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REVIEW

Habituation and Conditioning: Salience Change in Associative Learning

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Repeated presentation of a single stimulus produces habituation—engages a learning process that results in a reduction of the ability of the stimulus to evoke its customary response. Repeated stimulus presentation is a feature of the standard procedure for classical conditioning, although, in this case, subjects experience repeated presentations of 2 stimuli occurring in sequence: S1–S2. We ask how habituation to each of these stimuli (S1 and S2) is influenced by this form of sequential presentation and what implications any effects might have for the understanding of both conditioning and habituation itself. Our review of the experimental evidence demonstrates no clear effect on habituation to S2 of preceding this stimulus with S1. Habituation to S1, however, is attenuated or prevented by the occurrence of S2: Some orienting responses are maintained when S2 follows S1 inconsistently; other responses (habituation of which may be taken to indicate a reduction in the effective salience of the stimulus) are maintained when a salient S2 reliably follows S1. We discuss the implications of these changes in the properties of S1 for associative theories of conditioning and, in particular, for the proposal that the rules that govern changes in the associability of a stimulus differ from those governing changes in its effective salience.

Keywords: habituation, conditioning, association, stimulus salience, associability

For a wide variety of species and training parameters, the response initially evoked by a stimulus (the unconditioned response, or UR, in Pavlov's terminology; Pavlov, 1927/1960) declines in magnitude with repeated presentation of the stimulus; that is, habituation occurs. The effect is most obvious over the course of a training session with closely spaced stimuli (short-term habituation), but it is also evident in the longer term, with the level of responsiveness declining from session to session (Thompson & Spencer, 1966). Standard conditioning procedures involve repeated presentations of stimuli (of the conditioned stimulus and unconditioned stimulus, or CS and US, in classical conditioning). They thus involve the procedure necessary for habituation of these stimuli to occur.

If one takes habituation as being simply the reduced ability of a stimulus to evoke its UR, this may be of little consequence—for Pavlov (1927/1960) the significance of habituation of the response that is initially evoked by a stimulus to be trained as a CS was just that it eliminated a response that got in the way of the development of a conditioned response (CR). But the mechanism responsible for the waning of the initial response needs to be specified, and current accounts have suggested that habituation reflects a change in the effective properties of the stimulus. There are, in fact, rather few theories of habituation to consider (in his recent history of the topic, Thompson, 2009, came up with only three proposals). One of Thompson's proposals was his own dual-process theory (Groves & Thompson, 1970). This makes a number of interesting predictions (particularly with regard to the phenomena of sensitization and dishabituation), but when it comes to habituation itself, it does little more than restate the basic observation that with repeated presentation a stimulus becomes less effective at eliciting its normal response. The other two theories considered by Thompson, although they differ in the details of the mechanisms they propose, seem to agree on the general notion that there is a change in the effectiveness of the stimulus. Specifically, the well-known theory of Sokolov (1963) specifies that the stimulus is rendered ineffective when it comes to match some central representation established by prior experience of that event. Thompson's third theory, referred to by him as the Wagner-Konorski theory (see Konorski, 1967; Wagner, 1976, 1979) has something in common with Sokolov's. It proposes that the central representation of a stimulus is less sensitive to the occurrence of that stimulus when it has recently been activated (by prior presentation of the stimulus, in the case of short-term habituation and also, in Wagner's account of long-

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term habituation, by an event that has signaled the likely arrival of the stimulus).

What, then, are the implications, for the analysis of associative learning, of the fact that its basic training procedure seems likely to produce a reduction in the effectiveness of the stimuli involved? If psychological theories of habituation have been scanty, even less has been said about the implications of the phenomenon for learning generally. It has received some consideration from psychophysiologists studying the orienting response (the OR; see below) in the tradition of Sokolov (1963). Öhman (1983), in particular, has analyzed closely the role of the OR (and its habituation) in Pavlovian conditioning. But, with the important exception of Wagner (e.g., Wagner, 1981), general learning theorists have been largely content, having acknowledged the existence of habituation in their opening chapter or first lecture, to move on to other, seemingly more interesting phenomena, such as those displayed in conditioning and associative learning generally. We suggest that this neglect may be inappropriate. As we have noted, habituation might be expected to occur during the conditioning procedure, and if one accepts the view that habituation reflects an inability of the stimulus to activate fully its central representation, then the implications for the analysis of associative learning could be profound.

In what follows we begin by reviewing the experimental literature that provides information about the consequences of presenting a pair of stimuli serially (as in the conditioning, CS–US, procedure) on the course of habituation to each. This allows the conclusion that habituation can occur in these circumstances but is moderated by the CS–US arrangement. In the final section of this article we consider what this conclusion means for the understanding of the process of habituation and also how the findings might be incorporated into associative accounts of conditioning, as well as the potential implications of doing so.

Habituation of the CS During Conditioning?

Repeated presentation of a CS followed by a US results in the development of the ability of the CS to evoke a conditioned response (CR). The standard associative account of conditioning attributes this to the formation of an associative link between the central representations of the two stimuli. Presentation of a stimulus produces activity in its representative "node," and the co-occurrence of activity in two nodes allows link formation to occur (e.g., Hall, 1996). When subsequently the CS is presented alone, activation of the CS node will result in a CR by way of its acquired ability to activate the US node.

However, repeated presentations of the stimuli during conditioning will have another consequence—habituation will occur. For the CS the most obvious consequence would be a decline in the vigor of the orienting response (OR) that is elicited by any novel stimulus. From one point of view, this is no problem; indeed, as we have already noted, Pavlov (1927/1960) suggested that the OR might constitute an "obstacle" to conditioning, and that conditioning might be seen as a process whereby the OR is replaced by the CR. An issue arises, however, when habituation is interpreted as involving a reduction in the ability of a node to respond to its proper stimulus (or what amounts to the same thing—to a reduction in the effective salience of the stimulus). A fully trained CS will evoke a powerful CR, but if such training produces habituation, that CS will be unable to activate its node and should thus be unable to elicit a response.

Postasymptotic Decline of the CR

The most obvious solution to this problem is to adopt the assumption that habituation proceeds fairly slowly so that when the association has reached its asymptotic strength, habituation is not complete and the CS still retains some power to activate its node. The implication of this suggestion is that extensive training, beyond the point at which the magnitude of the observed CR has reached an asymptote, should lead to a loss in the vigor of the CR. Such training would allow habituation to take its course, making the CS less effective in evoking the CR. Examples of such postasymptotic decline are not uncommon—they are particularly evident in studies using the conditioned suppression technique in which a brief aversive US is preceded by a much longer CS (e.g., Annau & Kamin, 1961; Ayres, Berger-Gross, Kohler, Mahoney, & Stone, 1979; Bouton, Frohardt, Sunsay, Waddell, & Morris, 2008), but the effect was observed and, discussed in some detail, by Pavlov (1927/1960) himself for his original salivary conditioning procedure.

The source of the effect is not fully clear, but it does not seem to lie in CS habituation. Although Ayres et al. (1979) acknowledged habituation of the CS as one possible explanation for their results (among three or four others), they could cite no evidence to compel its acceptance, and Bouton et al. (2008) pointed out features of their findings that are inconsistent with this analysis. The explanations currently available make no mention of habituation but emphasize the notion that further associative learning is occurring with extended training. Thus, one possibility is that extended conditioning has its effect because it augments the associative strength of the cues that define the context in which the training is given. According to some accounts (see, e.g., Urcelay, Witnauer, & Miller, 2012), contextual cues serve a modulatory role that controls the degree of responding observed to the CS. Another possibility is that postasymptotic decline reflects the occurrence of some form of inhibitory learning that opposes the excitation established in initial conditioning. In particular, postasymptotic decline could be a consequence of the development of inhibition of delay (e.g., Schachtman, Channell, & Hall, 1987; Zielinski, 1966; see also, Bonardi, Brilot, & Jennings, 2016). In this, the postasymptotic reduction in the overall magnitude of the CR occurs because a temporal discrimination develops, so that conditioned responding comes to be concentrated toward the end of the CS (immediately prior to the occurrence of the US). Thus, rather than indicating a loss of effectiveness by the CS, this phenomenon implies that there is enhanced control by details of the CS. The implication is that, because the CS continues to be learned about postasymptotically, it is still being processed effectively and that any loss of effectiveness produced by habituation can only be minor.

A further possible source of postasymptotic decline, at least for the case in which the US is shock, is that the properties of the US change with extended training. Repeated presentation of the shock might reduce its aversiveness (itself an instance of habituation), and some accounts of conditioning hold that the CR to a signal for shock involves an opponent process that reduces the aversiveness of the shock (e.g., Young & Fanselow, 1992). These issues are taken up later (in the Habituation of the US During Conditioning? section, which addresses changes in the US). For the time being, we pursue the implications of our tentative conclusion that habituation of the CS does *not* occur during conditioning (or, at least, does so only rather slowly). If the CS does not habituate during conditioning, this must be an effect of following it by another event (the US). Accordingly, one can seek further evidence on this matter by looking at evidence from other procedures that involve the presentation of two stimuli (to be referred to henceforth as S1 and S2) in the sequence S1–S2.

Poststimulus Events and Habituation: Effect of S1–S2 Pairing on Habituation of S1

If repeated presentation of a stimulus normally produces habituation, why should this fail to occur during conditioning? The only procedural difference between habituation and conditioning is that in the latter the stimulus of interest is followed by another (salient) event. Could this prevent the occurrence of habituation? One needs to consider, therefore, experimental studies investigating the effects of presenting a poststimulus event on the progress of habituation of the target stimulus.

Interest in this topic was aroused by Wagner's (1976, 1979) theory of habituation that suggested that habituation was (in part) a consequence of the formation of an association between the target stimulus and the context in which it was presented. According to this theory, a poststimulus event would prevent or attenuate habituation by interfering with the processing necessary for association formation. Even if one does not accept this account (and Hall's, 1991, review of the evidence then available concluded that habituation was not context-dependent in the way required by Wagner's theory), the experiments that support it, and that it generated, are relevant to consider. These experiments monitor the change in the UR to a target stimulus (S1) when its presentation is followed by another (i.e., in the sequence S1–S2). This procedure is, of course, that used in conditioning itself (where S1 and S2 are referred to as CS and US); it differs only in that the event used as S2 usually lacks the motivational significance of a standard US. If one assumes that the effectiveness of an S2 in influencing habituation to S1 will depend on the salience of S2 (in the limiting case a stimulus too weak to be detected could have no effect), the effects demonstrated in these experiments are likely to underestimate those that would be generated in conditioning with a standard US.

We have referred to monitoring *the* UR, but it is important to note that a novel stimulus is likely to evoke a complex of responses. The orienting response (OR), of central concern to Sokolov (1963), is itself a complex, including behavioral orienting and a set of changes (in heart rate, skin conductance, and so on) mediated by the autonomic nervous system. A distinction has been made (e.g., Graham, 1979) between this and the different autonomic pattern that constitutes the defensive response (DR) that is evoked by intense or aversive stimuli. The function of the OR has been taken to enhance stimulus processing, whereas the DR functions to reduce rather than enhance interaction with the stimulus. (In addition, the DR is sometimes distinguished from the startle response, characterized by a widespread flexor jerk and evoked by the sudden onset of a brief intense stimulus.) It remains to be determined whether these different URs respond in the same way to the presentation of a poststimulus event during habituation.

It should be acknowledged that the distinction between the OR and the DR can be difficult to make at the behavioral level, and it has been suggested (e.g., Graham & Clifton, 1966) that they might be differentiated in terms of the way in which heart rate changes on presentation of the stimulus. Unfortunately, no heart-rate data are available for the experiments to be discussed (and work by Nivison, Ursin, & Gjestland, 1983, has challenged the notion that there is a simple relation between heart rate and behavioral orienting in the rat). To this extent, therefore, the assignment of responses to the different headings used in the following sections, is only tentative.

Defensive responses. A freely moving rat will freeze during the presentation of a novel stimulus, such as a bright light or loud noise, and this unconditioned suppression will habituate with repeated stimulus presentations. Although the effect is not always found (see, e.g., Mercier & Baker, 1985), the degree of habituation can be attenuated by the presentation of a poststimulus event. Cross (1975; reported in Pfautz, Donegan, & Wagner, 1978) examined the effects of following the target stimulus (an electric shock) by another and found that habituation of unconditioned suppression (to S1) was attenuated in subjects given an S1–S2 sequence, compared with subjects given unpaired presentations of S1 and S2.

This procedure has been investigated more extensively for the neophobic response of the rat to a novel foodstuff. The decline in neophobia that occurs with experience may be multiply determined, but at the descriptive level it has the properties of being a form of DR that undergoes habituation. Green and Parker (1975) demonstrated that consumption of a novel substance was enhanced by prior exposure to that flavor, but that effect was attenuated when a different novel flavor intervened between the two presentations of the test substance. The attenuation was greater the more closely the presentation of the second flavor followed the first presentation of the flavor being tested. This posttrial distractor effect has been confirmed in a number of subsequent experiments: Dopheide, Smith, Bills, Kichnet, and Schachtman (2005); Kaye, Gambini, and Mackintosh (1988); Robertson and Garrud (1983); Shanks, Preston, and Stanhope (1986). This last study also showed that the effectiveness of the distractor depended on its novelty; a distractor that was familiar (i.e., that had itself undergone habituation) did not disrupt habituation to the target flavor. In a study using a related procedure, Hall, Blair, and Artigas (2006) tested the properties of the target flavor indirectly by assessing its ability to interfere with consumption of a positively valued substance (on the assumption that habituation would reduce such interference). They found that interference was reduced (i.e., habituation was less profound) after preexposure in which the target flavor had been followed by some other.

Although this issue is complex (see, e.g., Sokolov, Spinks, Näätänen, & Lyytinen, 2002) the vasoconstriction evoked by the presentation of an intense or aversive stimulus has often been taken to be a DR. Wagner (1976) reported a study of vasoconstriction in the pinna of rabbits exposed to presentations of two different tones. One tone was presented alone; the other was followed by a visual–tactile distractor. On test the response to the latter was found to be maintained at a higher level than the response to the former.

Orienting responses. The sample of evidence just described confirms the hypothesis that, at least for some URs, presentation of S2 in the S1–S2 sequence can limit the development of habituation to S1. The position is less clear when it comes to studies of the OR, which, from the work of Sokolov (1963) onward, have been central to the analysis of habituation. That the OR should show a different pattern from that seen with DRs will not be surprising if one accepts the view that its functional significance is quite different. The DR is (almost by definition) protective. The functional significance of the OR, by contrast, is attentional; according to Spinks and Siddle (1983), it provides a mechanism for controlling changes in information processing. In some circumstances it could be useful to maintain or even enhance the OR to a certain stimulus, even one that is familiar.

There are many studies of the OR that have examined the effects of presenting sequences of stimuli (e.g., Ben-Shakhar, 1980; Furedy, 1969; see Siddle, Stephenson, & Spinks, 1983), but few have allowed assessment of the S1–S2 sequence of interest here. An exception is that by Lovibond (1969), who reported a study of habituation of what was then called the galvanic skin response (GSR) to a series of presentations of a light S1 that was followed immediately, for some subjects, by a tone S2. The GSR to the light declined over presentations, and it did so both for subjects that received the S2 and for those that did not. Strikingly, however, this was true only for subjects that received S2 on all trials; when the S2 was presented on a random 50% of trials, habituation of the response to S1 was much attenuated. The implication is that the OR tends to be maintained when the subject is uncertain about the outcome of the eliciting stimulus. Similar results have been obtained by Higgins (1971) in a study that used heart rate and vasomotor activity as the dependent variables and varied the probability that a tone of a certain intensity would follow a signal light.

These results, which contrast with those just described for DRs, in finding attenuation only when S1 is an unreliable predictor of S2, have been largely confirmed by experiments using a quite different procedure. These experiments (reviewed by Pearce & Hall, 1992) have looked at the behavioral orienting response of rats to the brief illumination of a discrete light. The initial response of the rat is to turn toward the light and approach it with his snout. This response declines when the light is repeatedly presented alone and also, although the rate of decline is less, when the light is followed reliably by some other event, such as the presentation of a food pellet (Kaye & Pearce, 1984). The response is maintained, however, when the light is followed by inconsistent consequences. Thus, Kaye and Pearce (1984) found that the OR was maintained when a food pellet was presented after only a random 50% of the presentations of the light; Pearce, Wilson, and Kaye (1988) found that it was maintained when the light was followed by a tone on 50% of trials but declined when the tone occurred on all trials; Swan and Pearce (1988) found that the OR was maintained when the value of the event that followed (a cue associated with imminent reward vs. one associated with delayed reward) varied randomly from trial to trial.

These effects were interpreted (Pearce & Hall, 1992) in terms of the model of conditioning proposed by Pearce and Hall (1980). This account supposes that the *associability* of a potential CS (represented by a parameter labeled alpha, in the formal model) can change with experience, declining when a stimulus reliably predicts its consequences but being maintained when it does not.[1] The OR, or at least the aspect of it recorded in the experiments just described, appears to track the level of alpha predicted by the theory. Support for this interpretation comes from studies in which the preexposed light has subsequently been used as the CS in a standard conditioning procedure. As its name implies, the associability of a stimulus determines the readiness with which that stimulus will enter into an association, and the experiment by Swan and Pearce (1988) confirmed that subsequent conditioning occurred more readily for a light that had been followed by inconsistent consequences during preexposure.

The analysis just offered can be reconciled with the wider literature on the OR by taking account of the distinction made by Liddell (1950) in his discussion of the Pavlovian orienting reflex. Pavlov (1927/1960) referred to the response to a novel event as the "what-is-it?" reflex; Liddell suggested that such an event will also elicit a "what-happens-next?" reflex. Both of these will change with experience and may do so according to different rules. The first, which implies the formation, or modification, of a central representation, has been the primary focus of work on habituation. Thus, Sokolov's (1963) theory, with its notion of a neuronal model, makes the formation of a central representation a primary explanatory construct; Wagner's (1976) theory, which allows the formation of associations among the components of a complex stimulus, has something in common with this. The "what-is-it?" reflex will decline with experience as the properties of the central representation change, a decline that is attenuated when presentations of the stimulus are followed by another event. The "what-happens-next?" reflex, by contrast, declines as the consequences of the stimulus become known but is maintained (or restored) when these are uncertain.

Poststimulus Events and Habituation: Indirect Measures

The studies considered in the preceding section focused on the effects of S1–S2 training on the ability of S1 to evoke its UR—the most obvious and direct measure of habituation. But a change in the effective salience of S1 will have more general effects. We now consider attempts to detect these using test procedures that assess the effectiveness of the preexposed stimulus by using it as a CS or as a US in a further stage of conditioning.

Latent inhibition. A stimulus that has undergone habituation training will be learned about only slowly when it is subsequently used as the CS in a conditioning procedure, a phenomenon referred to as latent inhibition (e.g., Lubow, 1989). Lubow's (1989) conditioned attention theory explains latent inhibition by suggesting that on its initial occurrence a stimulus will evoke an attentional response but that this will decline with repeated presentation; the attentional response is necessary for the stimulus to function effectively as a CS. According to the theory, the decline in the attentional response will be attenuated when some other stimulus

[1] It is worthwhile to clarify at this stage that in the Pearce and Hall (1980) model a distinction was drawn between the associability of a stimulus and its salience (the latter being determined, essentially, by stimulus intensity). Associability was concerned solely with the ability of the stimulus to enter into associations; salience would influence other aspects of performance. Other theorists have used the terms differently or sometimes interchangeably.

follows the target stimulus during preexposure. If one regards the loss of the attentional response as an instance of habituation (although Lubow does not use the term), this amounts to the proposal that the latent inhibition effect could be used to demonstrate attenuation of habituation to S1 by presenting it initially in the S1–S2 arrangement.

Experimental tests of this suggestion have produced inconsistent results. Using the conditioned suppression procedure and auditory and visual stimuli, Szakmary (1977) found that conditioning proceeded more readily to S1 (i.e., latent inhibition was attenuated) after preexposure to S1–S2 than after preexposure to uncorrelated presentations of S1 and S2. Lubow, Schnur, and Rifkin (1976) failed to replicate this result but did find an attenuation when comparing S1–S2 training with a condition in which S1 was presented alone. This latter result was not obtained, however, in a similar experiment by Mercier and Baker (1985). Experiments using flavor-aversion conditioning in the test phase have been similarly inconsistent. Thus, Kaye, Swietalski, and Mackintosh (1988a) and Best, Gemberling, and Johnson (1979) have demonstrated a loss of latent inhibition when a second flavor immediately followed presentation of the target flavor during preexposure. But no such effect was found in similar experiments by Honey and Hall (1989) and by Westbrook, Provost, and Homewood (1982).

Given what has been said previously about the role of stimulus associability in the context of the orienting response, these discrepancies might well be expected. It may be that a reduction in some aspect of the effectiveness of the stimulus (such as the decline in the attentional response of conditioned attention theory) contributes to the latent inhibition effect, but a test involving new learning about that stimulus will not be a pure measure of this reduction. The rate of new learning will be determined partly (even largely) by the associability of the stimulus, the value of which will be determined by its predictive history. The experiments just described compare cases in both of which the target stimulus is reliably followed by another event (S1–S2) or by no event (S1 presented alone). In both, therefore, associability can be expected to decline, but which procedure will produce the greater decline will depend on the exact parameters employed (in particular on the initial salience of the stimuli; see Hall & Rodríguez, 2010a). The S1–S2 arrangement may attenuate habituation to S1, but if it also, for the stimuli chosen, results in a rapid loss of associability by S1, there will be no advantage on test when compared with the S1-alone treatment. Evidence supporting the role of associability as determined by the predictive accuracy of the stimulus in determining the outcome of these experiments comes from a study by Matzel, Schachtman, and Miller (1988). In this, the nature of the event used as S2 varied from trial to trial during preexposure. With this arrangement the associability of S1 should be maintained, and, indeed, the results showed that latent inhibition was abolished. This result constitutes a clear parallel to the effects observed in the studies of the OR that were discussed earlier (e.g., Lovibond, 1969; Swan & Pearce, 1988).

US preexposure. The latent inhibition experiments just discussed have used the rate of new learning, in which the target stimulus (S1) served as the CS, to assess the effects of S1–S2 preexposure. One should also consider the case in which the target stimulus is used as the US. There is plentiful evidence (e.g., Randich & LoLordo, 1979) that exposure to the US, presented alone, retards subsequent conditioning. If this US-preexposure effect is a consequence of habituation (an issue that is discussed explicitly subsequently) and the presentation of a poststimulus event attenuates habituation, then following the potential US by some other event during preexposure should attenuate the effect.

This issue has not been the subject of much experimental attention, and such evidence as is available allows no firm conclusions. Fanselow and Tighe (1988) monitored the development of contextual fear (presumed to be the consequence of the formation of an association between the context and the US) in rats given a series of unsignaled shocks. Although the conditioned response was greater when the shocks were more widely spaced (an outcome that might be expected on the basis of some accounts of habituation; e.g., Wagner, 1979, 1981), there was no effect of inserting a distractor stimulus (a brief tone) between shock presentations. Clearer effects might be expected from a procedure in which the distractor immediately follows shock presentation. Hancock (2007) gave rats initial exposure to a series of shocks prior to conditioned suppression training with a light as the CS. For one group the shocks were followed by a potential distractor stimulus (a 60-s noise) during preexposure. These subjects acquired suppression rather slowly and at much the same rate as a group given preexposure to the shock on its own; intriguingly, however, conditioning occurred readily when the distractor was presented on only a random 50% of the preexposure trials (see Hall & Rodríguez, 2010b).

Perhaps the absence of a clear effect in these procedures is not surprising. The events used as distractors were no doubt much less salient than was the shock, and the relative salience of the stimuli may be important in determining any effect. Certainly the shock, by virtue of its high salience, would be expected to show only slow habituation, even in the absence of a distractor. (Thompson & Spencer, 1966, presented the failure of strong stimuli to show habituation as one of its defining characteristics, and slow habituation of such stimuli has been observed in a range of testing procedures; e.g., Groves & Thompson, 1970; Raskin, Kotses, & Bever, 1969; Thompson & Glanzer, 1976). Accordingly, a demonstration of the reality of a distractor effect on US preexposure might be more readily obtained for a US of lesser salience than a shock. One possibility is to make use of the sensory preconditioning procedure in which the events (S1 and S2) equivalent to the CS and US of the conditioning procedure are both neutral and the CR to the S1 emerges after a subsequent treatment has rendered S2 motivationally significant. There is some evidence to suggest that, with this procedure, preexposure to the stimulus that equates to the US (i.e., S2) will cause a loss of effectiveness but that this loss is attenuated by the presentation of a poststimulus event during the preexposure. Artigas, Sansa, and Prados (2012) gave rats preexposure to a salt solution followed by pairings of salt with a novel flavor. They then tested consumption of that flavor after the induction of a sodium appetite. A high level of consumption would indicate that the salt had served as an effective US during the pairing, and this result was found for rats that had experienced a poststimulus distractor during preexposure. Although this finding is suggestive, it should be acknowledged that it was obtained with only a specific set of stimuli, and the complexity of the experimental design allows the possibility of other interpretations.

Conclusions

The data reviewed in this section allow the conclusion that the change in the UR evoked by a target stimulus is modified when that stimulus is followed by another event. When the response being measured is an OR, the decline that would normally occur is prevented or attenuated when the poststimulus event occurs unreliably. This result, we have suggested, reflects the operation of an attentional mechanism that acts to maintain the associability of events the consequences of which are uncertain. Whether this is relevant in accounting for the fact that the CS maintains the ability to evoke performance over the course of training is a matter for debate. Certainly the theory proposed by Pearce and Hall (1980) regards the OR as an index of the parameter alpha, the sole function of which is to modulate the course of acquisition. The value of alpha is not assumed to influence performance. The validity and implications of this assumption are developed in the Discussion section.

For other URs, habituation is prevented or attenuated when the target stimulus is consistently followed by another event; if the magnitude of the UR is an indication of the salience of the stimulus, this means that the effective salience (and the ability to evoke a response) is maintained in these circumstances. This training procedure is, of course, just the arrangement that holds for conditioning (the CS is followed by the US), and accordingly one can expect that habituation of the CS over the course of conditioning trials would be limited or might fail to occur at all. This is not to say that that extended training has no effect on the CS—we have already acknowledged, for instance, that extended training could allow the subject to come to discriminate its temporal properties—but there is no real puzzle as to why a well-trained stimulus should continue to be able to evoke its CR. The further implications of our general conclusion are taken up in the Discussion section of this article.

Habituation of the US During Conditioning?

We reached the conclusion that a CS maintains its effectiveness (resists habituation) during conditioning because it is followed by another event (the US). But the US itself is not normally followed by another event during conditioning. The obvious implication is that the US might undergo habituation and, if so, as a consequence, might lose its ability to maintain the effectiveness of the CS (leaving things back where they started). This problem may, however, be more apparent than real; the events used as USs are typically high in salience (food for a hungry animal; electric shock), and as we have already said, there is good evidence (e.g., Thompson & Spencer, 1966) that salient stimuli are slow to habituate (but see McSweeney & Swindell, 1999). It will be worth considering, nonetheless, whether the relation between two stimuli presented in sequence may be reciprocal. That is, if following a CS by a US retards habituation of the CS, does preceding the US by a CS influence habituation of the US?

Conditioned Diminution of the UR

Direct study of changes in the strength of the UR evoked by the US over the course of conditioning itself does not lead to any simple conclusion. It is true that the UR will generally decline, and in some conditioning preparations this decline is found to be more substantial when the US is preceded by a CS than when it is presented alone or is not paired with or signaled by the CS (e.g., Baxter, 1966; Fanselow & Bolles, 1979; Grings & Schell, 1969, 1971). This phenomenon is known as *conditioned diminution of the UR* (H. D. Kimmel, 1966). It is supportive of Wagner's (1981) theory of conditioning, which supposes that associative activation of a US representation by a CS will reduce the response of that representation when the US then occurs—this is, indeed, Wagner's account of (long-term) habituation.

These results are not, however, enough to compel acceptance of the general principle that habituation of the UR proceeds more readily when the US is explicitly preceded by another event. One problem is that the conditioned diminution effect is found with only some response systems. In other preparations (e.g., the rat's startle response: Leaton & Cranney, 1990; or rabbit's eyeblink: Donegan, 1981), the presence of a predictive CS can potentiate the UR. These discrepancies may be a consequence of the fact that the behavior recorded in response to the US in this situation will reflect not just the UR but also the effects of the developing CR. For some training preparations, this response may mimic the UR (see, e.g., Donegan & Wagner, 1987), or it may enhance the general level of motivational arousal, thus potentiating responding (Leaton & Cranney, 1990; Wagner & Vogel, 2010). Conditioned diminution could thus be occurring in these circumstances, but its presence would be obscured by the effects of conditioning. By the same token, however, given that conditioning can establish CRs that may interfere with (or even be directly antagonistic to) the UR (see, e.g., Young & Fanselow, 1992), it is possible that instances of conditioned diminution are a consequence of such interference effects rather than indicating a change in the way in which the US is processed.

Wagner and Vogel (2010; see also Brandon, Betts, & Wagner, 1994; Brandon, Bombace, Falls, & Wagner, 1991) have conducted a close analysis of the interaction between the UR evoked by paraorbital shock in the rabbit and the various CRs that are established in conditioning. They presented a convincing case for the conclusion that, in this training procedure, UR to a signaled US is diminished. To this extent, their analysis supports the conclusion that the associative mechanism proposed by Wagner makes a contribution to the (long-term) habituation effect (e.g., Wagner, 1979, 1981). One may still ask, however, whether there are other sources of habituation and investigate whether these are influenced by signaling the US during exposure to it. To examine the issue of interest here one needs to eliminate the direct effect of the CR by comparing the performance of the two conditions (trained with a signaled US; trained with the US alone) in a final test in which both experience the US alone.

A few studies have included the required test, and these found that the UR that diminished during signaled training was restored in the test with the US presented alone (Baxter, 1966; Grings & Schell, 1969; E. Kimmel, 1967; H. D. Kimmel & Pennypacker, 1962). The apparent implication—that conditioned diminution derives solely from the direct associative effect of the CS—must, however, be treated with caution, because this test procedure introduces other factors. First, presenting the US alone during training does not preclude the possibility of conditioning—in the absence of a CS, the experimental context itself likely acquires associative strength. One might expect the context to elicit some form of CR in the unsignaled group, which, if it has opponent properties, would mean that the magnitude of the UR will be underestimated in this condition. Second, subjects in the signaled condition experience the US alone for the first time on test, and this stimulus may be perceived as a different event from that presented during training (which will have consisted of the US plus the aftereffects of the CS). The resulting generalization decrement could render the US on test effectively novel, underestimating the extent to which habituation occurred during training (see Mackintosh, 1987, for a discussion of this possibility). Both of these factors would work against the possibility of observing a diminished UR in subjects given signaled training.

Given these uncertainties, the safest conclusion at this stage is that there is no evidence from these experiments to support the proposal that habituation to the US is modified by signaling it with a CS, except by way of the associative mechanism of Wagner (1981). These uncertainties are reduced, to an extent, in the studies discussed in the first part of the next section. These experiments are analogous to those on conditioned diminution of the UR but make use of USs that have less motivational impact than do the stimuli used in studies of conditioning. This should, at least, eliminate or reduce any confounding effects that arise from the conditioning of emotional states.

Prestimulus Events and Habituation: Effects of S1–S2 Pairings on Habituation of S2

In a previous section (Poststimulus Events and Habituation) we considered experiments on habituation in which two stimuli were presented in sequence (i.e., S1–S2), and the effect of the poststimulus event (S2) on habituation to S1 was studied. Here we consider the parallel case, in which the target stimulus is S2, and ask whether preceding it by S1 influences habituation to it. As we have noted, this arrangement is that used for conditioning, where S1 and S2 are referred to as CS and US and the latter is an event of motivational significance. Such experiments were discussed in the previous section. Those discussed now can be regarded as studies of conditioning in which the S2 event is not of great motivational significance and is unlikely to endow S1 with the ability to evoke an overt CR. The absence of a substantial CR makes interpretation of the result easier, although complications arising from the possibility of generalization decrement still remain.

The role of context conditioning. Although the type of event used as S2 in the experiments under consideration here is unlikely to support the development of an overt CR, conditioning could still occur, with S1 acquiring the power to activate the representation of S2. Indeed, this notion is central to Wagner's (1976) account of habituation. This holds that the node that represents a given stimulus will be less responsive to the occurrence of that stimulus when it (the node) has recently been activated. In the case of long-term habituation, this activation is achieved associatively. Specifically, the theory assumes that when a target stimulus is repeatedly presented alone, the cues provided by the training context will come to activate the node for that stimulus. A seemingly simple, direct test of this hypothesis would be provided by testing the response of a habituated stimulus in a context different from that used for training. But although such experiments have often found the habituated response returns, as Wagner's theory requires, their results are open to other interpretations (Hall, 1991). In some the change of context has been such as to produce a change in the properties of the stimulus, allowing the possibility of generalization decrement effects; in others the test context has been quite novel and thus likely to promote responding simply by way of an increase in the subjects' general level of arousal. There are a few experiments that try to control for these unwanted effects, by careful choice of stimuli and by making the subject familiar with the test context prior to the test. Despite some early failures (Hall & Channell, 1985; Hall & Honey, 1989), more recent work, by Jordan, Strasser, and McHale (2000), has convincingly shown that the overt behavioral OR of the rat will be restored, after habituation, by a change of context. (Habituation of stimulus-evoked suppression of ongoing behavior also shows sensitivity to context, although this may simply be an indirect reflection of the change in the OR.) Although this result is consistent with Wagner's theory, other interpretations are possible. In particular. as we already discussed, the behavioral OR does not respond to habituation procedures in the way that other responses (such as DRs) do; and we suggested that the magnitude of the OR is determined (at least in part) by the value of the associability of the stimulus (the alpha parameter of the Pearce & Hall, 1980, model). In an elaboration of this model, designed to deal with stimulus-exposure effects, Hall and Rodríguez (2010a) demonstrated that the decline in alpha produced by exposure to a stimulus will be reversed by presenting the stimulus in a new context, thus accommodating the results of Jordan et al. This outcome can be expected for only a response system dependent on the value of alpha (i.e., an OR), and Jordan et al. have shown that habituation of the rat's startle response is not context-specific and that it transfers well to a new context.

However, whether or not one accepts this account of why habituation effects should vary across response systems, one may conclude that habituation is not routinely dependent on an association between context and stimulus in the way that Wagner's (1976) theory postulates. We turn now to consideration of studies in which the S1 is not a context but a discrete event.

Experiments assessing the UR. As was the case for investigation of the effects of poststimulus events, use has been made of the procedure in which a rat is given experience of two different flavors presented in succession, the focus now being on the effect of S1 on the response controlled by S2. Such studies have demonstrated that neophobia to a test flavor is still observed after preexposure in which that flavor was preceded by experience of another (e.g., Kaye, Swietalski, & Mackintosh, 1988b; Robertson & Garrud, 1983). They have thus implied that habituation might be attenuated by a prestimulus event. It should be acknowledged, however, that generalization decrement is likely to be an important factor with this procedure—a flavor presented for the first time on its own (on test) may well taste rather different from one experienced (during preexposure) immediately after consuming a different flavor. This interpretation is supported (although not proved beyond doubt) by the observation that no effect of the prestimulus event has been found in studies using stimuli less likely to interact in this way. Marlin and Miller (1981) monitored the startle response of rats to a brief tone after preexposure in which the tone had been preceded by a light stimulus. The extent of habituation was the same in these subjects as in control rats that had experienced unpaired presentations of tone and light during preexposure.

Indirect measures. In considering the role of poststimulus events, we discussed experiments in which, after S1–S2 preexposure, S1 was used as the CS or as the US in a standard conditioning procedure. The assumption was that the rate of conditioning would be determined, at least in part, by the state of habituation of the preexposed stimulus. We now consider the parallel case, in which S2 is the stimulus that is tested. We begin with experiments on latent inhibition, in which the target stimulus, the stimulus preexposed as S2, is now used as the CS in conditioning. This has not been much studied, but Lubow et al. (1976) provided some relevant evidence. They used a preexposure procedure in which presentations of a tone were a consequence of the rat's lever-press response. This response (and the set of stimuli associated with it) thus constituted S1, and the tone S2. When the tone was subsequently used as a CS for shock, subjects given this form of preexposure showed latent inhibition, learning less readily than did nonpreexposed subjects. The interesting result for present purposes, however, is that this latent inhibition effect was less profound than that shown by control subjects that experienced tone presentations in the absence of any response requirement during preexposure (i.e., in the absence of a reliable S1). Again, therefore, there is an indication that habituation can be attenuated by the presence of a pretrial event; but again we should note the possible role of generalization decrement—the failure of the effect of preexposure to transfer fully to the test would be expected if the change in the mode of stimulus presentation modifies how it is perceived.

One may also consider the case in which the target stimulus is used as the US in a conditioning procedure. How does S1–S2 preexposure influence the effectiveness of S2 when is subsequently used as the US? The basic US-preexposure effect is well established—prior exposure to the event to be used as a US retards conditioning when subsequently CS–US pairings are given. The effect is clearly shown for rats in the conditioned suppression procedure, with shock as the US, and also in flavor aversion conditioning, in which a nausea-inducing event (usually an injection of lithium chloride) serves as the US (for reviews see Randich & LoLordo, 1979; Riley & Simpson, 2001). The interpretation offered by Kamin (1961) for his original demonstration of the effect in conditioned suppression was in terms of a habituation process (adaptation of emotional reactivity to shock). If this is correct, then investigating the effects of signaling the US during the preexposure phase would provide information on the ability of a pretrial event to modulate habituation.

Several experimental studies have demonstrated that signaling the US during preexposure can attenuate the US-preexposure effect in the conditioned suppression procedure (e.g., Baker, Mercier, Gabel, & Baker, 1981; Randich, 1981). But this result is not always obtained; specifically, Randich (1981) found that signaling attenuated the US-preexposure effect when the US was a fairly strong shock but did not attenuate the effect produced after preexposure to a weak shock. This finding is problematic for an account in terms of habituation, given the fact that more intense stimuli appear to be less susceptible to habituation effects than are less intense stimuli. Further analysis confirms that the demonstration of an effect of signaling does not require the conclusion that the signal influences a process of adaptation to the shock, in the way postulated by Kamin (1961).

Recall that Wagner's (1976, 1979) account of (long-term) habituation was based on the notion that repeated presentation of a stimulus would result in the formation of an association between the context of training and the stimulus. Even if one does not accept this as the explanation of habituation, there is good evidence that such conditioning will occur when a shock is presented repeatedly in a given context (Randich & Ross, 1984). The US-preexposure effect could thus be a consequence of blocking (Kamin, 1969); the presence of a pretrained signal for the US (in this case the context) could block acquisition of strength by the discrete CS used in the formal conditioning phase. Signaling the US during preexposure could attenuate the US-preexposure effect because it restricts the acquisition of strength by the context and thus reduces the magnitude of the blocking effect. Direct support for this hypothesis is scarce for studies of shock preexposure, but it is well supported for US-preexposure effects in flavor-aversion conditioning. A series of experiments by De Brugada, Hall, and Symonds (2004; see also De Brugada, González, Gil, & Hall, 2005; Hall, 2009) has shown that, in this procedure, the US-preexposure effect is entirely to be explained in terms of blocking. In this case the set of cues associated with the administration of an injection during preexposure comes to signal the state of nausea that constitutes the US, and these block conditioning to the flavor CS when this is subsequently introduced. When the US is administered by a different route during conditioning, after preexposure in which it has been administered by injection, the US-preexposure effect is absent; that is, there is no sign of a habituation effect.

That the state of nausea should be resistant to habituation is perhaps not surprising (introspection suggests that episodes occurring recently are just as unpleasant as those experienced earlier in life). The situation may be different for cutaneous pain. Experimental studies with human subjects (and relatively weak stimulation) have shown that the perceived aversiveness of an unpleasant event will decline with repeated presentation. This has long been known for pressure stimuli (Burns & Dallenbach, 1933), and it is also true for thermal stimuli (e.g., Bingel, Schoell, Herken, Büchel, & May, 2007; Rennefeld, Wiech, Schoell, Lorenz, & Bingel, 2010) and, at least in the course of a session, for electrical stimulation (Ernst, Lee, Dworkin, & Zaretsky, 1986). Crombez, Eccleston, Baeyens, and Eelen (1997) reported that the tendency of a mild shock to disrupt performance of an auditory discrimination task declined over the course of training. If these results (admittedly from very different procedures) are any guide, one might conclude that some form of adaptation or habituation to the shock could well contribute to the US-preexposure effect shown by rats in the conditioned suppression procedure, particularly when a weak shock is used. With a strong shock, context conditioning is likely to occur during preexposure (Randich, 1981), and the effect of a preshock stimulus can be explained in terms of its ability to limit such conditioning. For information on the effects of a preshock stimulus on habituation, one needs to look at experiments in which the shock intensity is low. In these, signaling the shock during preexposure is found to have no effect on the US-preexposure effect (Randich, 1981), implying that such habituation as occurs is not influenced by the presence of the signal. (We should note that the suggestion that a consistently signaled US can suffer habituation provides a further mechanism for the phenomenon of the postasymptotic decline of the CR that was discussed at the start of this review.)

Conclusions

Our review of evidence on habituation of the CS during conditioning led to the conclusion that the conditioning procedure (i.e., following the CS by a US) would prevent or attenuate habituation of the CS. The evidence on habituation to the US during conditioning allows no clear conclusion. As has been seen, the CS–US arrangement introduces a range of other factors (generalization decrement, the acquisition of a CR, interaction with context-conditioning effects) that precludes an easy assessment of possible changes in the effective salience of the US. Certainly, the results suggesting that US habituation might be attenuated by the presence of a consistent CS can be explained away in terms of the operation of these other factors. It should be acknowledged that most of the relevant studies have used powerful stimuli as USs, for which there is precious little evidence of habituation in the first place. There is some evidence for habituation with weaker USs and no indication that this is modified by the presence of a signal. It may be doubted that this process plays much part in standard conditioning procedures, which usually use more intense USs, that is, events having high motivational impact.

Discussion

The central conclusions of this review can be summarized briefly. The repeated presentation of a pair of stimuli, CS and US, in a standard conditioning procedure, allows the possibility that both might undergo habituation. Taking habituation to involve a reduction in the effective salience of a stimulus raises the question of how, in these circumstances, conditioning can occur, and a CR be maintained, over the course of prolonged training. The answer supplied by the evidence reviewed here is as follows: The effective salience of the CS is maintained (i.e., habituation is attenuated) because the stimulus is reliably followed by a salient event (the US); a salient event is resistant to habituation and thus retains its effectiveness. How can these conclusions be accommodated by current theories of habituation and associative learning?

Theoretical Interpretations

As we have noted, the account of conditioning proposed by Wagner (1976, 1979, 1981) is unique in its attempt to integrate an account of habituation with one of association formation. Although it has been successful in many ways, an ability to deal with the phenomena of interest here has been only partial. Specifically, a central notion of Wagner's theory is that a stimulus representation becomes less responsive (i.e., habituation is evident) when that representation is activated by an event that previously has predicted the occurrence of its stimulus. There is indeed some evidence to support the view that the effectiveness of a stimulus can be influenced by the extent to which it is predicted. But the central phenomenon that one needs to explain is that habituation is modified by the pairing of the CS with a consequence (the US), that is, by what the stimulus predicts.

Associability-change theories. The notion that the ability of a stimulus (a CS) to command processing will depend on how it predicts its consequences is found in the models of conditioning proposed by Mackintosh (1975) and by Pearce and Hall (1980). Both theories suppose that presentations of CS and US change not only the associative strength of the CS as a signal for the US but also value of a parameter (abbreviated to alpha) representing the associability, or "conditionability," of the CS. The value of associability is assumed to be high for a novel CS. The theories differ on their specification of the rules by which it changes, and those proposed by Mackintosh have the potential to explain the findings on CS habituation. Mackintosh proposed that the value of alpha will increase for a CS that is a good predictor of its consequences (more precisely, when it predicts an outcome better than do other stimuli) but will decrease when it is a poor predictor or, as is usual in studies of habituation, is not followed by an outcome. Thus, if Mackintosh's alpha is taken to control or to index the effectiveness of the CS, these changes match the results from studies of habituation.

Mackintosh (1975) referred to his model as a theory of attention, allowing one the simple summary that a good predictor commands attention whereas a poor one does not. But in choosing to refine his concept of attention by using the term *associability,* he was emphasizing its role in the acquisition of associations. Associability is essentially attention-for-learning, and subsequent tests of predictions of the theory have focused on attentional factors in new learning. What we seek to explain, however, is why responding is maintained to a well-trained CS. It is therefore necessary for the proponent of this analysis to suppose that the level of alpha determines not only attention-for-learning but also attention-for-performance. Although he preferred to treat alpha simply as a learning-rate parameter, the alternative possibility was acknowledged by Mackintosh himself.

On the face of things, the associability-change theory of Pearce and Hall (1980) is poorly equipped to deal with the habituation results. According to this theory, the alpha value of a stimulus declines when the stimulus is associated with a consistent consequence, and it is maintained or increases when the consequences are inconsistent. These rules allow a ready explanation for those studies of the transfer of learning (summarized, e.g., by Hall & Rodríguez, 2010b; but see also Le Pelley, 2004) that show that subsequent learning about a stimulus pretrained with consistent consequences is poor, whereas a stimulus trained initially with inconsistent consequences is learned about readily. And, as we described in the section of this article devoted to orienting responses, these rules also accord with those in studies of changes in the OR, on the assumption that the vigor of this unconditioned response is determined by the level of uncertainty about the consequences of the stimulus, as represented by alpha. In these respects, the Pearce–Hall rules for alpha-change have an advantage over those proposed by Mackintosh (1975). But they cannot supply a general account of the changes in stimulus effectiveness revealed by studies of habituation. ORs may track changes in alpha, but other URs do not; and, critically, a fully trained CS, one that has been reliably followed by a given US, is very effective in evoking responding even though its alpha value will be low.

Given the last point, it is evident that the alpha parameter in the Pearce and Hall (1980) model could be only a learning-rate parameter—attention-for-learning—and that other aspects of attention must be controlled in other ways. To this end the original model included two parameters associated with CS in conditioning procedures: In addition to alpha, associability, there was S, salience, the level of which was assumed to be determined, in part, by the intensity of the stimulus. S will contribute to the rate of learning (an intense CS conditions more readily than does a less intense one), but, unlike alpha, it will also influence performance—the response (conditioned or unconditioned) to an intense stimulus is more vigorous than to a less intense stimulus. Although not formalized in the original model, it was assumed that habituation corresponded to a decline in the value of S associated with a stimulus. No consideration was given to the possibility that habituation might occur during the course of conditioning. The evidence just reviewed makes it necessary to assume that the CS–US arrangement attenuates or prevents this decline and to extend the theory to allow this. Next we outline briefly one possible way in which this might be done.

Stimulus–no event learning. Several theorists (e.g., Bouton, 1993; Hall, 1991; Lubow, 1989; Westbrook & Bouton, 2010) have supposed that the latent inhibition procedure (habituation training followed by conditioning) might involve, in its first stage, a form of learning in which the subject learns that the preexposed stimulus is not followed by anything. This idea was formalized by Hall and Rodríguez (2010a), who treated stimulus–no event learning in terms of the inhibitory learning mechanism proposed in the Pearce and Hall (1980) model.

Hall and Rodríguez (2010a) assumed that presentation of a novel stimulus would arouse the expectation that some event would follow and characterized this as involving a stimulus–event association. The strength of this expectation will be determined by generalization from similar stimuli that the subject had experienced in the past, followed by some outcome. (Each of these stimuli would tend to activate the representation of the particular outcome with which it had been associated, but the representation activated most effectively overall would be the representation of any feature all hold in common, i.e., the occurrence of "an event.") A salient or intense stimulus would activate more representations and thus evoke a greater expectation of an event. In latent inhibition training (or habituation), no event follows the stimulus; an inhibitory learning process is then engaged that results in the development of a stimulus–no event association that acts to oppose the original stimulus–event association. The assumed mechanism is in principle identical to the inhibitory learning mechanism responsible for extinction in the Pearce and Hall (1980) model. The difference is that, in extinction, the inhibitory effect arises from the acquisition of a CS–no US link, the latter being specific to the US used in conditioning; in the case of habituation, one needs to assume an association between the stimulus and a generic no-event representation.

Hall and Rodríguez (2010a) were concerned chiefly with the implications of this form of learning for changes in associability and the consequences for the course of conditioning in the second phase of the latent inhibition procedure. They did not develop the obvious implications for habituation of the changes that occur during the preexposure phase. These are that the response evoked by a novel stimulus will depend not solely on its own properties (such as its intensity) but also on its activation of the representations of other events. Some of its effective salience will be "borrowed" from its associates. Repeated presentation of the stimulus, by eliminating the original stimulus–event association, will remove this borrowed contribution and produce a reduction in the effective salience of the stimulus. Such a reduction may be taken to characterize (at least some instances and aspects of) habituation.

It would be foolish to put this forward as a complete account of the phenomenon of habituation (indeed, it seems unlikely that any single mechanism could accommodate effects as disparate as those seen with the human orienting response and in the gill withdrawal response of *Aplysia*). But it would be worthwhile to note two further positive implications of the analysis just offered. The first is that it supplies an explanation of the observation central to our discussion—that CS–US pairings retard CS habituation. If habituation depends on learning that no event follows a stimulus, then clearly, training in which some event does follow will preclude the occurrence of habituation and maintain (or even enhance) the effective salience of the target stimulus. Those URs that are determined by the effective stimulus of the target stimulus (as we have noted, some, ORs, are determined by other factors) will be maintained. The second is that it supplies a possible interpretation of the finding that salient events, of the sort used as USs, tend to be resistant to habituation. We have suggested that the important result of repeated stimulus presentation is that the subject can learn that no consequence follows. But for motivationally significant events (USs), this may not be the case. Certainly for a food US, the immediate sensory experience is reliably followed by certain consequences—acquisition of nutrients and alleviation of hunger. The same sort of thing could also apply to certain aversive USs, with cutaneous stimulation being followed by pain or distress. In such circumstances the effectiveness of these stimuli would be expected to be maintained.

Implications

Leaving aside speculations about the mechanism, we end with a brief discussion of the implications of the conclusion that salience change during exposure to a stimulus is modulated by the conditioning procedure. This conclusion has particular relevance for studies of the transfer of learning and for theories of stimulus processing based on them. For some time, theories of attention in learning have made use of a procedure in which training is given on two tasks sequentially, with the same stimuli being used in both (see, e.g., Sutherland & Mackintosh, 1971). With appropriately chosen tasks it is possible to demonstrate effects that must depend on changes in the properties of the stimuli produced by the first phase of training (see, e.g., Le Pelley, 2004).

The simplest example is the latent inhibition procedure in which presenting a stimulus on its own in the first phase reduces its effectiveness as CS in a subsequent conditioning phase. Although other analyses have been offered (e.g., Stout & Miller, 2007), this finding invites the conclusion that the ability of the stimulus to command attention has been reduced during the first phase (e.g., Lubow, 1989), an interpretation that has been formalized in theories of associability change (e.g., Mackintosh, 1975; Pearce & Hall, 1980). The arguments advanced in this article imply that this notion of attention is unduly simplified. Associability may indeed decline in the way posited by these theories, but the evidence considered here suggests that stimulus exposure will also, by way of habituation, produce a reduction in the effective salience of the stimulus. Given that the salience of a CS will contribute to the readiness with which it enters into associations (and the Pearce & Hall, 1980 model makes this explicit with its separate parameters for salience and for associability), this loss of salience will contribute to the retardation of subsequent conditioning; and it will also play a role in performance, given that a cue low in salience will be poor at evoking a response (such as the newly acquired CR).

In this context we note that a phenomenon referred to as latent inhibition during CS–US pairing (Hall & Pearce, 1979) is inaccurately labeled. In this procedure a CS was trained as a signal for one US before a second phase of training in which it signaled a different US. The retardation of conditioning seen in the second phase, taken to reflect the lowered associability produced by the first phase, is indeed an aspect of latent inhibition. But another aspect, the loss of salience, will not contribute to the results of this procedure because the CS–US pairings of the first phase will have maintained the salience of the CS.

The conclusion that changes in associability and changes in salience obey different rules, exemplified by the example just given, complicates the interpretation of an experimental design that has been widely used in the analysis of attentional factors in learning. This design, sometimes referred to as acquired distinctiveness (e.g., Lawrence, 1949) or learned predictiveness (e.g., Le Pelley, Oakeshott, Wills, & McLaren, 2005), takes a variety of forms but in outline is as follows: Experimental subjects are trained initially on a discrimination in which stimulus A is reliably followed by one outcome and B by another; for subjects in a control condition, either outcome can follow A or B, unpredictably. In the test phase, all subjects learn a new discrimination task with A and B as the cues. Which group will learn the test more readily? It is difficult to say. According to some accounts, the associability of A and B for the experimental group will have declined during the first phase, whereas that for the control subjects will have been maintained, suggesting that the latter should do well on test. On the other hand, the training given to the experimental group might be expected to maintain the effective salience of A and B, so that learning would be rapid and performance facilitated. Clearly a necessary next step is to formalize and quantify the notions presented here in order to generate firm predictions about experiments such as this.

Finally, we note that the evidence reviewed here is pointing in the direction of an account of attentional processes in learning that has two separable attention-like factors. This is in line with a number of hybrid theories of attention that have been put forward in recent years (e.g., Esber & Haselgrove, 2011; George & Pearce, 2012; Le Pelley, 2004; Pearce & Mackintosh, 2010). This consensus is reassuring, but it must be acknowledged that the attentional factors proposed by other theorists do not map precisely on to those identified here. We would argue in favor of the distinction we have made between associability and salience. These are not chosen arbitrarily but fit with the empirical evidence and the following general principles. An animal given a novel event must pay attention to it to see what it signifies (e.g., danger, food). In simple habituation it signifies nothing of importance, and attention can be reduced. In conditioning it does have a consequence, and attention must be maintained. Once the relation between CS and US has been fully encoded, attention-for-learning can be turned off. But such a stimulus must not be ignored—it needs to evoke responding appropriate to its consequence—and attention-for-performance must be maintained.

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