*A* and *B*) is formed. This link prevents retrieving the representation of one unique stimulus (e.g., *A*) on trials in which the fellow exposed unique stimulus (e.g., *B*) is present. This mechanism will only work if exposure occurs in an alternated schedule. In a blocked presentation of trials, the excitatory within-compound associations formed between the elements of the stimulus compound first exposed (e.g., between *X* and *A*) will undergo extinction during the presentation of the second stimulus compound, preventing the formation of an inhibitory link. It is commonly assumed that in a generalization test response originates from the common elements' ability to retrieve the unconditioned stimulus (US) representation through two sources: Directly, through the excitatory associative link formed between these common elements and the US during conditioning, and indirectly by the way of an $X \rightarrow A$ association. The inhibitory link formed during alternated but not during blocked exposure between *A* and *B* will impede this latter source of generalization. As a result, generalization following blocked stimuli exposure will be greater than after alternated exposure.

Based on Gibson's idea of stimulus differentiation (Gibson, 1969), Honey *et al.* (1994) and also Symonds and Hall (1995) proposed that alternated exposure permits the operation of comparison mechanisms able to alter the perceptual characteristics of the stimulus features, increasing the perceptual effectiveness of the unique elements and reducing those of the common elements facilitating discrimination. Hall (2003) suggested a specific mechanism under which the perceptual effectiveness would change. Associative models usually assume that the strength of a stimulus representation depends directly upon the stimulus's physical characteristics such as its intensity. The term salience is used to denote such characteristics. According to Hall, direct presentation of a stimulus can cause it to lose effectiveness. This loss of effectiveness is exemplified by the phenomenon of habituation in which the effect of repeated presentations of a stimulus could be characterized as a reduction of the stimulus sensitivity or salience. Conversely, indirect activation of the stimulus representation by way of an associative link will restore the stimulus's lost salience by a process that could be conceptualized as negative habituation. Exposure to *AX* and *BX* will therefore reduce the stimulus salience in both alternated and blocked pre-exposure schedules. As a consequence of alternated exposure, however, the representation of *A* will be associatively activated (by way of the *X*→*A* link) on *BX* trials, and the representation of *B* will be activated on *AX* trials (through the *X*→*B* link). This associative activation of *A* and *B* will attenuate the loss of salience during exposure. Blocked exposure, on the contrary, will not favor this associative activation because the excitatory links formed during the first blocked stimulus presentation will be subject to extinction during the next block. As a result, the effective salience of *A* and *B* will be higher following alternated than blocked exposure and generalization between *AX* and *BX* reduced.

Both, McLaren and Mackintosh and Hall's approaches may very well constitute an associative based mechanism underlying what Gibson (1969) referred to as *differentiation* processes. Differentiation was defined as an increase in the ability to detect (to respond to) distinctive features of the stimuli that were not initially responded to by a process of abstraction guided by experience of contrasted instances. Alongside differentiation, Gibson (1969) postulated an additional perceptual process by virtue of which irrelevant features of the stimuli, those aspects that fail to distinguish one stimulus from another, are progressively ignored. That is, the perceptual effectiveness of the features that the stimuli hold in common will be reduced. This latter process can probably be identified as latent inhibition but as noted above it is not clear that latent inhibition to *X* should be influenced by the schedule of stimulus exposure to *AX* and *BX* (but see Mondragón and Hall, 2002).

McLaren and Mackintosh's (2000) notion of latent inhibition merges the concepts of associability and salience making them depend upon the degree of expectancy or familiarity of the stimulus. Thus, a stimulus that is well predicted will lose associability, and therefore salience, and will be more latent inhibited than one not so well predicted (see also, Wagner, 1981). Alternated stimulus preexposure could result in a weak association between *X* and the unique features (*A* and *B* will be less well predicted) that might protect the unique stimulus from latent inhibition but there is no obvious way by which this preexposure arrangement may reduce the associability of *X*. Alternated preexposure however should not result in a weak *A*→*X* or *B*→*X* association, therefore *X* will be equally predicted after both preexposure conditions. Consequently, although it is clear that latent inhibition contributes to many perceptual learning effects, it is widely assumed that it cannot explain the schedule effect we are investigating. This assumption however may be wrong at least to the extent that perceptual learning may be partially due to differences on the effectiveness of the stimulus common features.

Nonreinforced exposure to a stimulus has another well known effect, that of habituation. The progressive reduction of the unconditioned response, such as orienting response (OR), that a stimulus elicits during preexposure will certainly contribute to the latent inhibition outcome but can be differentiated from it. Evidence, like the differential effects of context change, suggests that latent inhibition can be attributable to a loss of the associability whereas habituation effects are better explained as a decline on the stimulus perceptual effectiveness or salience (for a review, Hall, 1991). This distinction between associability and salience may prove useful in producing an associative mechanism to Gibson (1969) processes for disregarding common features.

As the main source for generalization from one stimulus to another, the role played by their common features in perceptual learning surely deserves further investigation. The purpose of this research is to analyze the effectiveness of these common features in an appetitive conditioning procedure.

2. Experiment 1

The variety of procedures employed to investigate the effect suggests that perceptual learning may be expected to occur quite generally and yet, to our knowledge, no report has shown perceptual learning with a standard appetitive Pavlovian conditioning technique in rats. On the contrary, a study on the effects of stimulus familiarity and novelty reported by Honey (1990) that tested generalization from one stimulus *A* to another *B* as a function of exposure yielded the opposite result. Honey (1990) exposed rats to two auditory cues *A* and *B* (a tone and a clicker) in a semi-random arrangement. Experiment 1 tested generalization to *B* after appetitive conditioning to *A* and found that rats given preexposure to the stimuli showed more generalization on the test than subjects not given pre-exposure. Group B/A of his Experiment 2 also showed more generalization to *B* than to a novel stimulus *C* in a within subjects test design. Honey’s results could, however, be interpreted solely as a consequence of differences in stimulus familiarity.

One possible 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. Unlike in flavor aversion experiments, standard conditioning procedures often involve very distinctive stimuli. The differences between a tone and a click, for instance –the stimuli tested in Honey (1990) experiments– might be too evident *per se* making redundant any learning mechanism able to enhance such differences. The rationale underlying this assertion arises from the empirical observation that perceptual learning is more likely to be obtained when the stimuli to be discriminated are rendered more similar by the addition of a common feature (Mackintosh *et al*., 1991). The following experiment sought to eliminate this problem by employing two similar stimulus compounds formed by two pure tones as unique features. Moreover, to increase similarity and to allow manipulation of the common features, white noise delivered through an additional speaker was superimposed on each tone. All animals were exposed to the stimuli, namely *AX* and *BX*, prior to conditioning to *AX.* In the experimental condition, Group ALT, the stimuli were presented in an alternated schedule whereas in the control condition, Group BLK, exposure to the stimuli was given in two separated blocks of identical trials; that is, a set of *AX* was followed (or preceded) by a sequence of *BX* trials. This exposure arrangement guaranteed that the two groups were matched in their exposure to the stimuli, a procedure developed by Honey *et al*. (1994) and Symonds and Hall (1995) for controlling the contribution of latent inhibition to the perceptual learning effect. Differences in discrimination were assessed by comparing responding during a generalization test to *BX.* If the alternated exposure regime is more effective at reducing generalization between the stimuli, *BX* should elicit less responding following the alternated preexposure than after a blocked preexposure schedule.

2.1. Method

2.1.1. Subjects

The subjects were 16 experimentally naïve male hooded Lister rats (Charles-River, London) with a mean weight of 348.3 g (326 - 372 g) at the start of the experiment. They were housed in pairs in a colony room on a 12 hour light-dark cycle with training taking place during the light part of the cycle (lit from 7am to 7pm) 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.

2.1.2. Apparatus

Eight identical conditioning chambers (30.5 X 24.1 X 21.0 cm) from MED Associates were used. The chambers were inserted in sound and light attenuating shells with background noise produced by ventilation fans (≈ 65 dB). The floor of each chamber consisted of 19 tubular steel bars 4.8 mm in diameter and 11.2 mm apart within a polypropylene frame. These bars were perpendicular to the wall where the food tray was located. This wall and the opposite one were made of aluminum. The ceiling and remaining walls were of clear polycarbonate. Each chamber was dimly illuminated by a shielded houselight (operating at 20V) located on the wall opposite the food tray. A magazine pellet dispenser (Model ENV-203M, Med Associates) delivered 45-mg Noyes (Lancaster, NH; Improved Formula A) pellets into the food tray. A head entry into the food tray was recorded by interruption of an LED photocell. A jewel light operating at 28V (Model ENV-221M, Med Associates), which was located above the food tray, provided illumination used as the response cue. A speaker (Model ENV-224DM, Med Associates) located at the ceiling of each chamber delivered two tones of 3.2 KHz and 9.5 KHz (approximately 80 dB) produced by a programmable audio generator (Model ANL-926, Med Associates). A heavy duty relay attached to the top center of the front wall was used to deliver a 6.25 Hz click of approximately 78 dB. A speaker mounted on the inside front wall of the shell could be used to deliver a 75 dB white noise, produced by a Campden Instruments Ltd noise generator. A Pentium III 800MHz computer running Med-PC for Windows (Version 4.0) controlled experimental events with 10ms resolution.

TABLE 1 ABOUT HERE

2.1.3. Procedure

Table 1 shows the designs employed in this and subsequent experiments. Throughout all the experiment phases rats were presented with trials separated by a variable ITI with mean of 315s. They received two exposure training days to two compound stimuli, *AX* and *BX*. Two tones of 3.2 KHz or 9.5 KHz and intensity of 80 dB served as *A* and *B* (counterbalanced) and a 75 dB white noise delivered from a different speaker was used as the common *X* element. The stimuli were 15 seconds long. Each exposure day consisted of 10 stimulus presentations, 5 of each compound type. The initial order (counterbalanced) in which the stimuli were exposed was reversed on day 2 and the identity of the first stimulus counterbalanced. In Group ALT-AX:BX the stimuli were exposed in an alternated fashion (e.g., *AX/BX/AX/BX*…). In Group BLK-AX:BX stimuli were presented in two separated 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. A test day was run next. The test consisted of 4 presentations of *BX* in extinction. The amount of time the animals kept their head in the food tray was recorded during the stimulus presentation and during the 15 seconds that preceded it (PCS). A difference score in which time responding during the PCS was subtracted from that recorded during the stimulus presentation was computed and used as a response measure. The rejection level adopted here and in all subsequent analyses was $p < 0.05$.

2.2. Results and Discussion

Response times during conditioning and during the PCS were averaged across 4 blocks of 5 trials to calculate difference scores. Inspection of these data indicated that responses during the presentation of *AX* increased progressively and similarly for both groups of animals. Mean time responding ($\times 10^{-2}$ s) along the four conditioning blocks for Group ALT-AX:BX were -19.8, 5.0, 22.8, 138.0; and 17.8, 22.7, 66, 97.0 for Group BLK-AX:BX. Statistical analysis conducted with preexposure condition (alternated *vs.* blocked) and trial block as variables showed that conditioning was sufficient to generate responding to *AX* [F(3,42) = 6.28]. No other differences, between preexposure conditions or in the interaction between the variables, were significant (Fs < 1). PCS responses as a measure of background activity also appear to increase as a result of training (Means: 30.9, 62.4, 59.6, 90.6 and 15.4, 57.3, 58.8, 94.4 *per* block and groups ALT-AX:BX and

BLK-AX:BX respectively) but this increment failed to reach significance [F(3.42) = 2.82] . No other variable effect or interaction was significant (Fs < 1).

FIGURE 1 ABOUT HERE

Mean time responding during the critical test of generalization to *BX* over two trial blocks is shown in Figure 1. Animals that were preexposed to the stimuli in alternation, Group ALT-AX:BX, responded less during the test presentation of *BX* than did animals in Group BLK-AX:BX. This pattern of responding would indeed be expected if alternated preexposure had resulted in an improved discrimination between the stimuli, that is, if generalization between the conditioned stimulus and the test stimulus had been reduced as a consequence of the alternated arrangement more than after the blocked stimulus presentation. An analysis of variance (ANOVA) with preexposure condition and trial block as variables was conducted with these data. This analysis confirmed the statistical reliability of this difference in responding. Animals in Group BLK-AX:BX responded significantly more to *BX* [F(1,14) = 5.16] than animals in Group ALT-AX:BX. No other effect, trial blocks or interaction between the variables, was significant (Fs < 1). Responding during the PCS periods (Means: 23.7, 16.4 and 10.1, 11.1 *per* block and groups ALT-AX:BX and BLK-AX:BX, respectively) did not statistically differ across trials and/or groups (Fs < 1).

To the best of our knowledge this result is the first report of perceptual learning in standard appetitive Pavlovian conditioning, that is, of reduced generalization as consequence of the schedule of exposure.

Similar experiments reported by Honey (1990) found more generalization when conditioning occurred after exposure than when the stimuli where not preexposed. There are, however, several differences between this experiment and those reported by Honey. For example, the stimuli used in his experiments were unmistakably more dissimilar than the ones employed here. As previously suggested, a learning mechanism intended to facilitate discrimination might only be evident when the stimuli are initially undifferentiated. The exposure arrangements were also different. In Honey's experiments the stimuli were either exposed in a semi random arrangement or not exposed at all. In the experiment described here, exposure within a day in the experimental condition followed a strict alternation, an arrangement known to be critical to obtain the effect (Blair and Hall, 2003; Dwyer, Bennett and Mackintosh, 2001; Dwyer and Mackintosh, 2002; Symonds and Hall, 1995). It was not the purpose of this experiment to elucidate the differences between Honey's procedure and ours nor to assess the specific conditions that favor the effect but rather to obtain clear evidence of perceptual learning in a standard appetitive Pavlovian conditioning.

3. Experiment 2

Schedule effects in perceptual learning designs control for differences in latent inhibition by comparing discriminative performance following an exposure arrangement in which only the regime of exposure to the stimuli – not the amount – varies within conditions. It is assumed that any perceptual learning effects attributable to differences in the schedule of exposure cannot be explained in terms of differential latent inhibition of the common features (e.g., Honey *et al*., 1994; Symonds and Hall, 1995). Yet, it can be questioned whether the common features are really equally effective acquiring associative strength. More specifically, is the common element *X* equally effective transferring generalization after an alternated preexposure than after a blocked one? Some evidence implies that it is.

Bennett and Mackintosh (1999) and Mondragón and Hall (2002) found no significant differences in the acquisition of a conditional response to *X* following alternated or blocked exposure to *AX* and *BX*. Nonetheless, Mondragón and Hall gave further test sessions in extinction and found that learning about *X* following alternated exposure was less robust than that shown by the blocked group.

Generalization from one stimulus to another is mainly the result of the associative strength acquired by the common features, but typically the whole stimulus (i.e., *AX*) and not just the common feature (i.e., *X*) undergoes conditioning. Thus, the extent to which response to *AX* may generalize to *BX* will perhaps be better assessed testing *X* following conditioning to *AX*. In Bennett and Mackintosh's (1999) Experiment 1b, animals were conditioned to *AX* and the strength acquired by *X* was then tested. They found no differences depending on the preexposure conditions. All the animals in their experiment, though, had previously received a *BX* test that could have attenuated any differences in strength due to the exposure conditions. Mondragón and Hall (2002) conducted a similar test but immediately after conditioning *AX*. Their experiment did find a reliable difference, indicating that learning about *X* was weaker in the alternated than in the blocked condition.

None of the accounts of perceptual learning mentioned earlier predicts direct changes in the effectiveness of *X*. However, a mechanism such as the one proposed by Hall (2003) able to modify the salience of *A* differentially depending on the schedule of exposure might account for different levels of *X*'s associative strength following *AX* conditioning. If alternated exposure restores the loss of salience of *A*, conditioning to *X* can differ as a result of stronger overshadowing by *A* than that caused in the blocked condition by a less salient *A*. Weaker learning to *X* following alternated preexposure and *AX* conditioning could also be easily accommodated by McLaren and Mackintosh (2000) theory. Compared to a blocked preexposure, the associability of *A* after an alternated *AX* / *BX* regime is expected to be higher since this preexposure schedule will protect *A* from undergoing latent inhibition. Then, during *AX* conditioning the relative more salient *A* in the alternated condition could overshadow conditioning to *X* in a greater degree than *A* could following blocked preexposure arrangement.

Experiment 2 was designed to provide further evidence for variations in the effectiveness of *X* following *AX* conditioning as a consequence of the differential exposure schedule.

Table 1 shows the experimental design. The group labels refer to the successive experiment phases: Preexposed schedule (ALT or BLK), conditioned stimulus and test stimulus. Group ALT-AX:X was given alternated preexposure to *AX* and *BX* and Group BLK-AX:X received blocked stimulus exposure. Conditioning trials followed in which all animals were conditioned to *AX*. The strength of learning governed by *X* was tested in two subsequent blocks of 5 extinction trials. If as a consequence of alternated exposure of *AX* and *BX* *X* became less effective transferring generalization than after blocked stimulus preexposure responding during test in Group ALT-AX:X was expected to be lower than in the Group BLK-AX:X .

3.1. Method

3.1.1. Subjects and Apparatus

The subjects were 16 male hooded Lister rats (Charles-River, London) with no previous experimental experience and with a mean *ad lib* weight of 369.2 g (348 - 395 g) at the start of the experiment. They were housed and maintained exactly as in Experiment 1. The apparatus was the same as that used in Experiment 1.

3.1.2. Procedure

Initial exposure training and conditioning were identical to those of Experiment 1. Following conditioning all animals received a single test day consisting of ten presentations of *X* in extinction. All other parameters remained identical to those of Experiment 1.

3.2. Results and Discussion

Response times ($x\ 10^{-2}$ s) during conditioning and during the PCS were averaged across 4 blocks of 5 trials to calculate difference scores. Over the course of conditioning, responding increased progressively during the presentation of *AX*. This increment was similar for both groups of animals. Mean time responding along the four conditioning blocks for Group ALT-AX:X were 28.4, -45.3, 62.7, 284.0; and -29.2, 41.2, 87.9, 281.1 for Group BLK-AX:X. Statistical analysis conducted with preexposure condition (alternated *vs.* blocked) and trial block as variables showed that conditioning was effective producing responding to *AX* [F(3,42) = 19.27]. No other differences were significant (Fs < 1). PCS responses did not significantly increase as a result of training (Means: 54.3, 163.5, 202.6, 129.0 and 64.9, 98.7, 77.5, 87.6 *per* block and groups ALT-AX:X and BLK-AX:X respectively) nor differentiated the groups in any way (Fs ≤1.44).

FIGURE 2 ABOUT HERE

More interesting were the results of the test phase. Figure 2 shows response times during the presentation of stimulus *X* for each group during the first and last block of 5 trials of this test. A visual inspection of the data reveals that animals that were exposed to stimuli in blocks responded more than animals preexposed to the stimuli in alternation. This difference was constant throughout test. If anything, extinction to *X* appeared to develop faster in Group ALT-AX:X. This pattern of responding is fully consistent with the proposal that *AX* / *BX* alternation would result in a loss of the effectiveness of *X* to acquire associative strength during conditioning to *AX* and was confirmed by a statistical analysis. An ANOVA performed with preexposure condition (alternated or blocked) and blocks as variables produced a significant main effect of preexposure condition [F(1,14) = 8.47]. The interaction between these variables and the effect of the extinction blocks were not statistically significant (Fs <1). PCS scores did not differ during test or across groups (all Fs <1). Means: 26.38, 34.47 and 23.58, 17.03 for blocks 1 and 2 and groups ALT-AX:X and BLK-AX:X, respectively.

These results seem to suggest that alternated exposure to the stimuli may have indeed reduced the effectiveness of *X* to acquire, or at least to express, associative strength during *AX* conditioning and support those of Mondragón and Hall (2002). If alternated exposure in Group ALT-AX:X had effectively restored some of the salience that *A* lost during exposure as predicted by Hall (2003), *A* could more easily have overshadowed *X* during conditioning than in Group BLK-AX:X. This result also fits the predictions of McLaren and Mackintosh (2000) model. That is, if alternated exposure had protected *A* from latent inhibition keeping its relative salience higher than the salience of *A* in Group BLK-AX:X, its ability to overshadowing *X* would be lesser in the latter than in the former.

No doubt, the fact that the ability of *X* to gain associative strength may be dependent upon the schedule of the compound stimuli preexposure would certainly contribute to the perceptual learning effect. However the question about whether the schedule of exposure would have a direct effect on the effective salience of *X* remains unanswered. Experiment 3 was designed to try to answer this question.

4. Experiment 3

If the effectiveness of the common element is reduced as a consequence of alternated exposure, it would be reasonable to expect differences both in the acquisition of a conditional response to *X* conditioned alone and in its expression. As above mentioned, McLaren and Mackintosh's (2000) theory of latent inhibition, that fails to distinguish between associability and salience effects, does not predict differences on the effectiveness of *X* due to this particular preexposure schedule, neither does Hall's (2003). From the perspective of a theory (e.g., Pearce and Hall, 1980) that assumes a distinction between associability and salience, variations in the stimulus salience able to modify the effectiveness of *X* during preexposure would be concurrent and interacting with the associability effects. During preexposure to *AX* and *BX*, each common stimulus feature will appear on twice as many occasions as each unique feature; its associability will therefore be severely reduced and a substantial latent inhibition is to be expected. Besides, these two exposure schedules may differentially reduce the associability of *X* according to Pearce and Hall's (1980) model. For the sake of clarity, the analysis of the implications of this later prediction will be postponed to the general discussion. Experiment 3 attempted to counteract latent inhibition with extensive conditioning training under the assumption that stronger conditioning will grant more room to detect any differences that could emerge. Therefore, in Experiment 3 (summarized in Table 1) twice as many conditioning trials to *X* were given as in the previous experiments. That is, animals received 40 conditioning trials to *X*. Four extinction test trials followed. In all other respects the procedure was identical to that used in Group ALT-AX:BX and Group BLK-AX:BX in Experiment 1.

4.1. Method

4.1.1. Subjects and Apparatus

The subjects were 16 experimentally naïve male hooded Lister rats (Charles-River, London) with a mean *ad lib* weight of 375.3 g (345 - 414 g) at the start of the experiment. Housing, maintenance and apparatus were the same as in Experiment 1.

4.1.2. Procedure

Group ALT-X:X and Group BLK-X:X received preexposure training identical to that of each group in Experiment 1 with the exceptions described next. All animals received 4 days of conditioning to *X* and a single test day consisting in 4 trial presentations of *X* in extinction. All other parameters remained identical to those of Experiment 1.

FIGURE 3 ABOUT HERE

4.2. Results and Discussion

The left panel of Figure 3 shows response times over the course of conditioning averaged across 10 blocks of 4 trials. As conditioning progressed, responding to *X* increased. Contrary to our prediction, learning progressed similarly for both groups of animals. Although during initial training animals in Group ALT-X:X appeared to learn somewhat slower than those in Group BLK-X:X these differences were not statistically reliable. An analysis of variance showed that only the effect of training [F(9,126) = 12.85] was significant; neither the effect of group nor the interaction between these two variables were statistically significant (Fs < 1). PCS response times during conditioning (Means: 43.3, 68.0, 70.4, 107.4, 67.3, 90.3, 43.7, 58.9, 79.7, 60.8 and 18.7, 22.3, 34.7, 77.3, 95.4, 30.7, 45.6, 68.8, 94.0, 81.9, *per* block and groups ALT-X:X and BLK-X:X respectively) did not statistically differ in any way (Fs <1). Test results (right panel of Figure 3), however, showed that animals in Group ALT-X:X responded less than animals in Group BLK-X:X during the first block of trials. These differences were not evident by the end of the test phase. An ANOVA confirmed this pattern of results and showed a significant interaction between group and test block [F(1,14) = 4.75]. No other effect was significant (Fs < 2.05). *Post hoc* analysis revealed that animals in Group ALT-X:X responded less than did animals in Group BLK-X:X during the first block of trials [F(1,14) = 5.87] but not during the second (F < 1). PCS scores during test (Means: 31.7 and 14.7; 4.8 and 0.0 *per* block and groups ALT-X:X and BLK-X:X, respectively) did not differ statistically differ in any way[Fs(1,14) < 1.63].

Experiment 3 replicated the effect found in Experiment 2, that is, relative to blocked exposure alternated exposure to *AX* and *BX* reduced the effectiveness of the feature *X* common to the compound stimuli. However, unlike in Experiment 2, this difference could not be attributable to an indirect effect product of differences in the effectiveness of the unique feature *A*. Remarkably, this effect was only evident when stimulus effectiveness was tested in extinction. Despite this, since responding to *X* differentiated the groups early during test, it seems unreasonable to consider the effect as a product of differential extinction rates. The absence of differences between the alternated and blocked exposure conditions during acquisition to *X* replicates the findings of both Bennett and Mackintosh (1999) and Mondragón and Hall (2002). It is possible that the failure in finding a reliable difference might simply be due to the insensitivity of the measure used but this is mere speculation. The reason why this schedule effect on *X* only appears evident during an extinction test remains a puzzle.

Since evidence supporting a reduction in the effectiveness of the common elements following alternated preexposure seems to elude a direct conditioning test, in Experiment 4 we used and indirect test to substantiate it.

5. Experiment 4

Consistently with the proposal that alternated exposure reduces the perceptual effectiveness of common elements, Experiments 2 and 3 extinction tests of *X* following *AX* or *X* conditioning, respectively, showed that animals appeared to have learned less readily about these elements during conditioning. Experiment 4 (see Table 1) was designed to seek for a different sort of evidence for changes in the perceptual effectiveness of the common elements. The rationale for this experiment was as follows. An indirect way to assess the effectiveness of a stimulus during conditioning would be to test its ability to overshadow other stimuli that are present. That is, if alternated exposure to two compound stimuli *AX* and *BX* reduces the effectiveness of *X* more than is observed after blocked stimulus exposure, then *X* should also be less able to overshadow a novel stimulus *Y* when conditioned in a simultaneous compound following alternated exposure. Accordingly, it was predicted that conditioning to *XY* will result in more responding to *Y* following alternated exposure thus providing an indirect test for the effectiveness of the common elements after alternated or blocked exposure.

5.1. Method

5.1.1. Subjects and Apparatus

The subjects were 16 male hooded Lister rats (Charles-River, London) with no previous experimental experience and a mean *ad lib* weight of 375.7 g (330 - 406 g) at the start of the experiment. They were housed and maintained exactly as in Experiment 1. The apparatus was the same as that used in Experiment 1.

5.1.2. Procedure

Initial exposure training and conditioning were identical to those of Experiment 1 except for the following changes. Animals in Group ALT-YX:Y received alternated exposure to *AX* and *BX* whereas animals in Group BLK-YX:Y where exposed to a blocked schedule. Following preexposure all animals received conditioning trials to a compound stimulus *XY* formed by a simultaneous presentation of a click of 6.25 Hz and approximately 78 dB (*Y*) and the noise delivered from different sources. All animals received then a single test day consisting of four presentations of *Y* in extinction. Data from this laboratory showed an enormous variability in the responding times when using the click as CS therefore in this experiment we recorded number of responses. The number of times that the animals introduced their head in the food tray was recorded during the stimulus presentation and during the 15 seconds that preceded it (PCS). A difference score was calculated subtracting responding during the PCS from that recorded during the stimulus and was used as a response measure. All other parameters were identical to those of Experiment 1.

5.2. Results and Discussion

Conditioning to *YX* progressed similarly for both groups of animals. Responses were averaged across 4 blocks of 5 trials to calculate difference scores. The mean number of responses per minute along the four blocks of conditioning trials for Group ALT-YX:Y were 0.7, 6.5, 8.2, 13.7; and 0.1, 6.5, 8.8, 12.5 for Group BLK-YX:Y. An ANOVA with preexposure condition and trial block as variables confirmed the original observation. Only the effect of blocks was statistically reliable [F(3,42) = 18.02]. No other differences were significant (Fs < 1). An analysis conducted on the PCS responses (Means: 1.2, 2.7, 3.5, 2.3 and 2.2, 1.4, 1.8, 2.9 *per* block and groups ALT-YX:Y and BLK-YX:Y, respectively) showed no significant interactions [F(3,42) = 2.04] nor a simple main effect of the variables (Fs < 1).

FIGURE 4 ABOUT HERE

More interesting were the results found during the overshadowing test. A visual inspection of the data, depicted in Figure 4, shows that animals in Group ALT-YX:Y responded more to *Y* than animals in Group BLK-YX:Y. This response pattern is consistent with the idea that motivated the experiment – that the less perceptually effective the common element *X* becomes as consequence of an alternated preexposure, the less will it be able to overshadow conditioning to *Y*, therefore resulting in more vigorous conditioned response. An ANOVA with preexposure condition and test block as variables statistically confirmed these observations. Both the effect of block and the interaction between block and preexposure condition were significant [Fs (1,14) = 4.95]. The main effect of preexposure was not [F(1,14) = 1.57]. An analysis conducted to explore the source of this interaction revealed that the differences in responding were reliable during the second block of trials [F(1,14) = 18.42] but not during the first (F <1). An analysis of the PCS responses through the test blocks (Means: 0.25 and 1.0 for Group ALT- YX:Y; 1.25 and 3.0 for Group BLK-YX:Y) showed no effect of blocks [F(1,14) = 1.87] nor an interaction between blocks and preexposure condition (F < 1). However, the main effect of preexposure condition just reached significance [F(1,14) = 4.7; p = .05], stemming from the fact that background responding in Group BLK-YX:Y was somewhat stronger. This different level of PCS responding was explored further. No differences in responding were found when the test blocks were individually analysed [Fs(1,14) < 2.4]; besides, a similar analysis conducted with CS rates alone showed a significant effect of groups on the second block of trials [F(1,14) = 6.10] thus ruling out the possibility that PCS scores might have contributed decisively to the critical test results.

This result provides further evidence of variations in the effectiveness of the element common to the two compound preexposed stimuli. Differential responding in extinction revealed differences in the associative strength of the conditioned response acquired by *Y* during conditioning but also may suggest that the speed of learning during the *Y* extinction phase differed. However, being the extinction phase identical for both groups, any observed difference must be a consequence of what was learned during the previous phases that would generalize to the extinction test. There are two sources of generalization. Direct generalization through the excitatory associative link formed between *Y* and the *US* and indirectly by the way of an *Y*→*X* (→US) association.

Conditioning to an equally novel stimulus *Y* will be expected to produce similar rates of conditioning. Differences of this rate due to a direct source of generalization should therefore be attributed to differential overshadowing by *X*. That the differences appear late during test should not be surprising. Since *Y* was a novel stimulus, conditioning should have developed faster and stronger for both exposure conditions compared to that gained by a substantially latent inhibited *X*. Thus, high levels of responding to *Y* could be expected initially during test that could mask differences between groups. However, as extinction proceeds, differences between groups could emerge. Conditioning of *Y* in Group ALT-YX:Y was more resistant to extinction indicating that animals exposed to the stimuli in alternation learned more readily about the novel stimulus *Y* presented in compound with *X* than animals exposed to them in blocks, therefore suggesting that the effectiveness of the common stimulus *X* was preferentially reduced as a result of this schedule of preexposure.

Although weaker, there is, however, a second source of generalization that may contribute to the difference rates of extinction by the way of an *Y*→*X* (→US) association. Other conditions remaining equal, a stronger conditioning to *X* or a stronger *Y*→*X* association in Group ALT-YX:Y will result in more generalization from *XY* to *Y*. Given that conditioning was identical and *Y* equally novel in both conditions, differences in conditioning to *X* or in the *Y*→*X* association strength between the two groups could have only been produced by difference in the effective salience of *X*. Thus, to produce a stronger *X*→*US* or *Y*→*X* association in Group ALT-YX:Y, *X* should be more salient in

Group ALT-YX:Y than in Group BLK-YX:Y at the beginning of conditioning. This hypothesis is precisely the opposite of what it has been proposed in this paper and elsewhere, implying that alternated preexposure of *AX* and *BX* would have increased the salience of *X* in Group ALT-YX:Y (or reduced the salience of *X* in Group BLK-YX:Y) contrarily to what previous results seem to suggest. Attributing the source of the observed differences to this secondary source of generalization without any other fact to support it seems in some way perverse.

There is a further possible explanation. If as a consequence of preexposure and conditioning the salience of the stimulus *Y* was somehow reduced on Group ALT-YX:Y (or enhanced in Group BLK-YX:Y), then, according to Rescorla and Wagner's model (Rescorla and Wagner, 1972) faster extinction should be expected to develop in Group BLK-YX:Y. No grounds, however, can be found to support this preliminary assumption according to which the salience of *Y* may have differentially changed during conditioning.

6. General discussion

An important set of perceptual learning studies assess the degree of generalization from one stimulus *AX* to another similar stimulus *BX* following different schedules of stimulus preexposure. When compared with a blocked stimulus presentation, alternated exposure often enhances stimulus discrimination. Although such a perceptual learning effect might be expected to occur quite generally, and regardless of the apparently diverse range of procedures in which the effect has been found, it has proved difficult to obtain in experiments using standard appetitive classical conditioning. Pilot experiments carried out by, among others, the first author in this laboratory and in Hall's laboratory at the University of York and by Ward-Robinson's laboratory at the University of Nottingham have repeatedly failed to obtain the effect (Ward-Robinson's personal communication). Besides, no report employing what is perhaps the more paradigmatic procedure of Pavlovian conditioning has never been published. Experiment 1 demonstrated for the first time, a perceptual learning effect in standard appetitive conditioning in Skinner boxes using auditory stimuli as discriminative stimuli thus proving the generality of the effect.

The primary source of generalization between two compound stimuli such as the ones employed in perceptual learning experiments is determined by the associative strength acquired by the feature, *X*, common to the stimuli. Despite being the basis for generalization, the role played by these common features in perceptual learning has been relatively ignored (but see, Bennett and Mackintosh, 1999; Mondragón and Hall, 2002; Symonds and Hall, 1997). All in all, the experiments reported here suggest that preexposure conditions that engender perceptual learning reduce learning about the common features. Unlike blocked stimulus exposure, alternated preexposure seems to reduce what has been referred to as the *effectiveness* of the common elements. Both a direct test of the common feature's associative strength in extinction and an indirect test, through its ability to overshadow a novel stimulus, are consistent with a diminished learning capability. It remains however unclear why such an effect would not be observed during conditioning.

One well known effect of exposing a stimulus is that it will reduce its associability, retarding subsequent conditioning –the latent inhibition effect. The designs employed in this research are intended to control for latent inhibition effects. All the stimuli are exposed and the amount of each stimulus exposure is equal to all the experimental conditions. However, it remains possible that latent inhibition to a feature *X* that is experienced as part of two different stimulus compounds might be influenced by the schedule of exposure. Latent inhibition to *X* could progress less readily during blocked exposure than when exposure involves alternated stimulus presentations. It must be noted, however, that the Pearce and Hall (1980) model makes just the opposite prediction. According to this account the accuracy with which a stimulus predicts the events that follow determines its associability; but the model asserts that the less accurate predictor a stimulus is the higher its associability will be. Applied to this particular case, we might assume that at the end of blocked preexposure in which, for instance, a set of *AX* trials precedes a series of *BX*, the feature *X* will become a good predictor of its associate stimulus *B*. In contrast, after an alternated exposure of *AX* and *BX*, the feature *X* will not have a consistent associate and, therefore, it will be a less accurate predictor than in the blocked case. That is, the associability of *X* will remain higher after alternated exposure and conditioning should be stronger – the opposite of what our test results revealed. A mechanism in the spirit of that proposed by Mackintosh (1975) that predicts higher associability for good predictor stimuli could perhaps cope with these results.

It is also possible to speculate that the operation of Hall's (2003) mechanism in which the *perceptual salience* of the unique feature increases when is associative activated by *X*, would also alter the salience of *X*. Specifically, we propose a simplified attentional mechanism that only requires assuming that a stimulus that associatively activates another will lose some of its own effective salience in a selective attention process that could be analogous to that of overshadowing. Alternated stimulus preexposure will guarantee that *X* will associatively activate either *A* or *B* in all trials but the first one, resulting in *X* losing more salience than after a blocked exposure schedule in which *X* will only activate the representation of its first associate during the initial second blocked trials. Whereas Hall's proposal could constitute a specific mechanism for explaining how *differentiation* might develop, the mechanism that we propose might refine Gibson's secondary perceptual process that assumed that irrelevant features of the stimuli, those that will not help to distinguish one stimulus from another, are progressively ignored. The operation of a mechanism such as the one we propose could perhaps give a more detailed account –and, at the same time, be of more general application– of how this secondary Gibsonian process might work. Associatively activated distinctive features could overshadow the salience of the feature that they hold in common and that associatively activates them. This salience reduction mechanism could operate in parallel to associative ones, such as associability effects, modulating the stimulus effectiveness. This explanation however is not exempt of problems. If as consequence of the compound stimuli exposure, the common element loses effectiveness to gain associative strength by associatively activating the unique elements, it could be assumed that it will also progressively lose its ability to activate them in the forthcoming trials because of the intermixed extinction trials that the alternation regime involves. Therefore, this process would imply limiting the amount of perceptual improvement that preexposure would generate to an asymptotic level of salience change that would be parametrically dependent.

The experiments reported in this paper were intended to analyze the role played by the common features, that is, to provide evidence of their contribution to the perceptual learning effect. We have shown that the effectiveness of common elements does change as consequence of preexposure and that this effect is to be taken into account when elaborating a perceptual learning theoretical approach. We propose a mechanism that could explain how the effective salience of the common stimulus may decrease as consequence of an alternated regime of preexposure. This mechanism does not exclude nor is presented as an alternative explanation to other theories that focus on the unique stimulus features (Hall, 2003; McLaren and Mackintosh, 2000) but as a complementary mechanism that would also contribute to the scheduled perceptual learning effect.

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Figure captions

Figure 1. Mean time of magazine approach response calculated from difference scores CS- PCS (s x 10^{-2}) during the two test trial blocks for Group ALT-AX:BX and Group BLK-AX:BX. Vertical bars represent SEM.

Figure 2. Mean time of magazine approach response calculated from difference scores CS- PCS (s x 10^{-2}) during the five test trials blocks for Group ALT-AX:X and Group BLK-AX:X. Vertical bars represent SEM.

Figure 3. Mean time of magazine approach response calculated from difference scores CS- PCS (s x 10^{-2}) during the ten conditioning four trial blocks (left panel) and during the two trial test blocks (right panel) for Group ALT-X:X and Group BLK-X:X. Vertical bars represent SEM.

Figure 4. Group mean rates of responding calculated from difference scores CS- PCS during the two test trial blocks for Group ALT-YX:Y and Group BLK-YX:Y. Vertical bars represent SEM.