

Flattening of a generalization gradient following a retention interval: Evidence for differential forgetting of stimulus features



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ABSTRACT

In two experiments, rats received exposure to a compound consisting of a solution of salt plus a distinctive flavor (A), followed by an injection of furo-doca to induce a salt need. Experiment 1, established that this procedure successfully generated a preference for flavor A in a subsequent choice test between A and water. Experiment 2 used this within-event learning effect to investigate generalization, testing the rats with both A and a novel flavor (B). For different groups the interval between the training phase and the test phase was varied. Subjects tested immediately after training showed a steep generalization gradient (i.e., a strong preference for A, and a weak preference for B). Subjects given a 14-day retention interval showed a flattened gradient, a reduced level of preference for A and an enhanced preference for B. These results are interpreted in terms of changes in stimulus representations over the retention interval that act to reduce the effectiveness of the distinctive features of stimuli (the features that are necessary to ensure discrimination between them).

1. Introduction

Accounts of the learning produced by classical conditioning procedures give a central role to the notion that pairing the conditioned stimulus (CS) and the unconditioned stimulus (US) strengthens an associative link between them. The strength of this link determines the ability of the CS to evoke a conditioned response (CR), and will determine, in part, the ability of other similar stimuli to do so. This phenomenon, generalization, is taken to indicate that the test stimulus has features or elements in common with the CS, and the degree of generalization is assumed to be determined by the associative strength of the trained elements and the number of elements the stimuli share. The study to be reported here addresses the proposal that training procedures, in addition to modifying associative strength, may also change the nature of the effective stimulus, that is, the nature and number of elements of the stimulus. The proposal is that generalized responding depends, in part, on a perceptual learning process that determines how the stimulus is encoded and perceived.

Evidence taken to support this proposal has been sought from studies in which a delay (a retention interval) intervenes between initial

conditioning and the generalization test. This procedure often results in a reduction in the strength of the CR to the trained CS – a result that can be interpreted as indicating simply that the associative strength acquired in acquisition declines (forgetting occurs) over the retention interval. But in addition, imposing a retention interval usually results in a flattening of the generalization gradient; although responding to the CS is reduced, responding to the test stimulus occurs at a fairly high level. This outcome has been obtained in a range of training procedures: in operant responding in pigeons (e.g., Thomas and Lopez, 1962), appetitive responding in rats (e.g., Perkins and Weyant, 1958), and shock-reinforced aversive conditioning in rats (e.g., McAllister and McAllister, 1963). It has been interpreted (e.g., Riccio et al., 1984) as reflecting a change in the way in which the stimulus is represented. During conditioning the subject will have encoded the details of the CS and, when tested immediately with a different but similar stimulus, it will detect the differences and respond rather little. Over the course of the retention interval, however, details of the CS will be lost (a reversal of the perceptual learning process that established them in the first place). A test stimulus that has the same general features as the CS will thus be responded to as if it were the CS.¹

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¹ An analogous argument has been applied to results obtained from studies using the spontaneous object recognition procedure (Angulo et al., 2017). In this procedure initial training consists simply of exposure to an object. Loss of the ability to discriminate between this object and a similar object, when both are presented after a retention interval, could reflect loss of information about the details of the preexposed object.

Unfortunately, as Riccio et al. (1984) themselves acknowledge, these experimental demonstrations of a flattening of the gradient are open to a simpler, and less interesting, explanation. They may reflect simply a general loss of associative strength over the retention interval, rather than any change in the nature of the stimulus representation. Specifically, imposing a retention interval might reduce responding to all stimuli, but could have more of an effect at the training value than with other stimuli, simply because the higher level of responding at the CS supplies a more sensitive baseline against which to detect changes. The result would be a flatter gradient.

This problem is avoided in an experiment by Richardson et al. (1984); but here another issue arises. In this study (Richardson et al., 1984, Experiment 2) rats were given flavor-aversion conditioning with one concentration of sucrose, followed by a test with this and with other concentrations. The rats showed aversion to the test stimuli but less so than to the trained concentration. This generalization gradient was flatter after a retention interval, but not because there was a greater loss of response to the CS than to the test stimuli. There was no loss to the test stimulus (all subjects showed a profound aversion to it). The authors interpreted the flattening of the gradient as showing that the animals had forgotten the specific attributes of the concentration of the CS and thus avoided another concentration as if it were the CS. The problem with this result is that it is equally well explained in terms of the possibility that the general strength of the aversion had increased over the retention interval. Such an incubation effect has frequently been demonstrated for the flavor-aversion procedure (e.g., Batsell and Best, 1992; Marcant et al., 1985). Test performance to the CS itself could, in principle, allow an assessment of this possibility, but unfortunately, in the experiment by Richardson et al., the aversion to the CS was complete at all retention intervals making it impossible to detect any differences among the groups.

In summary, the results of studies of generalization after a retention interval are consistent with the view that initial training has established a stimulus representation that changes over the interval; but the results are not decisive. In the study reported here (as Experiment 2) we attempted to find a procedure and a set of parameters that can generate the critical result – that is, a flattening of the gradient after a retention interval that cannot be interpreted in terms of a general change in the associative strength of the stimuli. Encouraged by the results of Richardson et al. (1984) we used flavors as the stimuli, but we avoided using an aversive conditioning procedure given the possible issue of incubation. Instead we used a procedure, based on the induction of a salt need, that was designed to generate a preference for the test flavors. A preliminary study (Experiment 1) was conducted to determine the efficacy of this procedure. A further advantage of this training procedure, in contrast to flavor aversion learning, is that it allows multiple presentations of the CS during conditioning (in Richardson et al.'s experiment only one conditioning trial was given). If we are seeking evidence that the details of a stimulus representation are lost over a retention interval, it is important to give sufficient initial exposure to the stimulus to ensure that those details are encoded in the first place.

2. Experiment 1

In the version of the sodium-depletion (or salt-need) procedure, introduced by Fudim (1978), rats are given access to a flavored solution to which salt has been added. This allows the possibility of within-event learning – of the formation of an association between the flavor and salt (see, e.g., Westbrook et al., 1995). This association will be “silent”, but it can be revealed by injecting the rats with a substance producing sodium depletion. After such treatment the rats will show a preference for the flavor that has been associated with salt. In this experiment we assessed the effectiveness of this procedure and established parameters that would produce a clear preference for the flavors to be used in Experiment 2. There were two groups of rats (see Table 1). Both were given initial training consisting of access to and consumption of a salt

Table 1
Experimental Designs.

Experiment 1				
Group	Training		Test	
FD	6 A + Sal		FD inj	A vs W
Control	6 A + Sal		Saline inj	A vs W
Experiment 2				
Group	Training	Delay	Tests	
Immediate (I)	6 A + Sal	0–days	FD inj	A vs W and B vs W
Delayed (D)	6 A + Sal	14–days	FD inj	A vs W and B vs W

Note: Sal refers to a 0.5 (w/v) % NaCl solution; A and B to a 2% solution of either almond or vanilla; W: water; FD inj: subcutaneous injection of furo-doca. In Experiment 1, and for the Immediate group of Experiment 2, injections were given 3 h after the last training trial.

solution flavored with either vanilla or almond (flavor A in the table). Prior to the test, one group (the FD group) received an injection of furo-doca (see Section Method below) in order to produce a state of salt need. The control group was injected with physiological saline. For the test, all subjects were given access to two bottles, one containing flavor A and the other water. We expected those in the FD group to show a preference for the flavor.

2.1. Method

2.1.1. Subjects and apparatus

The subjects were 16 male hooded Lister rats of approximately 4 months of age, obtained from Charles River Laboratories (UK), with a mean free-feeding weight of 469 g (range: 425–525 g). They had previously served as subjects in an experiment involving operant responding, but they were naive with respect to the current stimuli and procedures. They were housed individually in home cages measuring 35 × 22 × 19 cm, made of translucent white plastic, with wood shavings as bedding. Access to water was restricted, as described below. Laboratory chow was available throughout training, but was removed prior to the test (see below). The colony room was illuminated from 8:00 a.m. to 8:00 p.m. each day. All the experimental procedures were conducted in the home cages and during the light phase of the cycle. The flavors used were a 2% (v/v) solution of almond (almond flavoring supplied by Supercook; Leeds, UK) and a 2% (v/v) solution of vanilla (Supercook vanilla flavoring). For the training phase these were made up with a 0.5% (w/v) solution of sodium chloride; for the test they were made with water. The solutions were given to the animals in 50-ml graduated tubes fitted with a rubber stoppers and stainless steel, ball-bearing tipped, spouts. Fluid intake was measured by weighing tubes before and after sessions. The treatment used to induce the sodium appetite consisted of a subcutaneous injection of 0.5 ml of a mixture of 10 mg of furosemide (furo) and 0.5 mg of deoxycorticosterone acetate (doca) dispersed in 20 ml of distilled water with 1 drop of the dispersant Tween 80. Animals in the control condition received an injection of 0.5 ml of isotonic saline.

2.1.2. Procedure

The rats were randomly assigned to two equal-sized groups (FD and saline control) at the beginning of the experiment. To initiate a schedule of water deprivation, the standard water bottles were removed overnight; over the next two days, access to water was restricted to two 30-min sessions per day (starting at 10:30 a.m. and 4:30 p.m.). The next six days constituted the training phase. On each of these the subjects received access in the morning drinking session to 15 ml of a flavored salt solution. For half the rats in each group the flavor was vanilla, and for half it was almond. Water continued to be available during the 30-

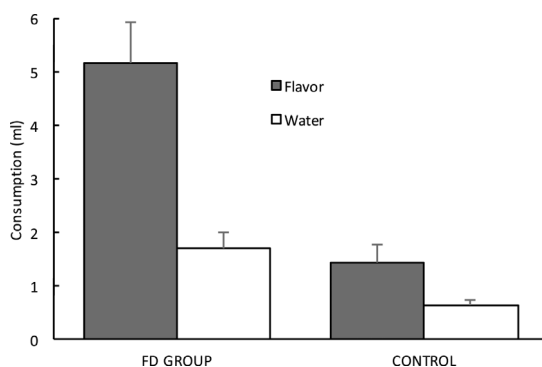


Fig. 1. Experiment 1: Group mean consumption scores during test for the group injected with furo-doca (FD) and the control group given a saline injection. Vertical bars represent SEMs.

min afternoon drinking session. On the last day of training, 3 h after presentation of the flavored salt solution, rats in Group FD were given an injection of furo-doca. Rats in the control group received an injection of physiological saline at this time. After this injection, the standard food was removed from the cages, but each subject was given access to 22 g of salt-free food and distilled water overnight. The distilled water was removed 3 h prior to the start of the test, which was given in the morning session on the next day. During this preference test, the rats had access to two bottles, one containing the trained flavor (vanilla or almond as appropriate) and the other containing distilled water. The left/right position of the bottles during the test was counterbalanced within each group.

2.1.3. Results and discussion

During the training phase all animals consumed almost of the fluid available. The mean intakes on the final day of training were 13.41 ml for the FD group and 14.07 ml for the control group. An ANOVA failed to show any differences between groups on this trial, $F(1,14) = 2.32$, $p = 0.151$, $\eta_p^2 = 0.152$.

Group means for consumption of the flavor and of water during test are shown in Fig. 1. Rats in the FD group drank more of both than did the control subjects, but the difference was especially marked for the flavor. An analysis of variance (ANOVA) with group (FD or control) and solution (flavor or water) as the variables yielded a main effect of group $F(1, 14) = 29.18$, $p < 0.001$, $\eta_p^2 = 0.68$, a main effect of solution $F(1, 14) = 21.89$, $p < 0.001$, $\eta_p^2 = 0.61$ and a significant interaction between these variables, $F(1,14) = 8.79$, $p = 0.010$, $\eta_p^2 = 0.38$. Analysis of simple main effects revealed a significant difference between groups for the flavor, $F(1, 28) = 34.84$, $p < 0.001$, $\eta_p^2 = 0.58$ but not for water, $F(1, 28) = 2.83$, $p = 0.104$, $\eta_p^2 = 0.47$. These results suggest that all rats have something of a preference for the flavor over water, but that the preference is more substantial in those given FD. This is made evident when the results of Fig. 1 are expressed as preference ratios: flavor consumption/total consumption. Both groups showed a preference for the flavor but this was stronger in the FD group (mean: 0.72) than in the control group (mean: 0.62). One-sample t tests showed that the FD group differed significantly from 0.5, $t(7) = 14.63$, $p = 0.001$, $d = 0.62$, whereas the control group did not, $t(7) = 2.10$, $p = 0.074$, $d = 1.64$. We conclude that our training procedure successfully reveals a preference for a flavor paired with salt.

3. Experiment 2

In this experiment we used the procedure of Experiment 1 to investigate how a conditioned preference will generalize to a different flavor, and, critically, to assess how generalized responding might be modified by the passage of time. The design of the experiment is shown in Table 1. All subjects received training identical to that given to the

FD group of Experiment 1 – that is, presentations of a flavor A in compound with salt, followed by an injection of furo-doca. They then received two tests, one involving a choice between A and water, the other a choice between water and a novel flavor (B). For subjects in the immediate (I) condition the tests were given immediately after the training phase; for subjects in the delay (D) condition an interval of 14 days was interposed between training and testing. For all subjects, we can expect there to be a preference for the flavor A (previously paired with salt); and, if the effectiveness of the associative learning responsible for this preference declines over a retention interval, the preference would be stronger in the I group than in the D group. A (generalized) preference for could also occur in subjects tested with flavor B. If the passage of time increases generalisation between stimuli, then we would anticipate that subjects in the D condition could show a preference for B at least as strong as that shown by subjects in the I condition.

3.1. Method

3.1.1. Subjects and apparatus

The subjects were 32 male Lister rats (from Charles River, UK) of approximately 3 months of age, with a mean free-feeding weight of 306 g (range: 300–315 g). They had previously served in an experiment involving operant responding, but were naive with respect to the current stimuli and procedures. They were housed and maintained under the same conditions as those described for Experiment 1. The flavored solutions were the same as in Experiment 1.

3.1.2. Procedure

After the water deprivation schedule had been established, the subjects were assigned to two equal-sized groups, immediate (I) and delayed (D). The next 6 days constituted the training phase; on each day all subjects were given access in the morning drinking session to 15 ml of a flavored saline solution (vanilla + saline for half the subjects in each group, and almond + saline for the others). On the last training day subjects in the I group received an injection of furo-doca, 3 h after the morning experimental session. After this injection, the food and water were removed and the rats were given access to distilled water and salt-free food overnight. Three hours prior to the test session on the next day the water bottles were removed and a two-bottle preference test followed. Half the subjects were tested with the trained flavor (A), either vanilla or almond, in one bottle and water in the other; the rest were tested with the novel flavor (B) versus water. The second test was given on the next day (distilled water and salt-free food having been made available overnight). This test was identical to the first, except that subjects first tested with A now received B, and vice versa. Subjects in the D group received an identical test procedure, but after an interval of 14 days during which they remained in their home cages. For the first 13 days that had free access to standard laboratory diet and to water each morning and afternoon. On Day 14 they received the furo-doca injection following the procedure described for, and at the same time of day as, the I group. Tests with A and with B followed, as described for the D group. Procedural details not specified here were the same as those described for Experiment 1.

3.1.3. Results and discussion

As in the Experiment 1, the animals drank almost all of the fluids presented during the training phase. On the last trial of this phase, the mean intakes were 13.65 ml for the I group, and 14.31 ml for the D group. An ANOVA failed to show any differences between the groups on this last trial, $F < 1$.

Group means for consumption of each flavor and of water on the test trials are presented in Fig. 2. It is evident that for both groups the flavor was preferred over water, and that this was true both for the trained flavor (A) and for the novel flavor (B). Group I showed a strong preference for flavor A and a lesser preference for the test flavor B (i.e.,

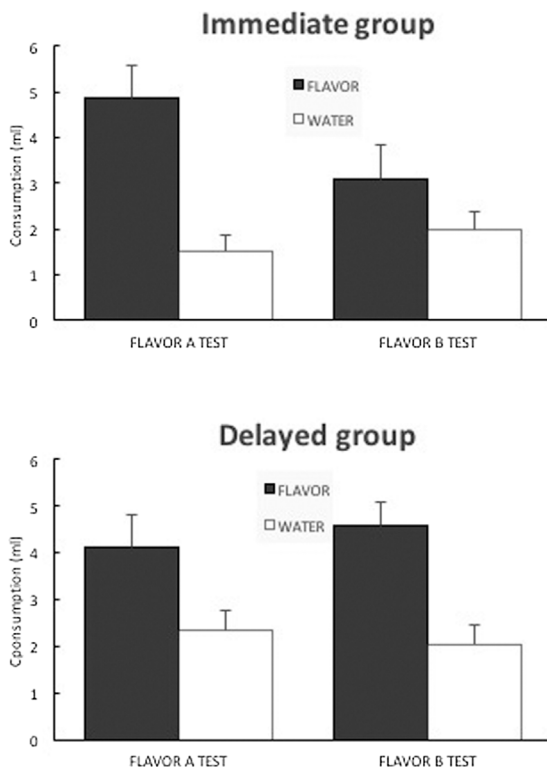


Fig. 2. Experiment 2: Group mean consumption scores for choice tests between Flavor A and water and between flavor B and water. The Immediate group was tested on the day after the last training session, the Delayed group after an interval of 14 days. Vertical bars represent SEMs.

showed a standard generalization gradient). Group D, on the other hand showed a lesser preference for A, and much the same level of consumption of B as of A (i.e., a flattened gradient). An ANOVA was conducted on the flavor consumption data summarized in the figure with the between subject variable of group (I or D) and the within-subject variable of flavor (A or B). This revealed no significant effects: for the main effects of group and flavor, $F_s < 1$; for the theoretically critical interaction, $F(1, 30) = 2.68$, $p = 0.11$, $\eta_p^2 = 0.082$. A parallel analysis on water consumption showed no significant effects; all $F_s < 1$, except for the main effect of group where $F(1, 30) = 1.79$, $p = 0.194$, $\eta_p^2 = 0.058$.

The pattern of result shown in Fig. 2 accords with the proposal that the generalization gradient becomes flatter over a retention interval, but the mean consumption scores presented in the figure hide substantial within-group variability in the total amount consumed, and the critical difference falls short of statistical significance. In order to attenuate the effects of this variability, we computed preference ratios, and these are presented in Fig. 3. Again, the I group showed a generalization gradient, having a higher preference for A than for B. Group D showed a reduced preference for A, a preference that was even less than its preference for B. An ANOVA with group and flavor as the variables yielded no significant main effects, but a significant interaction between the variables, $F(1,30) = 7.67$, $p = 0.009$, $\eta_p^2 = 0.20$. Analyses of simple main effects showed that the difference between the two flavors was significant for the I group, $F(1, 30) = 7.02$, $p = 0.013$, $\eta_p^2 = 19$, but not for the D group, $F(1, 30) = 1.60$, $p = 0.205$, $\eta_p^2 = 105$. Then groups differed significantly in their scores both for flavor A, $F(1, 60) = 4.59$, $p = 0.036$, $\eta_p^2 = 0.07$, and for flavor B, $F(1, 60) = 4.01$, $p = 0.049$, $\eta_p^2 = 0.06$. Although the size of these effects is fairly modest, they allow the conclusion that imposing a delay between training and test results in a flattening of a generalization gradient, both because of a reduced response to the trained flavor and of an enhanced tendency to respond to the test flavor.

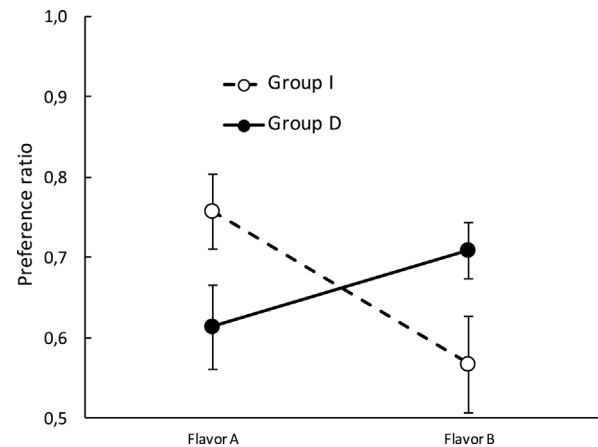


Fig. 3. Experiment 2: Test results expressed as preference ratios (flavor consumption/total consumption). Group I: Immediate test; Group D: Delayed test. Vertical bars represent SEMs.

4. General discussion

As we outlined in the Introduction, there have been several previous studies showing that generalization gradients will become flatter when there is an interval between conditioning and the test. But as we also argued, these results may not be of major theoretical significance; they may reflect simply a change in the general level of responsiveness rather than a change in the processes responsible for generalization (and generalization decrement). Our present results cannot be dismissed in this way. There is certainly evidence of a loss of responsiveness, in that the preference governed by the trained CS was reduced after a retention interval; but in spite of this, the generalization test stimulus, when presented after the delay still evoked a preference, that was as strong as (indeed numerically larger than) that evoked by the CS in the delayed test. This pattern of results has been taken as showing (e.g., Richardson et al., 1984; Thomas, 1981) that subjects can retain the conditioned response over a delay, but that they forget the specific attributes of the trained stimulus and thus respond to other similar stimuli as if they were the CS. We now attempt to specify the exact nature of the change that occurs over the retention interval, and how it influences responding and generalization.

As a starting point, we assume that generalization reflects the extent to which the trained and test stimuli have features or elements in common (and, of course, the associative strength of these features). Thus one flavor may be represented as ac (where a represents the unique features of almond or vanilla) and c the more general features shared by all flavored solutions. When given the test stimulus (bc) shortly after training, performance will be reduced (the contribution of the a elements is missing); but responding will still occur to some extent (the c elements are still present). If associative strength simply declines over a retention interval then only a general reduction in responsiveness both to A (i.e., ac) and B (i.e., bc) can be expected. If, however, the contribution of the a elements is particularly sensitive to the effects of delayed testing, then the pattern of results will be different. In this case, when tested with the CS (i.e., ac), only the c elements will be effective. Accordingly, the level of performance will be much the same as that evoked by the generalization test stimulus (which also contains the c elements), and will be less than that shown to the CS by subjects given the immediate test (for whom the a elements are effective).

This interpretation requires the assumption that the processes responsible for forgetting (whether decay, or some form of retrieval failure, e.g., Bouton, 1993) have substantial impact on the a elements but less of an effect on the c elements. Why should this be? Is it that the a elements lose associative strength more rapidly than the c elements? There is some evidence from related procedures that a and c elements differ in the ease with which they acquire associative strength.

Specifically, there are several studies, complementing that reported here, to show that generalization gradients become steeper with extended initial training (e.g., Rodríguez and Alonso, 2011; see Hall, 1991, for a review of earlier experiments). One interpretation of this effect is that the *c* elements of the CS (*ac*) acquire strength readily so that, after little training, they dominate test responding. With extended training, however, the *a* elements become effective, are learned about, and become able to affect test performance. This difference in the properties of the *a* and *c* elements is suggestive; but the hypothesis that *a* elements acquire strength slowly does not necessarily imply, what is required for the explanation of our present results, that they are likely to lose it quickly.

It would be good to have an account that avoided the need to make arbitrary assumptions about different rates of loss of associative strength. An alternative analysis of the process by which extended training leads to a sharpening of generalization gradients suggests a possibility that might be applied in explaining the effects of a retention interval. This analysis (discussed by Hall, 1991) supposes that the way in which the CS is perceived changes over the course of training. Initially only its more general features are perceived, but, as a consequence of a process of perceptual learning, its specific features become effective. Thus both *c* and *a* features acquire strength in the usual way; differences in the strength acquired (that determine the sharpness of the gradient) are determined by when they come to be perceived during reinforced training. We can apply this general notion to the effects of a retention interval if we assume that the effects of perceptual learning will be lost over the interval. This amounts to saying that, by the end of initial training the CS (*A*) will activate the representations of *a* and *c*, but that after a delay it activates only the *c* elements. That is, after training with *A*, both *a* and *c* features will have been learned about, and both will be effective in the immediate test. Both *c* and *a* elements may lose associative strength over the interval, but the critical source of the flattening of the gradient will be that, on the delayed test, only the general features of the CS will be perceived, making it effectively equivalent to the generalization test stimulus.

Either of the accounts just offered can accommodate the flattening of the gradient in subjects tested after the interval. Neither can explain, however, the crossover seen in Fig. 3. Specifically, why should animals given the immediate test respond less to test stimulus B than those tested after a delay? According to these accounts responding in both cases is determined just by the strength of the *c* elements which, if anything might be expected to be less after a delay. Some other process must be at work. Hall (1991) offered an interpretation in terms of habituation and unconditioned responding. This assumed that the presence of novel stimulus element (one that had not undergone habituation) would evoke unconditioned responses (URs; neophobic responses in this case) that would interfere with the expression of a

flavor preference. The presence of the *b* elements would thus be disruptive for both the I and the D groups. For the I group, however, there would be the additional factor of the omission of stimulus element A. Studies of habituation have shown that omission of an expected stimulus can evoke a UR (see, e.g., Siddle et al., 1983); that is, the mechanism responsible for evoking a UR is sensitive not only to the features that the input holds in common with a central stimulus representation, but also to the presence of features of the representation that are *not* matched by the input. Dishabituation by stimulus omission might thus be expected to disrupt the performance of the I group when tested with flavor B, resulting in a lesser preference than that shown by the D group.

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