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Blocking and Associability Change

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Blocking of learning about a conditioned stimulus (the "blocked" cue) occurs when it is trained alongside an additional stimulus (the "blocking" cue) that has been previously presented with the outcome. A number of theories (e.g., N. J. Mackintosh. 1975a. A Theory of Attention: Variations in the Associability of Stimuli With Reinforcement. *Psychological Review*, 82, 276–298; J. M. Pearce & G. Hall. 1980. A Model for Pavlovian Learning: Variation in the Effectiveness of Conditioned But Not Unconditioned Stimuli. *Psychological Review*, 87, 532–552) account for this attenuation in learning by proposing that attention paid to the blocked cue is restricted. In three experiments, we examined the associability of both blocked and blocking cues. In Experiment 1, rats were trained with a blocking protocol before being given a test discrimination composed of two components; one of these components required the use of the previously blocked cue as a discriminative stimulus, and the other component was soluble by using the blocking cue. To our surprise, the component that depended on the blocked cue was more readily solved than the component dependent on the blocking cue. The results of Experiments 2 and 3 suggest that this is due to the quantity of exposure that each stimulus received during initial training. Implications for theories of blocking, and more widely associative learning, are discussed.

Keywords: blocking, attention, cue competition, associability

Conditioning to one element of a compound is frequently found to be attenuated if another element of that compound has been separately paired with the reinforcer. In an experiment reported by Kamin (1969), two groups of rats received pairings of a noise-light compound with shock; one of these two groups had received prior pairings of the noise alone and shock, and this group exhibited a weaker conditioned response (CR) to the light than those rats that had not received the initial noise-shock pairings. In other words, the CR to a conditioned stimulus (CS) X was found to be weaker following AX+ training if it was preceded by trials in which A was paired with the unconditioned stimulus (US), A+. Kamin called this reduction in conditioning to X "blocking" to capture the notion that learning about X was somehow prevented by the presence of A. Blocking has since been reported in a wide range of behavioral preparations, including appetitive conditioning (Dopson, Pearce, & Haselgrove, 2009), flavor aversion learning (Willner, 1978), flavor preference learning (Dwyer, Haselgrove, & Jones, 2011), and spatial learning (Pearce, Graham, Good, Jones,

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& McGregor, 2006). Blocking has also been demonstrated in a variety of species, ranging from goldfish (Tennant & Bitterman, 1975) to humans (Dickinson, Shanks, & Evenden, 1984; Le Pelley, Oakeshott, & McLaren, 2005).

Rescorla and Wagner (1972) presented an elegant model of learning that readily explains the blocking effect. According to their theory, the US is less effective at supporting learning when it is well predicted by the CSs that precede it. Consequently, the X–US association will not be acquired when it is presented in compound with A, a good predictor of the US. This theory, then, accounts for blocking by proposing variations in the processing of the US. In contrast, other models of learning (Mackintosh, 1975a; Pearce & Hall, 1980) account for blocking by proposing variations in CS processing. These models differ in their mechanisms, but both suggest that the presence of A during AX+ trials reduces the associability of X, so that it is less able to enter into an association with the US, and hence evoke a CR. According to these theories, no variations in the processing of the US need take place in order for blocking to occur.

Mackintosh (1975a) proposed that the processing of a CS varies as a result of how well it predicts its consequences. Informally, an animal learns to pay attention to stimuli that are good predictors of events that follow it, and learns to divert attention away from stimuli that are poorer predictors than any available competitors. In the case of blocking, A becomes a good predictor of the US during initial A+ training. At the outset of AX+ training, therefore, X is presented alongside a better predictor of the outcome, and consequently suffers a decrease in processing. In other words, the associability of the blocked cue, X, declines because it predicts the US less well than the blocking cue, A. The Pearce and Hall (1980) model predicts a decrease in the associability of X during AX+ training for rather different reasons. According to the Pearce—Hall

model, a CS is processed by the organism to the extent that it is followed by a surprising outcome. In the blocking experiment described above, A+ training causes the US to become predicted by A, such that the associative strength of A increases toward the maximum level supported by the US. The associability of A, therefore, decreases but this occurs only once A has acquired associative strength. X, however, undergoes a reduction in associability before substantial learning about the relationship between X and the US has taken place. This is because, even at the outset of AX+ training, the outcome is well predicted. The capacity of X to become associated with the US is, therefore, restricted. The Mackintosh and Pearce-Hall theories, therefore, both predict that blocking occurs because the presence of A during AX+ trials reduces the associability of X, but for different reasons; according to Mackintosh it is because X is a poorer predictor of the US than is A, and in the case of the Pearce-Hall model it is because the US is rendered unsurprising by the presence of A.

Early evidence for variations in CS processing during blocking came from a study by Mackintosh and Turner (1971). Two groups of rats received pairings of a noise with a shock of moderate strength (N+), followed by pairings of a noise/light compound with a stronger shock (NL++). Interposed between these two stages, one of the two groups received a small number of pairings of the noise/light compound with the moderate shock (NL+). During testing with the light at the end of the experiment, the group that had received NL+ trials exhibited a weaker CR than those that had not. This is not the result anticipated by the Rescorla-Wagner model, which predicts either no difference in the CR to the light in the two groups, or a stronger CR in the group that had received extra pairings of the NL compound with a shock (albeit a moderate one). Reduced conditioning to the light in those rats that had received NL+ training is consistent, however, with the idea that NL+ trials following N+ training reduced the processing of L. This may be either a result of L being a poorer predictor of the shock than N (a la Mackintosh, 1975a), or of the NL compound being followed by the expected moderate shock (a la Pearce & Hall, 1980); in either case, this finding is in keeping with the idea that a blocked cue suffers a reduction in processing. Another result that provides support for changes in CS processing during blocking is that changing the value of the US at the time at which the blocked cue is introduced can attenuate the magnitude of the blocking effect. The Rescorla-Wagner model is able to explain this when the US increases in magnitude (e.g., Kamin, 1969; Mackintosh & Turner, 1971), but cannot easily be reconciled with the finding that blocking is also reduced by a decrease in US magnitude (e.g., Dickinson, Hall, & Mackintosh, 1976; Holland & Kenmuir, 2005; Mackintosh, Bygrave, & Picton, 1977). This "unblocking" effect is, however, consistent with CS-processing models of learning which permit an increase in the associability (and hence conditioning) of a blocked CS when the conditions of reinforcement change—this is to say, when the delivery of the US is once again surprising. Rather more problematic for CS-processing accounts of blocking are demonstrations of blocking after a single compound (AX+) trial. According to both the Mackintosh model and the Pearce-Hall model, the associability of a CS is modulated at the end of each trial in accordance with that trial's outcome, meaning that the associability of X will be unchanged from its starting value during the first trial. Learning about the relationship between X

and the US should, therefore, progress normally during this trial. US-processing accounts of blocking, such as that provided by the Rescorla—Wagner model, anticipate blocking of learning about X even on the first AX+ trial following A+ training, because the US is predicted by A and, therefore, less well processed from the outset. Although Mackintosh (1975b) has reported a failure of blocking after only one compound conditioning trial, numerous instances of one-trial blocking have been observed (Azorlosa & Cicala, 1986; Balaz, Kasprow, & Miller, 1982; Dickinson, Nicholas, & Mackintosh, 1983). It seems, then, that blocking can occur prior to changes in CS processing, provided that the US is predicted

One way of resolving this conflict, then, is to assume that changes in both CS and US processing take place during blocking. It is not difficult to imagine a combination of, for instance, the Rescorla-Wagner and Mackintosh models, in which the processing of a US decreases as it becomes predicted, and the processing of a CS is dependent upon its predictive power. Indeed, this kind of resolution, in which multiple concurrent processes are assumed to combine to determine the overall rate of learning, is adopted by a number of recent "hybrid" models of learning (e.g., Esber & Haselgrove, 2011; Le Pelley, 2004; Pearce, George, & Redhead, 1998; Pearce & Mackintosh, 2010). It is unclear, however, how exactly any changes in CS processing take place. The findings of Mackintosh and Turner, and the unblocking observed when the reinforcer decreases in magnitude, are equally compatible with the Mackintosh and Pearce--Hall models. In the current article, we sought to differentiate between these two very different theories of CS processing by directly assessing the associability of blocking and blocked cues. In each of the three experiments presented here, we used a compound discrimination procedure that allows the assessment of associability without the need to compare acquisition to stimuli with different associative strengths (e.g., Haselgrove, Esber, Pearce, & Jones, 2010; Jones & Haselgrove, 2011; Pearce, Esber, George, & Haselgrove, 2008). In this procedure, subjects are required to solve the discrimination AY+, AX-, BY- following training that, putatively, establishes A and B with a different degree of attention to X and Y. If A and B capture more of the organism's attention than X and Y then the subdiscrimination between AY and BY should be easier to solve than the subdiscrimination between AY and AX. This follows because AY and BY are distinguished by CSs that are salient, and AY and AX are distinguished by CSs that are not. Should X and Y capture more of the organism's attention than A and B, then the reverse outcome should be observed. Importantly, all compounds begin the discrimination with equivalent associative strength, which means that US-processing models of learning such as the Rescorla-Wagner model anticipate that the two subdiscriminations should be solved at the same rate. Experiments that we have conducted have revealed that this procedure is adept at revealing behavioral phenomena predicted by both Mackintosh's theory and the Pearce-Hall model (Haselgrove et al., 2010). The aim of the current experiments was to apply this compound discrimination procedure to the examination of CSs that have been used in a blocking experiment, in order to expose any changes in processing that have taken place as a result of blocking.

Experiment 1

The purpose of Experiment 1 was to provide a comparison of the associability of blocking cues and blocked cues, using the compound discrimination procedure just described. Rats received appetitive Pavlovian conditioning in three stages: In the first stage, two stimuli were followed by the delivery of food (A+ and B+). To discourage rats from learning simply that all stimuli are followed by food, presentations of an additional stimulus were given without reinforcement (P-). During the second stage, A+ and B+ trials were intermixed with simultaneous compound trials (AX+ and BY+). During these compound trials, it was anticipated that blocking would occur, that is, learning about X and Y would be restricted by virtue of being presented alongside A and B, respectively. P- trials also occurred during this stage. Rats were then trained with a final test discrimination, AY+, AX-, BY-. Mackintosh's theory predicts that A and B will have higher associability than X and Y, and, therefore, that the AY/BY discrimination will be solved more readily than the AY/AX discrimination. The Pearce-Hall model, on the other hand, predicts that the associability of A, B, X, and Y will all be low because, by the end of training, the US will be fully predicted by A, B, AX, and BY. As a result, the Pearce-Hall model anticipates no difference between the rates at which the AY/AX and AY/BY discriminations are solved. Likewise, the Rescorla-Wagner model predicts this result, because the prediction of the US is the same for each of the three test compounds at the start of the test discrimination. The Mackintosh model is, therefore, unique, among these three models at least, in predicting faster solution of the AY/BY discrimination than the AY/AX discrimination.

Method

Subjects. Thirty-two male Lister hooded rats served as subjects. All rats were experimentally naïve, and supplied by Harlan Olac (Bicester, Oxon, United Kingdom). They were housed in pairs in a holding room which was illuminated for 12 hr/day. Before the start of the experiment their weight range was 250–300 g, and rats were reduced to not less than 85% of this initial weight by restricted feeding. During the course of the experiment rats' weights were allowed to increase gradually in proportion with a separate group of rats that were allowed free access to food. Measured amounts of food were given at the end of each experimental session, when rats were returned to their holding cages. Experimental sessions were conducted at the same time each day, during the period in which the holding room was illuminated.

Apparatus. Experimental sessions were conducted in eight conditioning chambers, supplied by MED Associates (St. Albans, VT). Each measured 30.0 × 24.0 × 20.5 cm high, and was enclosed within a light- and sound-attenuating box. Exhaust fans within each box provided ventilation and a background noise of 70 dB. The two smaller walls of each chamber were made from aluminum, the larger walls of each chamber (one of which served as a door) and the ceiling were made of clear acrylic. The floor was composed of a series of 19 stainless steel rods, positioned parallel to one another and to the shorter walls of the chamber. Each rod was 4.8 mm thick, and positioned 1.6 cm apart center-to-center. A square, recessed magazine of 50-mm thickness was set into one of the shorter walls of the chamber, equidistant from the two adjacent walls and with the lower edge of the magazine 18 mm above the

grid floor. Food pellets (45 mg, traditional formula, P. J. Noyes, Lancaster, NH) could be delivered to this magazine. An infrared beam was sent from one side of this magazine to the other, and each interruption of this beam could be recorded by the computer as magazine activity. The magazine was also fitted with a 2.8-W lamp that could be used to illuminate the interior of the magazine, which remained off for the duration of Experiment 1. Two 2.8-W lamps were positioned on the same wall as the magazine, 1.5 cm from the floor. These lamps were fitted with 2.5-cm, circular covers made out of translucent plastic, and positioned 16 cm apart, center-to-center. Neither lamp was operated during the current experiment. Three loudspeakers were located on the opposite wall of the chamber: two square-shaped loudspeakers of 70-mm width located in the upper corners of the wall, and a rectangular loudspeaker measuring 35×70 mm located 35 mm from the ceiling and equidistant from the two adjacent walls. The upper left loudspeaker could be programmed to emit two auditory stimuli: a pulsed 77-dB, 8-kHz tone, with each 0.25-s pulse separated by a 0.25-s period of silence, and a 74-dB "buzzer" composed of a 500-Hz train of clicks. The upper right speaker could emit a 78-dB white noise, while the rectangular speaker could emit a 77-dB, 2.9-kHz tone. A relay was also incorporated into this wall, which could be operated in a pulsed manner to produce a 76-dB train of clicks, with a click every 0.08 s. Five auditory stimuli could, therefore, be produced, and each of these was 15 s in duration. On trials in which two stimuli were presented in compound, the onset and offset of these stimuli was simultaneous. These auditory stimuli were controlled by a computer that was programmed with the MED-PC programming language.

Procedure. The five auditory stimuli were assigned to serve as stimuli A, B, X, Y, and P. For half the rats, the white noise and 2.9-kHz tone were A and B, and the pulsed 8-kHz tone and the clicker were X and Y; for the remaining rats, this was reversed. Within each of these two subgroups of rats, stimuli serving as A and B were counterbalanced, as were stimuli serving as X and Y. The buzzer served as stimulus P for all rats.

Rats initially received one session of magazine training, during which a food pellet was delivered to the magazine every 60 s. This session was 30 min in duration, and all rats successfully consumed all pellets during this session, and in all experiments reported here. During each of the next 10 sessions, rats received A+, B+, Ptraining: Each presentation of A or B was followed immediately by the delivery of two food pellets to the magazine, whereas each presentation of P was followed by nothing. Sessions were 52 min long, and contained 10 trials of each of A+ and B+, and four Ptrials. These were block-randomized such that each block of 12 trials contained five of each of the reinforced trial types, and two P- trials. The intertrial interval (ITI), defined as the period from the end of one trial to the beginning of the next, varied randomly from 65-145 s, with a mean ITI for each session of 105 s. Following these 10 sessions, rats received four sessions of AX+, BY+, A+, B+, P- training. Each session in this stage contained five of each of the reinforced trial types, and four P- trials. These occurred in a random sequence throughout the session. Other details of these sessions were the same as for the previous stage.

During the final stage of the experiment, rats were trained for six sessions with an AY+, AX-, BY- discrimination. Each of these sessions contained 32 trials: 16 with AY+, and eight of each of the other two types. These were block-randomized such that each

block of eight trials contained four with AY+, and two of each of the other trial types. These sessions were 68 min in duration, and other details were the same as earlier training sessions. For all trials in this and subsequent experiments, the duration of magazine activity was recorded. For ease of exposition, these durations are expressed as a percentage of the total duration of the CS.

Results and Discussion

A Type I error rate of p < .05 was adopted for all experiments. Conditioning during the first stage of training proceeded smoothly, and the mean magazine activity during the final session of Stage 1 training was 47.5% during A and B (averaged between stimuli), and 9.6% during P. A within-subjects t test revealed a significant difference between these magazine activity rates, t(31) = 12.97. Following this stage, rats were trained with five trial types: A+, B+, AX+, BY+, and P-. The mean magazine activity percentages during the final session of this second training stage for the average of A and B, the average of AX and BY, and P were, respectively, 52.5, 52.2, and 8.9. A one-way analysis of variance (ANOVA) revealed an overall effect of trial type, F(2, 62) =189.39, MSE = 106.30. Post hoc tests conducted according to the Bonferroni procedure revealed no difference between the rates of responding during A/B and AX/BY, t(31) = 0.27; and a difference between both A/B and P, and between AX/BY and P, smaller t(31) = 13.86.

The left-hand panel of Figure 1 shows mean magazine activity for AY, AX, and BY, during each of the six sessions of the test discrimination. Surprisingly, responding was lower throughout training during AX than during BY. To simplify the analysis of these data, discrimination ratios were calculated for each of the two discrimination types. These were of the form p/(p+q), in which p is the rate of magazine activity for each rat during AY, and q is the rate during AX or BY. A score of 0.5 would, therefore, indicate equal responding during AY and the nonreinforced com-

pound, and a score of 1 would indicate perfect discrimination. These discrimination ratios are shown in the right-hand panel of Figure 1. A two-way ANOVA of these ratios with the variables of discrimination (AY/AX vs. AY/BY) and session (1 to 6) was conducted. This analysis revealed a significant effect of discrimination, F(1, 31) = 32.04, MSE = 0.017, and of session, F(5, 155) = 101.74, MSE = 0.007, and a significant Discrimination x Session interaction, F(5, 155) = 3.55, MSE = 0.005. Simple effects analysis revealed no effect of discrimination for the first session, F(1, 186) = 1.32, MSE = 0.007, but a significant effect of discrimination for all other sessions, smallest F(1, 186) = 5.80, MSE = 0.007. There was also a significant effect of session for each of the two discrimination types, smaller F(5, 310) = 46.10, MSE = 0.006.

In Experiment 1, rats were given pairings of each of A and B with food (A+ and B+), and these two stimuli subsequently served as blocking cues during A+, B+, AX+, BY+ training. According to Mackintosh's (1975a) model, this second stage of training should result in attention to A and B becoming higher than to X and Y, as a consequence of A and B being the best predictors of the delivery of food. This model, therefore, predicts that A and B will be more effective discriminative stimuli during the test discrimination, and that the AY/BY discrimination will be solved more easily than the AY/AX discrimination. Our results, however, show the opposite. The AY/AX discrimination was solved more easily than the AY/BY discrimination, suggesting that X and Y were better processed than A and B. This result was surprising to us; not only is it contrary to Mackintosh's model, it is also not the result that might be expected on the basis of the Rescorla-Wagner (1972) model or the Pearce-Hall (1980) model. According to Rescorla and Wagner, attention to all CSs remains constant during blocking. According to Pearce and Hall, stimuli suffer a decrement in processing when they are followed by a predicted outcome, and, because the outcome was entirely predictable after the first trial

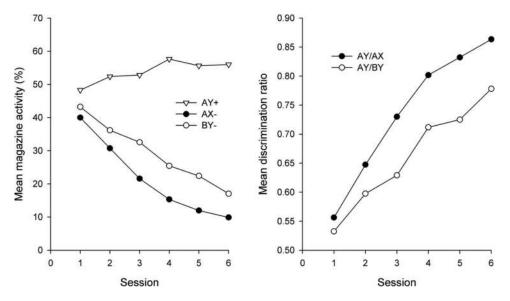


Figure 1. Results of the test discrimination from Experiment 1. Left-hand panel: Mean magazine activity during AY, AX, and BY for each session. Right-hand panel: Mean discrimination ratios for the AY/AX and AY/BY discriminations. The + and - symbols refer to food and no food, respectively.

during Stage 2, the associability of all stimuli should have fallen to the same level. In either case, the AY/AX discrimination and the AY/BY discrimination would be solved at the same rate. It might be possible, however, to reconcile the Pearce-Hall model with the results of Experiment 1 if we assume that the reduction in associability of a cue when it is followed by a predicted outcome happens slowly, over a large number of trials (Pearce, Kaye, & Hall, 1982). Although A, B, X, and Y were all paired with the predicted food US, rats received far fewer trials with X and Y than with A and B. In total, Stages 1 and 2 of Experiment 1 contained 140 trials containing each of A and B, but only 20 each for X and Y. It seems plausible that we simply did not give enough Stage 2 training for the associability of X and Y to be modified fully. We attempted to test this prediction in an unpublished experiment, the design of which was identical to Experiment 1—except that Stage 2 training was extended to 12 sessions, in comparison with the four sessions used here. This extended training regime might be expected to allow the associability of the blocked cues to decrease more fully; the pattern of results seen during the test discrimination was, however, the same as for Experiment 1.

An additional possibility is that the critical difference between the stimuli that produced these surprising results was not the number of times each stimulus was paired with the US, but the number of occasions on which each stimulus was presented to the animals. If the processing each stimulus receives were inversely related to the quantity of an animal's experience with it, then it would follow that stimuli that are presented to an animal on fewer occasions (X and Y) are able to function as more effective discriminative stimuli than those that are presented to the animal a greater number of times (A and B). The idea that exposure to a stimulus results in a decrement in processing is of course not new. It is well documented that the ability of a stimulus to enter into associations is hindered by exposure to that stimulus, both under conditions of nonreinforcement (latent inhibition; Lubow & Moore, 1959) and reinforcement (negative transfer: Hall & Pearce, 1979; Pearce et al., 1982). Many theories of learning include mechanisms that allow the associability of a CS to be reduced following prolonged exposure, both when that CS signals an important outcome such as the delivery of food, and when it signals nothing (e.g., Esber & Haselgrove, 2011; McLaren, Kaye, & Mackintosh, 1989; Pearce & Hall, 1980; Wagner, 1978, 1981).

It seems important, therefore, to evaluate the idea that the AY/AX discrimination was solved more easily than the AY/BY discrimination in Experiment 1 because the animals had received fewer prior presentations of X and Y than of A and B. This is quite different to the suggestion that X and Y were in receipt of higher levels of attention than A and B as a result of learning about X and Y being blocked by A and B, respectively. According to the argument that it was a difference in the number of exposures that was responsible, we should see the same pattern of results if rats are presented with A, B, X, and Y in the same manner as in Experiment 1, except that the delivery of food in the first two stages of the experiment is omitted, that is, no blocking occurs. On the other hand, if the higher associability of X/Y than of A/B seen here is a consequence of blocking and not of exposure, then the result should be the same if we use a blocking procedure that equates the numbers of exposures to A, B, X, and Y. We will deal with these two separate predictions in turn in the remaining two experiments.

Experiment 2

The purpose of Experiment 2 was to evaluate the idea that a schedule of stimulus exposure that was similar to that used in Experiment 1, except for the omission of food delivery following presentations of A, B, X, and Y, would produce a similar result in the test discrimination. The procedure for Experiment 2 was identical to that used for Experiment 1, except that food was only delivered during the first two stages of the experiment following presentation of P. Rats, therefore, received an A-, B-, P+ discrimination in Stage 1, before being trained with AX-, BY-, A-, B-, and P+ trials during Stage 2. The AY+, AX-, BY- test discrimination used in Experiment 1 was also used here. If differences in the amount of exposure in Stages 1 and 2 is sufficient to cause attention to X and Y to be higher than to A and B, then the AY/AX discrimination should once again be solved more readily than the AY/BY discrimination.

Method

Subjects and apparatus. Sixteen male Lister hooded rats served as subjects. These rats were experimentally naïve, were supplied by Harlan Olac, and were housed in the same room and under the same conditions as for Experiment 1. Before the start of the experiment their weight range was 250–295 g, and rats were maintained according to the same food restriction schedule described for Experiment 1. As in the previous experiment, experimental sessions took place at the same time each day and during the period in which the holding room was illuminated. These sessions were conducted in the same apparatus as for Experiment 1.

Procedure. As in Experiment 1, rats were initially given one session of magazine training. Ten sessions were then administered, during which rats were trained with an A-, B-, P+ discrimination. These sessions were identical to the A+, B+, P- sessions in the previous experiment, except that two food pellets were delivered following P and not following A or B. Four sessions then took place in which rats received an AX-, BY-, A-, B-, P+ discrimination. Food was delivered following P, but not following AX, BY, A, or B; in all other respects, these sessions were the same as Stage 2 training sessions given in Experiment 1. Finally, rats were trained for four sessions with an AY+, AX-, BY- discrimination, in the same way as for the previous experiment.

Results and Discussion

Rats solved the Stage 1 discrimination with ease. During the final session of conditioning, mean magazine activity was 3.3% during A/B, and 29.7% during P; this difference was significant, t(15) = 7.33. During Stage 2, rats maintained a high level of magazine activity during P while withholding responding during trials containing A or B. The mean response rates for the final session of Stage 2 for the mean of AX and BY, the mean of A and B, and P were, respectively, 1.4%, 2.3%, and 24.2%. These scores differed significantly, F(2, 30) = 29.45, MSE = 90.02. Pairwise comparisons conducted according to the Bonferroni procedure indicated that the levels of responding during AX/BY and A/B did not differ, t(15) = 1.22; but that responding was higher during P than during either AX/BY or A/B, smaller t(15) = 5.36.

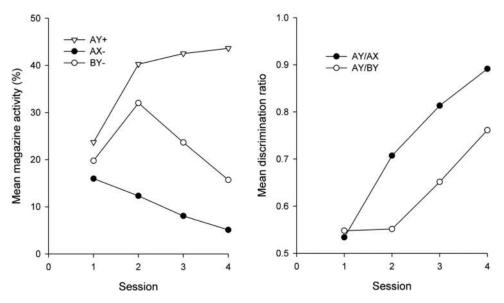


Figure 2. Results of the test discrimination from Experiment 2. Left-hand panel: Mean magazine activity during AY, AX, and BY. Right-hand panel: Mean discrimination ratios for the AY/AX and AY/BY discriminations.

Mean magazine activity during each of AY+, AX-, and BYis shown in the left-hand panel of Figure 2. It is immediately apparent that magazine activity was lower during AX than during BY, throughout training. Discrimination ratios for the AY/AX discrimination and the AY/BY discrimination are shown in the right-hand panel of Figure 2. The AY/AX discrimination was solved more readily than the AY/BY discrimination; A two-way ANOVA of these ratios with the variables of discrimination and session revealed a difference between the two types of discrimination, F(1, 15) = 7.35, MSE = 0.051, a significant effect of session, F(3, 45) = 24.19, MSE = 0.020, and a significant interaction between the two variables, F(3, 45) = 5.24, MSE = 0.010. Simple effects analysis revealed that there was a significant effect of session for both discrimination types, smaller F(3, 90) =10.597, MSE = 0.015; the difference between the two types of discrimination was not significant for the first session, F(1, 60) <1, but was significant for each of the remaining three sessions, smallest F(1, 60) = 6.56, MSE = 0.021.

The observation that the AY/AX discrimination was solved more easily than the AY/BY discrimination is in keeping with the idea that the amount of exposure used in Stages 1 and 2 of the current and previous experiments is sufficient to cause A and B to command lower attention than X and Y. It is, of course, possible that some additional process of attention change takes place during blocking that is not dependent on the amount of exposure to each stimulus, and that the effects of this process were occluded in Experiment 1 by the effect of differing stimulus exposure. A mechanism similar to that proposed by Mackintosh (1975a), for example, might cause changes in attention that are dependent on each cue's status as a better or poorer predictor of reinforcement, provided those changes are small enough to be obscured by the effects of stimulus exposure. It is impossible to determine on the basis of the experiments reported so far whether or not such a mechanism operates. In order to better examine the changes in attention that take place during blocking, we must turn our attention to a version of the blocking task in which all stimuli of interest are presented to the animal the same number of times.

Experiment 3

The aim of this experiment was to compare the associability of blocked and blocking stimuli when the numbers of exposures to these CSs were equal. For this purpose, a blocking group of rats was trained with an A+, B+, C+, AX+, BY+, CX+, CY+, P-discrimination, in which learning about X and Y was expected to be blocked by A, B, or C. Standard associative models predict the associative strength at asymptote to be high for A, B, and C, and low for X and Y. Crucially, X and Y receive as many presentations in this discrimination as A and B. If attention to these cues is based purely on the quantity of exposure, then the associability of all four stimuli should be the same; if, on the other hand, the predictiveness of the cues is important, then we might expect to see differing associability for the blocked and blocking stimuli.

Given the unconventional blocking design used here, we were keen to assess the extent to which learning about X and Y was restricted. In order to achieve this, a control group was trained with an A-, B-, C-, AX+, BY+, CX+, CY+, P+ discrimination. In this design, A, B, and C should be ineffective as blocking cues because they are nonreinforced when presented alone. At the end of training, the associative strength for these animals was expected to be high for X and Y, and low for A and B. By comparing magazine activity during presentations of X and Y in the blocking group and the control group, we can examine the extent to which learning about X and Y was restricted in the blocking group by separately pairing A, B, and C with the US. All rats received a test session during which conditioning to A, B, X, and Y was assessed by briefly presenting each stimulus in the absence of reinforce-

ment. Following this session, the associability of these four cues was tested in the blocking group using the same AY+, AX-, BY – discrimination as used for previous experiments. If the AY/AX discrimination is solved more readily than the AY/BY discrimination, as it was in the previous two experiments, then we will be unable to attribute this to differences in the number of exposures to the four critical stimuli. Instead, this result would suggest that blocking leads to higher attention for the blocked cue. Alternatively, if no changes in attention take place during blocking except those that result from stimulus exposure, or if changes in attention are such that A/B and X/Y command the same amount of attention (as may be predicted by the Pearce-Hall model) then we expect to see no difference in the rate of solution of the two parts of the test discrimination here. Finally, it is possible that the AY/BY discrimination will be solved more easily than the AY/AX discrimination. This would be consistent with the idea that, all other things being equal, better predictors of reinforcement are better processed (as in Mackintosh's model), and would suggest that the opposite result was obtained in Experiment 1 because any effect of predictive power was masked by an opposing effect of stimulus exposure. The data presented here are the combined output of three replications of this experiment. To foreshadow the results of the test discrimination, this was necessary because initial results showed a small tendency for the AY/BY discrimination to be solved more readily than the AY/AX discrimination that did not reach statistical significance. Replication was needed in order to distinguish between a null result and a lack of statistical power; this explains the high number of animals used.

Method

Subjects and apparatus. Ninety-six male hooded Lister rats served as subjects, 48 of which were assigned to each of the blocking and control groups. These were experimentally naïve, from the same supplier and maintained in the same conditions as for previous experiments. Before the start of the experiment, the weight range of these animals was 235–290 g, and each rat was reduced gradually to not less than 85% of its free-feeding weight and maintained according to the procedure described for previous experiments. The apparatus used was also the same as for previous experiments, except that illumination of the lamp located in the magazine for 15 s was used as an additional experimental stimulus. All experimental sessions occurred in the period during which the holding room was illuminated. Before the start of the experiment, rats were randomly assigned to one of two groups—the blocking group and the control group.

Procedure. One session of magazine training was given in the same way as for previous experiments. Following this, rats in the blocking group received 14 sessions of training with an A+, B+, C+, AX+, BY+, CX+, CY+, P- discrimination. The white noise, 2.9-kHz tone, clicker, and pulsed 8-kHz tone served as stimuli A, B, X, and Y, and were counterbalanced in the same way as for previous experiments. The buzzer served as stimulus P, and illumination of the magazine light served as stimulus C, for all rats. Two food pellets were delivered to the magazine immediately following all trials except those with P. Each session had a duration of 64 min, and contained 30 trials: nine trials with P- and three of each of the other trial types. These trials were blockrandomized such that each block of 10 trials contained three P-

trials and one of each of the other trial types. Other details of these sessions, including ITIs, were the same as for previous experiments. Rats in the control group received training on an A-, B-, C-, AX+, BY+, CX+, CY+, P+ discrimination. This was carried out in exactly the same way as training for the blocking group, except that food was not delivered following A, B, and C, but was delivered following P.

Following this training stage, rats were tested to measure the extent to which learning about A, B, and C had blocked learning about X and Y in the blocking group. This was assessed in a test session, which consisted of three blocks of trials, with these blocks following each other seamlessly. The first and third blocks of trials each consisted of one of each training trial type—that is, the blocking group received one trial of each of A+, B+, C+, AX+, BY+, CX+, CY+, P-, and the control group received one trial of each of A-, B-, C-, AX+, BY+, CX+, CY+, P+. The second block of trials consisted of two presentations of each of A, B, X, and Y, in a random order and with no food delivered following any of these auditory stimuli. This session was 52 min in duration, and was in other respects identical to the training sessions previously described. Following this test session, rats received eight sessions of training with an AY+, AX-, BY- discrimination, in the same manner as for previous experiments.

Results and Discussion

Conditioning during the first stage of training progressed smoothly for both groups. For the blocking group, mean magazine activity during the final session of Stage 1 was 40.2% for A+/B+, 30.0% for C+, 37.3% for AX+/BY+, 33.8% for CX+/CY+, and 4.6% for P-. A one-way ANOVA showed that the difference between these groups was significant, F(4, 188) = 137.43, MSE =71.01. Bonferroni-corrected t tests showed that A+/B+ did not differ from AX+/BY+, t(47) = 2.06, C+ did not differ from CX+/CY+, t(47) = 2.73, and AX+/BY+ did not differ from CX+/CY+, t(47) = 2.47, but that all other comparisons were significant, smallest t(47) = 4.32. For the control group, mean magazine activity during the final session was 14.9% during A-/ B-, 11.2% during C-, 42.9% for AX+/BY+, 39.3% for CX+/ CY+, and 38.4% for P+. The difference between these scores was significant, F(4, 188) = 99.99, MSE = 107.972. There was no difference in magazine activity between A-/B- and C-, t(47) =2.35, AX+/BY+ and CX+/CY+, t(47) = 2.56, or between CX+/ CY+ and P+, t(47) = 0.59; all other comparisons were significant, smallest t(47) = 3.19.

Following this training, conditioned responding to A, B, X, and Y was briefly assessed by presenting each of these stimuli separately in the absence of reinforcement. Mean magazine activity rates for the blocking group during this test were 20.6% for A and B, and 9.7% for X and Y; magazine activity for the control group was 9.1% during A and B, and 34.2% during X and Y. A two-way Group x Stimulus ANOVA revealed a main effect of group, F(1, 47) = 13.35, MSE = 154.99, a main effect of stimulus, F(1, 47) = 21.48, MSE = 112.73, and a significant interaction, F(1, 47) = 136.10, MSE = 114.03. Simple effects analysis showed that magazine activity was higher for A and B than for X and Y in the blocking group, F(1, 94) = 25.05, and that the reverse was true for the control group, F(1, 94) = 133.18, MSEs = 113.38. Magazine activity during A and B was higher for the blocking group than the

control group, F(1, 94) = 23.25; crucially, magazine activity during X and Y was lower in the blocking group than in the control group, F(1, 94) = 107.52, MSEs = 134.51. This latter result, weaker conditioning to X and Y for those animals that received pairings of A, B, and C with the US, is a demonstration of blocking. Following this, rats in the blocking group were trained for eight sessions with an AY+, AX-, BY- discrimination. Raw magazine activity rates and discrimination ratios for the AY/AX and AY/BY discriminations are shown in Figure 3. Casual inspection of this figure indicates that there was no difference in the rate at which the two discriminations were solved, and a two-way ANOVA confirmed this impression. There was a significant effect of session, F(7, 329) = 104.82, MSE = 0.011, but no effect of discrimination and no interaction between these variables, Fs < 1.

The most important finding from Experiment 3 is that the AY/AX and AY/BY discriminations were solved at the same rate. This is, at first glance at least, problematic for Mackintosh's account of blocking, which states that blocking occurs as a result of a loss of attention to the blocked stimulus. On each occasion that X or Y was presented to rats in the blocking group during Stage 1, they were accompanied by a better predictor of the US and attention to X and Y should have fallen. A and B, on the other hand, were presented alongside stimuli that were poorer predictors of the delivery of food, and attention to these stimuli should have increased. If this were the case, we would expect the AY/BY discrimination to be solved more readily than the AY/AX discrimination. The results of Experiment 3 are, however, consistent with the Pearce-Hall model; according to this account, attention to all stimuli should fall during Stage 1 because the US is fully predicted on each trial. In order to account for the results of Experiment 1, we suggested that the changes in attention described by the Pearce—Hall model might take place rather slowly, with the result that stimuli that are followed by a predictable outcome more often will suffer a larger decrease in associability. In the current experiment, such slow attentional changes should affect A, B, X, and Y approximately equally because they are each presented, and followed by a predictable US, on the same number of occasions. Attention to A, B, X, and Y should, therefore, all be equivalently low at the outset of the test discrimination. The results of the test discrimination are also fully compatible with the account of blocking provided by the Rescorla—Wagner model, which states that blocking is the result of changes in US processing, and that the processing of A, B, X, and Y need not change at all for blocking to occur.

General Discussion

The three experiments reported here represent an attempt to distinguish between several popular models of associative learning by comparing the associability of stimuli following blocking. In Experiment 1, we used a blocking procedure that did not equate the amount of training with blocked and blocking cues, and we found that the more commonly presented blocking cues had lower subsequent associability than the less frequently presented blocked cues. Experiment 2 demonstrated that the schedule of exposure used in Experiment 1 was sufficient to produce this effect, and Experiment 3 showed that blocking is not a sufficient condition for producing the effect if it occurs in the absence of a difference in exposure. The most striking feature of our data is that the associability of each stimulus was related not to its status as a blocking or blocked cue, but to the number of times it had been presented. We must draw a parallel here between the present findings and the results of a series of experiments examining the associability of stimuli after a different type of cue competition: overshadowing. Following an AB+, X+, Y+ discrimination, we showed that the associability of the overshadowed cues, A and B, was greater than that of the cues trained in isolation, X and Y (Jones & Haselgrove, 2011). Like the present Experiment 1, this was a surprising result

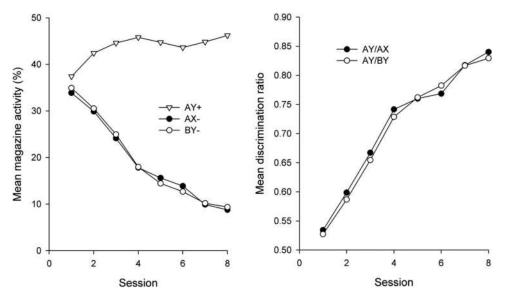


Figure 3. Results of the test discrimination from Experiment 3, for the blocking group only. Left-hand panel: Mean magazine activity during AY, AX, and BY. Right-hand panel: Mean discrimination ratios for the AY/AX and AY/BY discriminations.

that did not initially seem to be compatible with Mackintosh's (1975a) model of learning. Further examination, however, revealed that a similar effect could be produced by presenting the stimuli according to the same schedule in the absence of reinforcement (Jones & Haselgrove, 2013). We proposed that this was due to differences in the conditions of exposure (in compound or in isolation), and tested this prediction by using an overshadowing procedure that equated these conditions. In this case, we observed the opposite of our initial result—lower associability for the overshadowed cue than for a control cue that had higher associative strength (Jones & Haselgrove, 2013). The parallels between this series of experiments and the present examination of associability changes during blocking are obvious. In both cases, the manner in which the stimuli were presented has proved critical in producing higher associability for cues that can be regarded as less predictive of the outcome. In the case of overshadowing, we revealed the reverse of this effect by equating both the number of exposures of the different types of cue, but also the conditions of that exposure; in the present examination of blocking, we have equated the number of exposures only. This begs an obvious question: What would be the result if we presented both blocking and blocked cues under the same conditions with regard to presentation alone or in compound? We have attempted to answer this question in a series of unpublished experiments, but we have been unable to obtain a reliable answer. The tantalizing possibility is that, as with overshadowing, presenting all stimuli only in compound would reveal an underlying process that is consistent with the general view exemplified by Mackintosh's model.

Whether such a process exists remains to be determined; what we are able to say about Mackintosh's model on the basis of the present results is that its account of blocking is, at the very least, incomplete. The model contains no mechanism that would produce the striking exposure effects observed in Experiments 1 and 2. The model described by Pearce and Hall (1980), however, fares rather better. If attention declines on each occasion that a stimulus is followed by a predicted outcome, then it is a simple matter to explain both the difference in associability between often- and rarely-presented stimuli that was observed in Experiments 1 and 2, and the equivalence of associability observed when the number of presentations was equated in Experiment 3. Indeed, the Pearce-Hall model was suggested specifically to account for instances of associability declining under conditions of consistent reinforcement (e.g., Hall & Pearce, 1979). Although our results are not compatible with US-processing models such as that proposed by Rescorla and Wagner (1972), they are consistent with the general view that predicted stimuli are less well processed than unpredicted cues. By applying this concept to CSs as well as USs (e.g., Wagner, 1978, 1981), we can naturally predict a loss of associability to stimuli that come to be expected in the experimental context. Finally, there are a number of "hybrid" models of learning that provide approximate combinations of these various approaches and possess enormous explanatory power as a result (e.g., Esber & Haselgrove, 2011; Le Pelley, 2004; Pearce et al., 1998; Pearce & Mackintosh, 2010). These are easily compatible with our results, provided they restrict the action of any components that correspond roughly to Mackintosh's model, and emphasize processes that are broadly in line with the Pearce—Hall model.

To recap, the pattern of results observed here is suggestive of a general decline in associability that is dependent on the amount of exposure each stimulus receives. This poses an interesting question: If blocking cues (A and B in the present experiments) are paid less attention as a result of their comparatively frequent presentation, why are they able to function as effective blocking stimuli in the first place? The caveat to this question is, of course, that we did not measure blocking in the two experiments that produced a difference in the associability of the blocking and blocked cues. The general procedure, however, in which blocking cues are presented alongside the reinforcer in two stages of the blocking protocol, and the blocked cues are added only for the second stage, is one that has reliably produced a blocking effect in many different preparations (e.g., Kamin, 1969; see Introduction for additional examples). Presumably, a cue needs to command a certain amount of attention in order to effectively block an added stimulus. Is it possible that additional pairings of the blocking stimulus and the reinforcer could be detrimental to the magnitude of a blocking effect? To be clear, we are not suggesting that more initial training will always be harmful. While the blocking cue is still acquiring associative strength, additional pairings will allow it to more effectively predict the US and consequently block learning about any added cues more completely. Once learning about the blocking cue has reached asymptote, however, any additional training will only serve to reduce the attention paid to it. We are not aware of any systematic examination of the effect of overtraining on the blocking effect, but this seems an issue worthy of some attention.

It is entirely possible, of course, that attention is not a unitary phenomenon and that the kind of attention necessary for one cue to effectively block learning about another is not the same as that responsible for the different learning rates seen here. Beesley and Le Pelley (2011) have used eye tracking to examine the amount of overt attention capture by blocked, blocking, and control (overshadowing) cues in a study of human causal learning, In their study, as in our Experiment 1, the blocking cue was paired with the reinforcer a number of times before the addition of the blocked cue. They showed that dwell times to blocked cues were significantly shorter than to blocking or control cues, implying that overt attention follows a different pattern to the effect on learning rates seen in Experiment 1 here. This apparent divergence in findings is certainly consistent with the idea that these tasks tap into different kinds of attention, but without a principled reason for making this distinction it must be considered speculative.

In summary, the experiments presented here underline the prime importance of stimulus exposure in determining associability. They are most readily compatible with models of associative learning that allow the associability of a stimulus to fall during reinforced exposure (e.g., Pearce & Hall, 1980; Wagner, 1978, 1981), and are problematic for models which either emphasize the importance of predictiveness (e.g., Mackintosh, 1975a), or that predict no change in the associability of CSs during blocking (Rescorla & Wagner, 1972).

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