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Learned changes in the sensitivity of stimulus representations: Associative and nonassociative mechanisms

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Central to associative learning theory is the proposal that the concurrent activation of a pair of event representations will establish or strengthen a link between them. Associative theorists have devoted much energy to establishing what representations are involved in any given learning paradigm and the rules that determine the degree to which the link is strengthened. They have paid less attention to the question of what determines that a representation will be activated, assuming, for the case of classical conditioning, that presentation of an appropriately intense stimulus from an appropriate modality will be enough. But this assumption is unjustified. I present the results of experiments on the effects of stimulus exposure in rats that suggest that mere exposure to a stimulus can influence its perceptual effectiveness—that the ability of a stimulus to activate its representation can be changed by experience. This conclusion is of interest for two reasons. First, it supplies a direct explanation for the phenomenon of perceptual learning—the enhancement of stimulus discriminability produced by some forms of stimulus exposure. Second, it poses a theoretical challenge in that it seems to require the existence of a learning mechanism outside the scope of those envisaged by current formal theories of associative learning. I offer some speculations as to how this mechanism might be incorporated into such theories.

Associative learning and exposure learning

Those who do research in the area sometimes known as animal learning theory do so (usually) not because of any special interest in the behaviour of the laboratory rat or the domestic pigeon but because they hope that intensive study of such animals will reveal principles of general applicability. Some may feel (along with Mackintosh, e.g., 1983, 1994), that, with the concept of *association*, they have found such a principle; and certainly, in the guise of connectionism, this notion has been shown to be capable of supplying an explanation for a wide range of complex perceptual and cognitive phenomena, in both animals and men.

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But although the phenomena being explained may be complex, the basic notion is very simple. As applied to Pavlovian conditioning it runs as follows. An external event or stimulus is effective (is perceived) by virtue of the fact that it evokes activity in some central representational node. The magnitude of this activation is taken to depend on the intensity of the applied stimulation, which, for the sort of event traditionally used as a conditioned stimulus (CS), may be symbolized as S (for salience); the level of activity in the representation sensitive to the application of an unconditioned stimulus (US) is usually symbolized as λ. Co-occurrence of activity in two representations allows the formation, or strengthening, of a link between them, so that presentation of the CS is able to engender activity in the US representation (and thus, among other things, evoke behaviour appropriate to that US). Although they have disputed the details at length (e.g., Mackintosh, 1975; Pearce & Hall, 1980; Rescorla & Wagner, 1972; Wagner, 1981), most theorists agree that the degree of associative strengthening produced by a pairing of stimuli is some simple direct function of the level of activity in the CS node and the level of activity in the US node (i.e., of $S.\lambda$).

However general the consensus on this matter, the idea that the associative principle can provide a complete account of all instances of learning faces a direct challenge from experiments on what I will call *exposure learning*. In these it has been demonstrated that learning can be generated by exposure to a single event—a training procedure that, on the face of things, could not result in association formation. The phenomenon known as the US-preexposure effect provides an example. If rats are given exposure to a shock prior to its being used as the US in Pavlovian conditioning, acquisition is found to be retarded. This effect is not wholly to be explained in terms of the formation of an association between the shock and the context of preexposure (see Randich & LoLordo, 1979); rather it appears to be, in part, the consequence of some sort of habituation process that reduces the effectiveness of the shock as a US. One way of looking at this is to suggest that the value of λ (the degree of activation in the US node produced by presentation of the shock) is not determined solely by the physical intensity of that event, but can be modulated by a learning process engaged during exposure to the shock.

The phenomenon of latent inhibition seems to provide a parallel to the US-preexposure effect for the case of the CS. Conditioning is found to be retarded in animals that have been given preexposure to the event to be used as the CS, and again attempts to explain this effect in terms of the formation of associations between the context and the CS have not proved wholly successful (see Hall, 1991). It would be tempting to conclude, in line with what has been said about the US, that here is evidence that the value of S is not solely determined by the salience of the CS, but is modulated by some habituation-like learning process. I shall return to this possibility shortly. For the time being we should note that, in fact, for a variety of reasons (including, perhaps, a desire to find a formal place for the traditional notion of attention; see, e.g., Sutherland & Mackintosh, 1971), it has become customary to explain latent inhibition in terms of the operation of another CS-related parameter (α), the value of which can be changed by experience and which determines the associability or conditionability of the CS node. The mechanism responsible for this process has not been specified but various attempts have been made to delineate the learning rules that describe how α changes with experience (Mackintosh, 1975; Pearce & Hall, 1980).

A further challenge to the completeness of the associative analysis comes from work on the perceptual learning effect—studies showing that preexposure to a pair of similar stimuli can, in some circumstances, enhance their discriminability. For example, rats given flavour-aversion conditioning with stimulus AX as the CS will show generalization to a similar stimulus BX (here A and B represent the unique features of the two stimuli; X represents those features that the stimuli, being similar, will hold in common). But prior exposure to the stimuli will attenuate the extent to which generalization occurs (i.e., facilitate discrimination between them). This outcome is most readily obtained when the preexposure regime is one that might loosely be described as being likely to promote comparison between the stimuli, as when AX and BX are presented in alternation. Intermixed preexposure has been demonstrated to be more effective in limiting generalization between AX and BX than a procedure in which AX and BX are presented equally often but in separate blocks of trials (e.g., Mondragón & Hall, 2002; Symonds & Hall, 1995).

Results of this sort have again been interpreted in terms of learned changes in stimulus effectiveness. Gibson's (1969) notion of *stimulus differentiation* is essentially that in animals (or people) given exposure that allows them to compare a pair of similar stimuli, the perceptual effectiveness of features that distinguish these stimuli (A and B in the present example) will be enhanced, whereas that of features that the stimuli hold in common (such as X in the present example) will decline. After intermixed preexposure to AX and BX, a rat conditioned with AX as the CS will learn readily about A but less readily about X, and generalization to BX (which will depend largely on the associative strength governed by the X element) will be slight. Experimental evidence consistent with this view comes from the study reported by Mondragón and Hall (2002). In one of their experiments they gave rats exposure to AX and BX, either in the intermixed arrangement or in separate blocks of trials. All animals then received conditioning trials with X presented alone as the CS. Subsequent testing revealed that X governed more associative strength in the blocked-preexposure group than in the intermixed-preexposure group.

Analysis of the perceptual learning effect

The role of common stimulus features

Before reaching for the conclusion that intermixed preexposure engages a novel learning mechanism that reduces the perceptual effectiveness of common stimulus features, it is necessary to establish that the results reported by Mondragón and Hall (2002) cannot be explained in terms of known processes. In particular, we have already acknowledged that exposure to a CS can reduce its associability (the latent inhibition effect). Given that the factors that determine the occurrence of latent inhibition remain to be fully specified, we must also acknowledge the possibility that the result obtained by Mondragón and Hall is an instance of this effect—that latent inhibition to X presented in compound with A and B proceeds more readily when the two trial types are intermixed than when they are blocked. The results of a recent series of experiments by Blair and Hall (in press), demonstrating the perceptual learning effect using a within-subject design, allow us to reject this possibility.

The design of one of these experiments is shown as Experiment 1 in Table 1. The eight rats in this experiment received initial exposure to three compound flavours, AX, BX, and CX. A was a lemon solution; B and C were solutions of salt and sucrose (counterbalanced). A small amount of quinine (the common feature X) was added to each. Preexposure was given at two

TABLE 1
Experimental designs

Exp.	*Group*	*Preexposure*	*Conditioning*	*Test*
1		AX/BX & CX	AX+	BX & CX
2	X	AX/BX & CX	AX+	BX & CX
	no-X	A/B & C	A+	B & C
3		AX/BX & CX	Y+	BY & CY
4	B	BX/X & CX	B+	B
	C	BX/X & CX	C+	C

Note: A, B, C, X, and Y represent different flavours; + indicates an injection of LiCl.

trials a day, over 6 days. On four of these days (the first four for half the rats, the last four for the remainder), the trials consisted of alternating presentations of AX and BX, thus paralleling the intermixed arrangement of the between-subjects design. On the other two days, CX was presented on both trials (a version of the blocked arrangement). There followed two conditioning trials in which consumption of AX was followed by an injection of lithium chloride (LiCl) as the US. The animals then received generalization tests in which consumption of BX and CX was measured. Half the animals received BX on the first test day and CX on the second; half received the reverse arrangement.

The results of the generalization tests (group mean consumption scores) are shown in the left panel of Figure 1. There was no difference between the subgroup given the CX block at the beginning of preexposure and that given CX at the end of this phase, and their results are

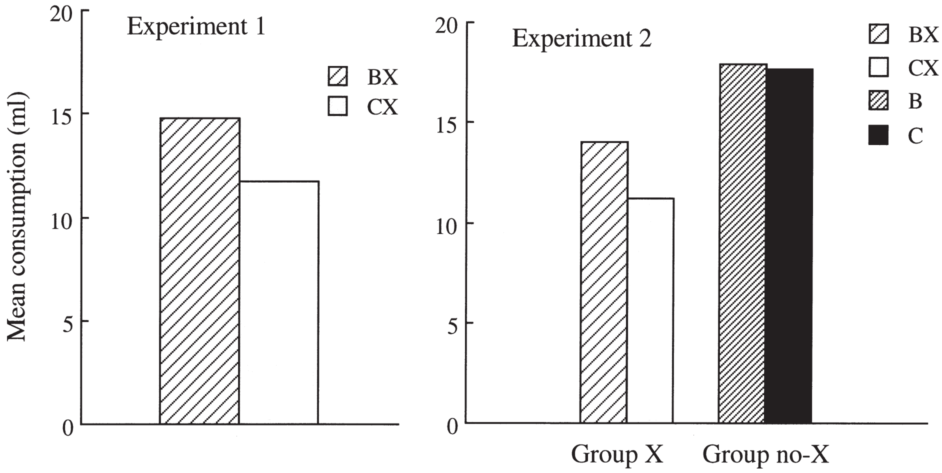

Figure 1. Experiment 1: Group mean consumption of compound flavours BX and CX after aversive conditioning with AX. Experiment 2: Group mean consumption of BX and CX or the simple flavours B and C after conditioning with AX (group X) or with A (group no-X).

pooled in the figure. It is evident that the rats drank significantly ($p < .05$) less of CX than of BX. This result constitutes a within-subject demonstration of the perceptual learning effect of Symonds and Hall (1995). The aversion acquired to one preexposed stimulus (AX) generalized to another similar stimulus preexposed in a separate block of trials (CX in this case), but generalization was less to an equivalent stimulus (BX) that was presented intermixed with presentations of AX during the preexposure phase. As I have acknowledged, it is possible that latent inhibition may play a role in the between-subjects version of the effect—that the effect could arise if latent inhibition of the common stimulus elements (such as the X element) were to develop more readily in the intermixed than in the blocked condition. Such a mechanism could not be responsible, however, for the effect obtained in the within-subject design in which each animal experiences the X element (and other elements common to the three stimuli) in both the intermixed arrangement (i.e., on the AX/BX days) and the blocked arrangement (on the CX trials). Whatever the contribution made by the aversion acquired by X on the reinforced AX trials to the performance shown on test, it must be assumed to be the same on both BX and CX tests. The difference in the aversion controlled by the two test stimuli must have some other source.

The logic of the argument just advanced seems to imply that the associative strength acquired by common stimulus elements is irrelevant to the results obtained in Experiment 1. Although it is impossible to eliminate them entirely (the flavour stimuli used in these experiments necessarily share some intrinsic common elements), it should be possible to reduce the salience of common elements dramatically by omitting the explicitly added X element—the quinine that was added to A, B, and C. In a further study (Experiment 2 in Table 1), Blair and Hall (in press) trained one group of eight rats (group X) with the stimuli and procedures used in Experiment 1, with expectation that these subjects would consume more of BX than of CX on test. A second group of eight (group no-X) was treated identically except that the X element was omitted throughout; that is, these rats were preexposed to A and B (intermixed) and to C, conditioned with A, and tested with B and C. The results are presented in the right-hand panel of Figure 1. Those for group X confirmed those of Experiment 1—generalization was less to BX than to CX. But no such difference (between B and C) was evident in group no-X. It seems that the within-subject version of the perceptual learning effect cannot be obtained in the absence of a salient stimulus element common to all the cues (for a similar finding in the between-subjects procedure see Mackintosh, Kaye, & Bennett, 1991). The attempt to develop an explanation for the perceptual learning effect will need to take account of this finding.

The role of unique stimulus features

If the effect obtained in Experiment 1 and in group X of Experiment 2 is not to be explained in terms of the response governed by common stimulus elements (such as the X element) then the difference in responding shown by these groups to BX and CX on test must be a consequence of a difference between the unique elements, B and C.

McLaren, Kaye, and Mackintosh (1989; see also McLaren & Mackintosh, 2000) have put forward an associative theory of perceptual learning effects that provides a possible explanation. They point out that the preexposure procedure used in perceptual learning experiments will allow the formation of associations among the various elements of the compound stimuli. In the present case, within-event learning can be expected to occur, producing excitatory association between A and X, B and X, and C and X. In addition, however, the alternating schedule used for AX and BX will allow the development of inhibitory associations between the unique features (A and B) of the preexposed stimuli, A being present on those trials when B is absent, and vice versa. When, after conditioning with AX, animals are tested with CX, their response will be partly determined by the ability of X (by way of the X–A association) to contact a representation of the US. This source of responding will not be available on the test with the BX compound as the presence of B will serve to inhibit activation of the representation of A.

The differentiation theory supplies an alternative interpretation. According to this theory, it will be recalled, exposure to intermixed presentations of AX and BX results not only in a reduction in the perceptual effectiveness of common stimulus elements but also enhances that of their unique features. The situation is shown schematically in Figure 2, where the trial-by-trial change in the size of the symbols A and B represents their increasing effectiveness, and the reduction in the size of X its growing loss of effectiveness. The unique element C of the CX compound, which is presented on a separate block of trials, not intermixed with some other similar stimulus, is also shown as losing effectiveness. The implications of these changes for the test trials are shown on the right of the figure. When the animals are tested with BX the B element of the compound will dominate, X will be less readily perceived, and the aversion conditioned to this stimulus will be unable to show itself fully; C, on the other hand, will be less likely to interfere with the perception of X, and a stronger aversion should be evident. Since the effect depends on the degree to which B and C interfere with the expression of the aversion governed by X, such a result would not be obtained when, as in group no-X of Experiment 2 the X element is omitted. (It should be added that, although Figure 2 shows A and B growing in effectiveness, the experimental results do not require us to assume this—all that is needed is that the effectiveness of the unique elements of AX and BX be maintained at a higher level than that of the C element of CX.)

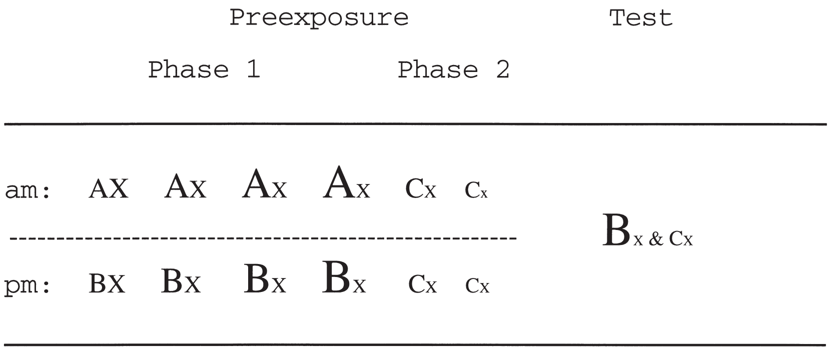

Figure 2. Schematic presentation of supposed changes in effectiveness undergone by the various components of compound stimuli (AX, BX, and CX) over the course of the preexposure procedures employed in the present experiments. An increase in font size indicates increased effectiveness; a reduced size indicates a loss of effectiveness. The consequence of these changes for the test phase are shown on the right of the figure. Note that the scheduling of trials was counterbalanced, with some animals receiving the arrangement shown, and others receiving the CX trials as Phase 1.

An implication of this analysis is that it should not be necessary to employ the AX compound as the conditioned stimulus in order to obtain the perceptual learning effect. In order to test this we (Blair & Hall, 2002) conducted the study referred to as Experiment 3 in Table 1. As before, the rats received preexposure to alternating presentations of AX and BX, and to CX on a separate block of trials. They were then conditioned with a novel stimulus Y as the CS prior to a test with BY and CY. The new flavour used in this experiment was a 1% solution of vanilla essence, chosen because other experiments in our laboratory have shown that there is very little generalization between vanilla and quinine. The design was counterbalanced so that half the rats received vanilla as X and quinine as Y, and half the reverse arrangement. The degree of aversion shown on the test trials may be assumed to depend on the rat's ability to perceive and respond to the conditioned Y element. The hypothesis being tested suggests that B, being perceptually more dominant than C, will be more likely to interfere with perception of Y and thus that a lesser aversion will be displayed to BY than to CY. The associative theory of McLaren et al. (1989) makes no such prediction. The mechanism proposed by this theory requires that the A element should undergo conditioning—the ability of B to inhibit the representation of A will be able to influence behaviour only when A has some associative strength. Conditioning with Y (rather than AX) precludes the operation of this mechanism, and the theory thus predicts no difference between BY and CY on test.

The experiment used eight naive rats given preexposure to AX, BX, and CX according to the procedures described for Experiment 1. They then received two conditioning trials with Y as the CS. This resulted in a more substantial aversion than was produced by conditioning with the AX compound, and consumption was low on the initial test trials. Accordingly testing was continued, in extinction, over the course of 6 days, with each rat receiving three presentations of BY and three of CY. The two trial types occurred in alternation. For half the animals the test sequence began with BY, and for half it began with CY.

The test results for Experiment 3 are shown in Figure 3. Consumption was suppressed to both stimuli on the initial test trials but recovered over the course of the test revealing significantly ($p < .05$) more consumption of BY than of CY. These results demonstrate that the aversion controlled by a conditioned flavour can be modulated by the presence of another, preexposed flavour. The aversion is less when the added flavour is one (B) that has been preexposed in alternation with some other similar flavour (i.e., has been experienced in a sequence of alternating AX/BX trials) than when the added flavour (C) has been preexposed on a separate block (of CX) trials. This outcome is not predicted by the associative account of preexposure effects developed by McLaren et al. (1989, or at least, not by the mechanism that depends on the formation of inhibitory links between A and B; it remains to be determined whether or not some other aspect of this multifaceted theory—for instance, the mechanism it includes for modulation of stimulus salience—might be applicable here). Central to the mutual inhibition mechanism proposed by this theory is that the test stimuli must be able to activate the representation of the conditioned element A in the test phase. This is not possible with design used in these experiments, in which the A element does not undergo conditioning. These results are entirely consistent, however, with the proposal that the perceptual effectiveness of the B element is greater than that of the C element and that the behaviour shown toward the test compounds is a consequence of the degree to which the added elements are able to interfere with the response governed by the conditioned element.

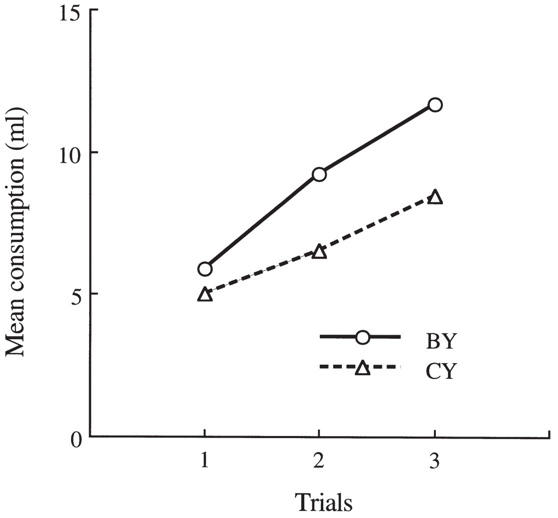

Figure 3. Group mean consumption of the compound flavours BY and CY after aversion conditioning with Y (Experiment 3). All animals received initial exposure to a block of CX trials and to trials with AX and BX presented in alternation.

Mechanisms for changing stimulus salience

The essence of the account of perceptual learning prompted by the results just described (and shown schematically in Figure 2) is that exposure to a stimulus can produce a change in its perceptual effectiveness. In terms of our current theories of learning this amounts to saying that the sensitivity of a stimulus representation can change, or, equivalently, that the value of S associated with a CS is not fixed but can be modified by experience. Our task now becomes that of attempting to specify the learning process by which such changes might occur.

As we have already noted, it is well established that repeated presentations of a motivationally significant event (a US) can cause it to lose effectiveness—the phenomenon of habituation is evidence of that. And although the details of the mechanism responsible for habituation remain to specified, the outcome of the learning process can be characterized as being a reduction in the sensitivity of the representational node corresponding to the US (effectively a reduction in the value of λ associated with that stimulus). If this is true of USs, why should we not accept the equivalent for the stimuli customarily used as CSs? The habituation process will not be so readily evident in behaviour (by their nature, CSs evoke no very obvious response when first presented), but changes in the sensitivity of representational nodes could still occur and should be detectable by means of other behavioural measures (for instance, a CS with a low S value will form associations with a US only slowly—a possible source of the latent inhibition effect). From this point of view, the loss of effectiveness that is assumed to occur to Stimulus X (and Stimulus C) during the preexposure phase of our experiments (see Figure 2) needs no special explanation—our basic assumption is that repeated presentation of a stimulus will reduce its effective intensity (the value of λ for a US and of S for a CS).

The real explanatory problem concerns the changes assumed to occur to Stimuli A and B of Figure 2—these stimuli are shown as gaining, not losing, effectiveness during preexposure. We need to assume, therefore, that there is something about the preexposure arrangement used for AX and BX that reverses, or at least attenuates, the usual habituation process for A and B. The only clue we have (the only thing that distinguishes A and B from Stimulus C) is that AX and BX were presented in alternation during preexposure. We chose this schedule on the grounds that it might allow stimulus comparison to occur, but it must be acknowledged that comparison, as it is usually conceived, is unlikely to be operating with the preexposure procedures that we use. It is usually supposed that comparison will occur when two events are presented concurrently and can be perceived simultaneously (or, at least, in close temporal succession). In our experiments, however, the minimum interval between presentations of AX and BX was about 5 h, making it unlikely that the activation produced by presentation of the first stimulus would still be present when the second was presented. The interaction between the two stimuli must be mediated by some longer term learning process.

One possibility has already been mentioned. The stimuli used in these experiments have been construed as being compounds consisting of a unique feature (A or B) and features held in common (such as the explicitly added X element). As McLaren et al. (1989) have pointed out, exposure to such a compound can be expected to result in the formation of within-event excitatory associations, between X and A and between X and B. When exposed to AX and BX in alternation the consequence will be that the representation of A will be associatively activated (by way of the X–A) link on the BX trials, and the representation of B will be activated (on all but the first of) the AX trials by way of the X–B link. Repeated presentation of the compounds will maintain the excitatory links and ensure that this process continues indefinitely. CX trials might also be expected to establish an excitatory X–C association, but, since these trials are given as a separate block, associative activation of the C representation is less likely to occur. Presentations of AX and BX could not activate the representation of C when the CX block follows exposure to AX and BX (the X–C association would not yet have been formed); and although the X-C association might be effective on the early AX/BX trials when the CX block comes first, we might expect that this association would extinguish in the absence of further presentations of the CX compound. In short, the intermixed preexposure procedure ensures that the representations of the unique features of the stimuli will repeatedly experience associative activation, something that will not occur for the unique feature of a similar stimulus presented on a separate block of trials.

This observation prompts the following hypothesis—that the two different ways in which a stimulus representation can be activated may have different consequences for changes in the sensitivity of that representation. Direct activation of a representation, produced by presentation of the appropriate stimulus, will, we have already argued, result in habituation—in a reduction in the ability to respond to further presentations of the stimulus. But indirect or associative activation of the representation, in the absence of the stimulus itself, may have the opposite effect, restoring the sensitivity of the representation (increasing the S value associated with the stimulus). Put more casually, the suggestion is that every presentation of a stimulus will reduce the impact it makes, but that if we think about (and expect) a stimulus that then fails to turn up, the impact produced by its next occurrence is heightened. Accepting this proposal generates the changes shown schematically in Figure 2. The representations of stimulus elements C and X, which are activated only directly, will suffer a loss of sensitivity, but those of A and B, which are also activated associatively on some trials, will benefit from the effects of what may be termed the "negative habituation" process. Their loss of sensitivity will be attenuated and perhaps (as shown in the figure) may actually be enhanced. Whether the salience of A and B will increase above initial levels remains to be resolved. What matters, for our present purposes, is that this hypothesis suggests that the effective salience of B will be greater than that of C at the end of preexposure. B will thus be more effective than C in overshadowing the aversive element X when the animals are tested with BX and CX, producing the pattern of results obtained in the experiments reported above.

Although clearly speculative, this hypothesis finds support in the final experiment to be described here (Experiment 4 in Table 1; again conducted in collaboration with Chris Blair). Two aspects of the hypothesis were tested, one concerned with the conditions necessary for stimulus effectiveness to be maintained, the other with the suggestion that changes in effectiveness can be equated with changes in the salience parameter. The subjects were 16 rats, all of which received preexposure consisting of a block of CX trials and a set of trials in which BX and X were presented in alternation. According to the hypothesis being tested, C should lose salience in these conditions. B, on the other hand, should not (or at least should suffer a lesser loss). Although BX was presented in alternation with X, rather than with AX, during preexposure, this procedure should still serve to maintain the salience of B. The hypothesis holds that the important consequence of presenting two similar stimuli in an alternating schedule is that the presentation of one of them produces associative activation of the unique features of the other. Since it is the association between common and unique features that is responsible for this activation, the effect should be obtained perfectly readily when only the common feature (X) is presented in alternation with the BX compound. In the test phase, the rats were divided into two groups; group B received four reinforced trials with B as the CS, and group C received four reinforced trials with C as the CS. All then received a series of 12 daily test trials in which the CS was presented in extinction. If the preexposure procedure has left B with more salience than C, this difference between them should be evident not only in the ability of these stimuli to interfere with the expression of an aversion governed by another stimulus (the test used in Experiments 1–3) but also in the rate at which further conditioning occurs—all our standard theories assume that the higher the value of S, the more rapid will be conditioning.

The aversion was acquired very rapidly in both groups, making it difficult to detect a difference between them over the course of the conditioning trials; nonetheless, as Figure 4 shows, acquisition proceeded somewhat more rapidly in group B than in group C. The difference between the groups became more evident over the course of the extinction test. Both groups showed a strong aversion on the initial trials but, as extinction proceeded, consumption of the conditioned flavour reappeared more rapidly ($p < .05$) in group C than in group B. These results are thus consistent with the suggestion that conditioning occurred more readily to Stimulus B than to Stimulus C, the result to be expected on the basis of the proposal that the preexposure schedule results in B having a higher level of salience than that associated with C.

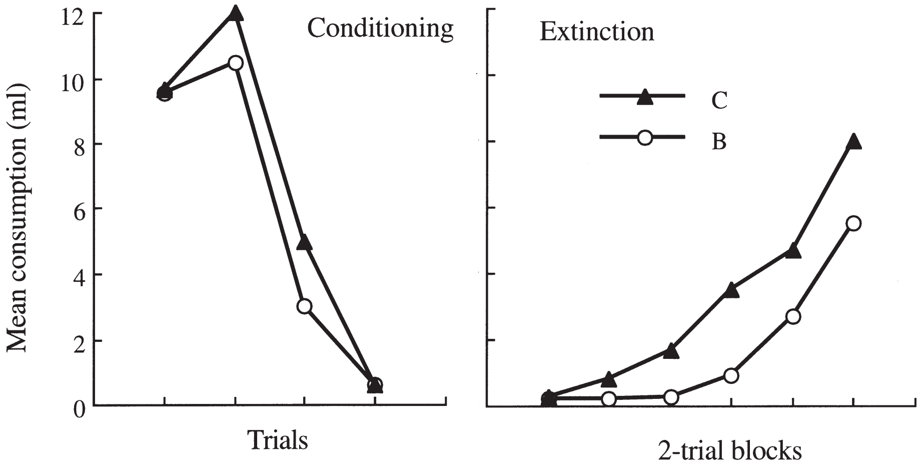

Figure 4. Group mean consumption during conditioning and on extinction test trials with flavours B and C. All animals have received preexposure consisting of a block of CX trials and trials in which BX and X were presented in alternation. The animals were given a fixed amount (10 ml) of fluid on Conditioning Trial 1, but free access to the fluid on the other trials.

Implications and conclusions

Given the central role of associative learning in cognitive functioning generally, a major task for the learning theorist is that of determining under what conditions associations will be formed. At one level the answer is simple—when (for the case of classical conditioning) two event representations are activated concurrently, the association between them will be strengthened, the magnitude of this increase in strength being some simple function of the level of activity in each representation. But what determines these levels of activity? It is common ground that a more intense stimulus will generate more activity than a less intense stimulus, but this is not the only factor. As far as the US is concerned, association formation itself may play a role. Much has been made of the suggestion that a predicted US will be less effective than one that is surprising (Rescorla & Wagner, 1972), a suggestion that is expressed in Wagner's (e.g., 1981) version of associative theory by the explicit proposal that a US will be unable to generate activity in its representational node when that node has already been activated by way of an associative link. What Wagner's theory does not fully acknowledge is that other, nonassociative, learning processes may also play a part in modulating the ease with which a given US can produce activation in its node. In particular, mere exposure to a US (in the absence of a predictive CS) appears to be able to produce long-term changes in US effectiveness, as evidenced not only by the US-preexposure effect but also by the many demonstrations of the phenomenon of long-term habituation. Perhaps we need to acknowledge, as a basic fact of learning, that repeated activation of a stimulus representation makes that node less sensitive to stimulation in the future. And given that associative learning depends on the ability of the stimulus applied by the experimenter to activate its representation, it becomes a matter of the first importance to specify the rules governing the way in which stimulus exposure has this effect.

The first implication of the studies of perceptual learning reported in this article is that what is true of the US also holds for the CS. That is, the results of our experiments can best be accommodated by assuming that preexposure to the flavour cues tends to reduce their perceptual effectiveness. Nothing very radical is being proposed here—the distinction between CS and US, prior to their being paired in a conditioning procedure, is simply that the latter is usually an event of motivational significance, but it is not necessary to suppose that the habituation process will be confined to events of this sort. More important is the further implication of these studies, that under some circumstances the habituation process may be reversed. The speculation that associative activation of a representation, in the absence of the stimulus itself, will increase the sensitivity of that representation has received some empirical support from our Experiment 5 and provides a coherent account of the perceptual learning effects demonstrated in earlier experiments. Whether further experimental work will confirm the validity of this speculation remains to be seen but, as I have already said, such work, designed to determine the rules governing changes in the sensitivity of event representations, will be necessary if we are to be able to provide a full account of the conditions in which associations will be formed.

Granted the assumption that the same rules will apply to all stimuli, both to those customarily labelled as CSs and to those labelled as USs, this work could be carried out as readily with the latter as with the former. As a first step I have been conducting experiments (in collaboration with J. Prados) exploring the way in which preexposure to a shock reduces the effectiveness of that event when it is subsequently used as the reinforcer (the US) in classical conditioning. Our unpublished observations to date (Hall & Prados, 2002) are in accord with the hypothesis advanced above. Preexposure to the shock, even when it is preceded by some other signal, reduces its efficacy when subsequently it is used as the US for conditioning with a novel CS. But this retardation of conditioning is less evident after equivalent preexposure in which nonreinforced presentations of the signal are intermixed with shock-preexposure trials. Our interpretation is that the associative activation of the shock representation that occurs on trials on which the signal is presented alone acts to reverse the habituation process that operated on those trials on which the shock is actually presented.

This apparent parallel between the CS and the US prompts one further, final speculation. We have argued that, for both these events, mere exposure will modify their effective intensities (will produce changes in the values of S and λ, respectively). There is an asymmetry, however, in that we have also allowed (following Mackintosh, 1975) that the readiness of a CS to enter into associations will be determined not just by S, but also by the value of a learning-rate parameter (α), the value of which will depend on how well that CS has predicted the US in the past. Although formal accounts of association formation usually incorporate a learning-rate parameter (often symbolized as β) associated with the US, it has not previously been supposed that the value of this parameter is susceptible to modification. But if α can change, then why not β? Just as the associability of the CS will depend on how well it has predicted in the past, perhaps the associability of the US can be similarly modified, perhaps in terms of how well it has been predicted. To disentangle the relative roles of changes in S and λ and of changes in α and β will be no easy matter but our understanding of the conditions under which CS–US associations are formed will remain incomplete until this has been achieved.

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