Stimulus Significance, Conditionability, and the Orienting Response in Rats

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Since the late 1970s we have been trying to understand the way in which attentional processes influence one sort of information processing—that involved in associative learning. The central idea guiding our work can be stated briefly. It is that one aspect of attention (that necessary for a stimulus to enter into associations) is paid only to stimuli that have uncertain consequences. Part of the evidence for this assertion comes from the study of the behavioral orienting response (OR) shown by rats to a localized stimulus, a response that we take to reflect this form of attention and, thus, to reflect stimulus conditionability.

The first part of this chapter summarizes the relevant evidence: Experiments showing that the likelihood of the OR depends on the predictive accuracy of the stimulus that evokes it; and experiments showing that the likelihood of the OR is correlated with the conditionability of the stimulus. But our survey of the evidence also reveals cases in which the likelihood of the OR changes without there being a change in predictive accuracy, and cases in which the level of the OR does not appear to correlate with the conditionability of the stimulus. The latter part of the chapter constitutes an
attempt to explain these discrepancies and lay the foundations of a more comprehensive account of the determinants of the OR. To anticipate, we see that the level of the OR reflects not only the information processing in associative learning but also that involved in the perceptual learning processes underlying habituation.

Our research started with the intuition that the attentional capacities of animals are limited and that to be used efficiently their deployment must vary during the course of associative learning (Pearce & Hall, 1980; Pearce, Kaye, & Hall, 1982). In a Pavlovian conditioning experiment, for example, the most efficient strategy would be for the subject to attend fully to the conditioned and unconditioned stimuli (CS and US) during the early stages of conditioning. But once conditioning has reached asymptote, attention to these events can decline because there is no need for further learning. Should the circumstances that follow the CS change then the attention it receives would need to be restored so that learning about this new relationship can take place rapidly. A further decline in attention would then be expected to occur once the necessary associative changes have been completed. These intuitions led us to propose that to ensure their resources are used efficiently animals will pay most attention to stimuli that have proved to be accurate predictors of the events with which they are associated. This will be the case when a CS is first paired with a US, and when the CS is first presented in extinction. On the other hand, minimal attention will be paid to stimuli that have proved to be accurate predictors of their consequences; for example when they have consistently been followed by the same reinforcer, or by nothing. Such stimuli will, of course, continue to command one form of attention—a CS that has accurately predicted a US is not ignored completely since it is capable of eliciting a conditioned response (CR). Our concern is not with such automatic processing however (see LaBerge, 1975; Schneider & Shiffrin, 1977; Shiffrin & Schneider, 1977), but with the mechanisms of controlled processing that are engaged when a subject is required to attend to and learn about a stimulus.

In order to facilitate the investigation of this latter form of attention, we have attempted to devise a behavioral index by making use of the investigatory or orienting behavior that animals will direct toward a localized stimulus, especially when that stimulus is novel. The functional value of such ORs may well lie in their capacity to increase the processing of sensory information. Accordingly, we present next a review of experimental evidence supporting the notion that the OR can play this role.

PREDICTIVE ACCURACY AND THE OR

The Importance of Predictive Accuracy

We have conducted a series of experiments that examined the effects of Pavlovian conditioning on the OR. If this response is a manifestation of the attention paid to a stimulus, and if our intuitions summarized earlier are correct, then we should expect the OR to be stronger when it is directed toward a stimulus that is an inaccurate rather than an accurate predictor of its consequences.

In the first experiment to test this prediction Kaye and Pearce (1984a) conducted appetitive conditioning in a darkened chamber containing a light bulb. The bulb was located 8 cm above the floor on a wall in which a food hopper was located. The first session contained six trials in which the light was illuminated for 10 sec at regular 4-min intervals. The purpose of this preexposure session was to examine the OR that the light elicited in rats when it was novel; and this was achieved by observing the subjects' behavior, with the assistance of a videorecorder, 4 sec and 9 sec into each trial. An OR was scored whenever subjects ran immediately in front of the light, or made contact with it with their snout or paws. In each of the three groups that were employed, approximately half of the observations revealed an OR when the bulb was illuminated, but when it was dark this activity was virtually nonexistent. That the initial level of the OR is less than 100% probably reflects, at least in part, a tendency for contextual cues to evoke their own investigatory responses that will tend to compete with the OR that we measure. Certainly an initial phase of preexposure to the context alone, which would allow such competing responses to habituate, results in a much higher level of orienting when the light is first presented.

Having established that the light elicited an OR, the next stage of the experiment was intended to investigate how this activity would be influenced when the predictive accuracy of the light was manipulated. In Group N (no food), the light was presented in the same manner as for the preexposure session and it was never paired with food. The expectation was that these conditions would result in a rapid loss of the OR, because subjects would soon appreciate that the light was an accurate predictor of nothing. The second group, Group C (continuous reinforcement), was treated in the same way as Group N, except that each presentation of the light was followed by a single pellet of food. On the basis of the argument developed earlier, we should expect the light to elicit a strong OR during the initial sessions of conditioning, while subjects learn that the light is a signal for food. But as soon as this learning is complete, and the light can be regarded as an accurate predictor of the food, then the frequency of the OR during the light should decline. Finally, Group P (partial reinforcement) also received conditioning with the light, but in this case the light was followed by food on a randomly selected half of the trials. In these circumstances subjects will never be able to

\[\text{The light might also be expected to come to elicit a conditioned response of goal-tracking that, in this preparation, is likely to involve approach to the magazine—see later. The complication that arises when the conditioned response involves sign-tracking, which is likely to be similar to the OR, is discussed in detail by Collins and Pearce (1985).}\]
predict accurately the outcome of every trial, that is the light will be a consistently inaccurate signal for its consequences, and the OR that it elicits should be sustained at a relatively high level. The upper panel of Fig. 6.1 shows the group mean percentages of observations of the subjects' behavior that revealed light orientation for each session. The frequency of the OR declined rapidly from its level in the preexposure session in Group N, whereas in Group C light orientation was sustained at its original level for several sessions before its frequency declined. In contrast, there was no hint of a decline in the OR in Group P, even though 14 sessions of training were given. Overall, this pattern of results is consistent with the predicted outcome.

In addition to observing the OR in this experiment, we monitored a second response of magazine activity, which consisted of making contact with the food magazine, or standing with the snout adjacent to the magazine. The results for this response are portrayed in the lower panel of Fig. 6.1 and it is evident that they conform to the pattern that has been shown with many different CRs. As a result of the continuous reinforcement schedule, magazine activity during the light in Group C increased until it was recorded on nearly every observation that was made. The same pattern of results was evident in Group P, but the intermittent pairings of the light and food resulted in a lower asymptote of responding. Very little magazine activity was observed in Group N. Although this pattern of results is not at all surprising, it is important because it suggests a theoretically uninteresting explanation for the results obtained with the OR. Conceivably, conditioning with the light strengthened light orientation in much the same way as magazine activity, but perhaps to a lesser extent. The decline in the OR during the later stages of conditioning in Group C could then be due to interference from the competing response of magazine activity, rather than to a loss of attention to the light. The absence of a similar decline in Group P could be a consequence of the relatively weak magazine activity in this group failing to disrupt the OR.

We have conducted a number of experiments to evaluate this competing response interpretation (Kaye & Pearce, 1984a, 1984b; Pearce & Kaye, 1985; Pearce, Wilson, & Kaye, 1988; Swan & Pearce, 1988), but the one we describe here is reported by Pearce et al. (1988). In the first stage of the experiment, three groups of rats received appetitive conditioning with a 30-sec tone; for two of the groups, the tone was paired with food on a continuous reinforcement schedule, and for the third group, a partial reinforcement schedule was employed. In the second stage, the groups received serial conditioning. The details of this training differed for the three groups, but they all received trials in which the same light as that used in the previous experiment was presented for 10 sec and followed immediately by the tone for 30 sec which in turn was followed by food. (see Table 6.1). For Group LT+ Lo these serial conditioning trials were intermixed with nonreinforced presentations of the light alone. Group LT+ just received the serial conditioning trials, and Group LT+ LTo received the serial conditioning trials among nonreinforced presentations of the light-tone sequence.

As a result of the serial conditioning in Group LT+ Lo, the light will be an

Table 6.1 Summary of the Design of the Experiment Reported by Pearce, Kaye, and Wilson (1988)

<table>
<thead>
<tr>
<th>Stage 1</th>
<th>Stage 2</th>
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<tbody>
<tr>
<td>Group LT+ Lo</td>
<td>Tone-food</td>
</tr>
<tr>
<td>Group LT+</td>
<td>Tone-food</td>
</tr>
<tr>
<td>Group LT+ LTo</td>
<td>Tone-nothing</td>
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</tbody>
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FIG. 6.1. The mean percentages of observations that revealed light orientation (upper panel) and magazine activity (lower panel) for the three groups employed in the experiment by Kaye and Pearce (1984a).
inaccurate predictor of the tone and food, which should ensure frequent orientation to the light throughout serial conditioning. For Group LT+, however, the light will initially be an inaccurate signal for the tone and food, but this should not be true after a number of sessions of serial conditioning and orientation toward the light can be predicted to decline eventually. The effects of serial conditioning on the OR can be seen in the upper panel of Fig. 6.2, which makes it clear that in the later sessions of conditioning the OR was observed with greater frequency in Group LT + Lo than Group LT +.

One interesting question that is raised by the aforementioned results concerns identifying the event that is responsible for making the light in Group LT + Lo an inaccurate predictor. In this group, the light could be viewed as an inaccurate predictor of either food, or the tone. Fortunately the

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**FIG. 6.2.** The mean percentages of observations that revealed light orientation (upper panel) and the mean duration of magazine activity per trial (lower panel) for the three groups in the experiment by Pearce, Wilson, and Kaye (1988).

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results of Group LT + LTo allow us to evaluate the relative importance of these events in determining the strong OR during the light in Group LT + Lo. If it was the intermittent relationship between the light and food that was responsible for this outcome, then the equivalent relationship in Group LT + LTo should lead to similar level of light orientation as in Group LT + Lo. But if the main determinant of light orientation in Group LT + Lo was the irregularity with which the tone followed the light then, because the tone always followed the light in Group LT + LTo, the OR during the light in this group should eventually decline to a low level. The results shown in Fig. 6.2 support this latter interpretation. By the end of the experiment the frequency of the OR was considerably less in Group LT + LTo than LT + Lo. These results thus strongly imply the strength of the OR during the light is determined principally by the accuracy with which it predicts its immediate consequences. This is not to say that the food was unimportant in Group LT + LTo. Obviously, the food is necessary to ensure that the tone has some appetitive value, but the reinforcement schedule with the food appears to be of relatively minor importance in determining orientation during the light. A more detailed discussion of this issue can be found in Honey, Schachtman, and Hall (1987).

The reason for adopting a design based on serial conditioning is that it ensures the light is temporally remote from the delivery of food. In contrast to the first experiment, therefore, the level of magazine activity during the light is likely to be relatively slight and it will be less disruptive of any tendency to perform the OR. To evaluate this argument we measured the duration of each trial that subjects spent in contact with the magazine (see the lower panel of Fig. 6.2). By the end of the experiment this activity occupied less than 2% of the time that was available during the light in each of the three groups. It is thus very difficult to argue that the pattern of results shown in the upper panel of Fig. 6.2 is due to the disruptive effects of magazine activity. We would therefore argue that during appetitive conditioning the OR directed at the light is not governed by the same principles as those applying to CRs such as magazine activity. Instead, we favor the proposal that the OR is an attentional response the strength of which is determined by the predictive accuracy of the stimulus to which it is directed.

**Other Determinants of the Orienting Response**

We started our study of the OR in the hope, no more, that it might prove to be useful index of the concept of attention that we have developed in our formal model of attention in conditioning (Pearce & Hall, 1980). From this viewpoint the results just surveyed are most satisfactory. It would be too much to hope, however, that the OR might be determined solely by the
predictive accuracy of the stimulus to which it is directed, and some of our experiments have revealed the operation of other factors.

Hall and Channell (1985) studied the way in which a change of context after exposure to a light can influence the strength of the OR that it elicits. The apparatus consisted of standard conditioning chambers with a light bulb and food hopper located in much the same position as for the experiments just reported. There were two sets of chambers, housed in different rooms. White noise was presented continuously to one set, which smelled of peppermint, but not the other, which smelled of violets. Using one of the contexts, subjects were exposed to eight 10-sec presentations of the light, with an average interstimulus interval of 3 min, in each of 18 sessions. They were then given a test session that was identical to the training sessions, except that the light was presented for the first time in the other context.

The upper panel of Fig. 6.3 shows the outcome of this study. Not surprisingly, the training sessions resulted in a substantial decline in orientation toward the light. But when the light was presented for the first time in the different context then, as the histogram shows, there was a substantial recovery in the frequency with which it elicited the OR. There is no reason to suppose that presenting the light for the first time in a new context will alter its predictive accuracy. These results thus establish that some additional factor governs the frequency with which the OR is performed.

From the point of view of later discussion, it is important to note that the recovery of the OR was observed only when the light was presented in an unfamiliar context. Hall and Channell (1985) conducted a second experiment that was identical to the one just described, except that subjects had been repeatedly placed in the second context before they received their test trials in it. The center panel of Fig. 6.3 shows the results from this study, and it is evident that on this occasion there was virtually no recovery of the OR in the test session. Nonetheless, the recovery of the OR that occurred when the light was first presented in an unfamiliar context suggests that the OR to a light can be modified without altering its predictive accuracy.

Further support for this conclusion can be found in a study by Hall and Schachtman (1987). A group of rats was repeatedly exposed to a light in each of 16 sessions. The group was then retained in its home cage for 16 days before being returned to the apparatus for a test session with the light. In keeping with the results from the previous experiment, the training sessions resulted in a substantial decline of the OR during the light, as revealed in the lower panel of Fig. 6.3. The histogram in the panel shows, however, that when the subjects were reintroduced to the light, after the retention interval, then the frequency of the OR was enhanced considerably. Once again, it is difficult to see how this outcome can be explained if the only factor that influences the OR is the predictive accuracy of the stimulus to which it is directed.

FIG. 6.3. The graphs in the three panels show the number of trials in each session in which an OR was recorded during 8- (upper two panels) or 10-sec presentations of a light. The histograms show the number of trials that elicited this response when it was subsequently presented in a different, novel context (upper panel) in a different familiar context (middle panel) or in the same context but after a retention interval of 16 days (lower panel).
These results are open to more than one interpretation. If we assume that the level of the OR is a direct measure of attention, then they mean that forms of training that do not influence predictive accuracy can modify attention. Alternatively, it may be that factors other than attention determine the level of the OR. Further discussion of these alternatives will be postponed until the relationship between the OR and stimulus conditionability has been considered.

THE OR AND CONDITIONABILITY

Our experiments allow the conclusion that one important determinant of the strength of the OR in our training preparation is the predictive accuracy of the stimulus. The results are thus consistent with our intuition that animals will pay more attention to stimuli that have uncertain consequences. Now we have argued that for efficient associative learning, animals need to pay full attention to the CS. It follows, therefore, that the conditionability, or associability, of a stimulus should vary with predictive accuracy and, to a large measure, therefore, with the level of the OR it evokes. If animals are paying a lot of attention to a stimulus then learning will be rapid when it is paired with a reinforcer, but if the stimulus is being ignored then subjects should experience difficulty in learning about its relationship with reinforcement.

Experiments Varying Predictive Accuracy

To test this argument, Swan and Pearce (1988) conducted an experiment in which, for the first stage, two groups of rats received training designed to make them pay different levels of attention to a light. The groups then received a further stage of training in which the conditionability of the light was assessed. The method for manipulating the attention paid to the light was slightly different from that used previously, and itself was composed of two phases. In the first phase, two auditory stimuli, X and Y, were separately paired with food. For the experimental group, Group E, X was always of 10-sec duration and Y was of 30-sec duration; whereas for the control group, Group C, X and Y were each of 10-sec duration for half the trials and of 30-sec duration for the remaining trials. As a result of this training it is likely that the appetitive value of X in Group E will be greater than of the longer duration Y. On the other hand, there is no reason to suspect that the value of X and Y will differ in Group C.

Training in the second stage of the experiment continued with the auditory stimuli in the manner just described, but each trial commenced with a 10-sec presentation of the same light that was employed for the previous experiments. The onset of the light was always followed immediately by the onset of an auditory stimulus that always terminated with food. This procedure is summarized in Table 6.2.

This procedure will result in the predictive accuracy of the light eventually being different for the two groups. The experiments described previously have shown that when the light is an accurate predictor of its immediate consequences then eventually the OR that it elicits will be relatively weak. This will be the case in Group C because, although the light will sometimes be followed by the tone and sometimes by the clicker, both stimuli share the same relationship with food and can be expected to be of equivalent value. Thus, upon the completion of serial conditioning the light will be an accurate predictor for the value of the stimuli that follow it. At this point the light should thus receive a minimal level of attention and elicit a relatively weak OR.

In contrast, X and Y will always be of different value for Group E and no matter how many conditioning sessions are given, the light will never be able to serve as an accurate predictor for the value of the stimulus that is presented immediately after its onset. In these circumstances we should expect no decline in either the attention that the light receives or the strength of the OR that it elicits. The effects of serial conditioning on the OR can be seen in the upper panel of Fig. 6.4. There was no difference between the groups at the outset of serial conditioning, but with extended training the frequency of the OR during the light declined in Group C and remained high in Group E.

The results summarized in the lower panel of Fig. 6.4 show the group mean percentages of observations of the subjects' behavior that revealed magazine activity during the light. The level of this activity was low, and there is no indication that it was more vigorous in one group than the other. As with the previous experiment, therefore, it is unlikely that the differences in the orienting behavior of the two groups is due to the disruptive influence of magazine activity.

In order to examine the conditionability of the light after the serial conditioning, half the subjects in Group E, Group E-E, and half the subjects in Group C, Group C-E, received excitatory (E) conditioning in which the light

| Table 6.2 Summary of the Design of the Experiment by Swan and Pearce (1988) |
|-----------------|----------------|----------------|----------------|
|                 | First Element  |                | Second Element |
|                 | Stimulus       | Duration       | Stimulus       | Duration       |
| Group E         | Light          | 10 sec         | X              | 10 sec         |
|                 |                |                | Y              | 30 sec         |
| Group C         | Light          | 10 sec         | X              | 10 or 30 sec   |
|                 |                |                | Y              | 10 or 30 sec   |

Note: For half the subjects in each group X was a tone and Y a clicker, this relationship was reversed for the remaining subjects.
was paired directly with food. We expected this training to enhance considerably the level of magazine activity during the light, but at a different rate for the two groups. If animals pay more attention to stimuli that are inaccurate rather than accurate predictors of their consequences, and if this attention facilitates learning, then the different serial conditioning schedules should result in more rapid conditioning with the light in Group E-E than Group C-E. The left-hand panel of Fig. 6.5 shows the group mean percentages of observations of magazine activity that were recorded during the light for the four conditioning sessions combined. It is evident that conditioning was more successful with Group E-E than Group C-E.

One explanation for this outcome, which makes no appeal to differences in the conditionability of the light, is that the initial phase of training resulted in the light being better associated with food in Group E-E than Group C-E.

This would then give an advantage to the former group during the final, test sessions. Inspection of the lower panel of Fig. 6.4 provides no support for this suggestion, by indicating that the level of magazine activity in Groups C and E was virtually identical throughout serial conditioning. Nonetheless, the conclusions that can be drawn from this study would be more convincing if this explanation could be discounted, and it was for this purpose that the remaining subjects in the experiment were employed.

Upon the completion of the serial conditioning, the remaining subjects from Group E, Group E-D, and the remaining subjects from Group C, Group C-D, received 10 sessions of discrimination (D) training. Trials in which a 10-sec clicker was paired with food were intermixed with nonreinforced presentations of the light and clicker together. According to a number of theories (e.g., Rescorla & Wagner, 1972) for the discrimination to be solved it is necessary for the light to become a signal for the absence of food. Such learning would progress rather slowly if the light had entered into an association with food in Group E-D prior to discrimination training. But if the serial conditioning ensured that subjects in Group E-D paid more attention to the light than in Group C-D, then the opposite outcome would be expected. In fact, the discrimination was mastered more rapidly by Group E-D. The results of the discrimination training are summarized in the right-hand panel of Fig. 6.5, which shows the mean percentages of observations that revealed magazine activity for the 10 sessions combined. It is apparent from this figure that although both groups showed more magazine activity during the clicker than the clicker-light compound, this difference was substantially, and significantly, bigger in Group E-D than Group C-D.

The previous experiment shows that consistently pairing a stimulus with
consequences that can be accurately predicted results in a weak OR and a loss of its conditionability. In the next experiment we examine whether this lost conditionability can be restored by changing the light from an accurate to an inaccurate predictor. For this experiment we reverted to the serial design employed by Pearce et al. (1988) that was considered earlier. In the first stage of the experiment two groups of rats received the same serial conditioning in which trials with the sequence light–tone–food were intermixed with trials of light–tone–no food. This training should result in the light becoming an accurate predictor of the tone, at which point it should elicit a weak OR and be of relatively low conditionability. This training continued in the same manner for the control group, Group C, during the eight sessions of the second stage; for the experimental group, Group E, however, the training was changed so that trials with the light–tone–food sequence were presented among nonreinforced presentations of the light alone. This treatment should now make the light an inaccurate predictor of the tone and increase the frequency with which the OR occurs during the light. The results for these two stages are shown in Fig. 6.6. The upper panel reveals the effect of serial conditioning on the OR, and both groups show a decline in this activity during the first stage of the experiment. In the second stage, there is a marked increase in the frequency of orientation to the light in Group E, whereas there is very little change in this activity in Group C.

The lower panel of the figure indicates that throughout both stages of the experiment magazine activity was performed at a similar low level in both groups.

On the basis of our theoretical proposals, as well as our results from the previous experiment, we can predict that at the end of the second stage of the experiment the conditionability of the light will be higher in Group E than Group C. To test this prediction, both groups received a number of sessions in which the light was paired with food. The outcome of this training is summarized in Fig. 6.7. The right-hand panel makes it clear that conditioning progressed more rapidly in Group E than Group C and, once again, this difference was significant. The results in the left-hand panel show that for both groups the OR during the light was relatively weak throughout the test sessions. One reason for this relatively low level of responding is that, especially in Group E, subjects spent most of their time engaged in magazine activity.

Other Determinants of Conditionability

Changing the attention that a stimulus receives is not the only means of modifying its associability. Conditioning with a stimulus may be slow if it

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3We are grateful to Paul Wilson and Patrick Bounphrey for their assistance with this study.

has previously signaled the absence of the reinforcer with which it is currently being paired (e.g., Rescorla, 1969), or if it has previously been paired with an event of opposite hedonic value to the current reinforcer (e.g., Dickinson & Dearing, 1979). In each of these cases it is conceivable that the stimulus will elicit a strong OR at the outset of the test stage. But even if this reflects a high level of attention being directed toward the stimulus, it may still not be sufficient to counteract the associative interference produced by the initial training.

More problematic for the theory being developed here are effects found after simple nonreinforced exposure to a stimulus. These include instances of
changes in conditionability that do not appear to be a product of associative interference but that occur without parallel changes in the OR. Nonreinforced exposure will produce a profound loss in the OR (Group N, Fig. 6.1) and, as might be expected, will also produce a retardation of subsequent conditioning—the latent inhibition effect (Lubow, 1973). Now it is well established that the loss of conditionability evident in latent inhibition can be attenuated if preexposure is given in one context and conditioning in another (e.g., Channell & Hall, 1983; Hall & Honey, 1989; Hall & Minor, 1984) and this is true whether the conditioning context is familiar or novel. But as we have already seen (Fig. 6.3), although a change of context can restore the loss suffered by an OR with nonreinforced preexposure, it does not always do so. In particular, Hall and Channell (1985) found that switching to a different but familiar test context attenuated the latent inhibition effect (i.e., restored lost associability) but failed to bring back the OR.

Hall and Schachtman (1987) have reported a finding that demonstrates a reverse dissociation—a procedure that restores the OR but not associability. In their study, which was referred to earlier, the OR to a light was first weakened by repeatedly presenting the light in sessions on successive days. They then discovered that the strength of the OR could be restored substantially by not exposing subjects to the light for 16 days. This recovery in the OR, however, was not accompanied by an equivalent recovery of the conditionability of the light—that is latent inhibition survived the retention interval.

These results do not invalidate our earlier demonstration that variations in the level of the OR generated by changes in the predictive accuracy of the stimulus tend to be correlated with the subsequent conditionability of the stimulus. What they do suggest is that other factors are involved that make the relationship between the OR and conditionability rather more complex than was anticipated in our earlier theorizing. It is time now to develop the theory to accommodate these complexities. We begin by considering the determinants of the OR.

6. STIMULUS SIGNIFICANCE

TWO SOURCES OF THE OR

Habituation and the Orienting Reflex

We have been largely concerned, so far, with experimental procedures in which the OR initially evoked by a light tends to decline. We have attempted to explain the phenomenon in terms of a theory that equates the OR with the attention governed by a stimulus, and that supposes attention to be determined by the extent to which the consequences of the stimulus are predictable. When the stimulus has been presented alone, the consequent decline in the OR has been attributed to the animal’s learning that the stimulus is reliably followed by nothing. But at the empirical level, the phenomenon being studied here is habituation—a decline in the probability of the unconditioned response that the stimulus initially evokes as a consequence of repeated presentation of that stimulus. We need, therefore, to examine the relationship between our approach and the interpretation offered by current theories of habituation. Is it possible to accommodate habituation more generally in terms of the framework we propose? Can more usual accounts of habituation deal with our results showing the importance of predictive accuracy? Or is it possible in some way to combine these different interpretations of habituation?

Current theories of habituation suppose that repeated experience of a given stimulus will establish some central representation of it—a “neuronal model” in the terminology of Sokolov (1963); or just the set of S–R pathways that have lost effectiveness in the dual-process theory of Groves and Thompson (1970; see also Thompson, Berry, Rinaldi, & Berger, 1979). A match between input and representation means that no response (in this case, no OR) will be evoked; and the representation is held to become better formed, in some way, with repeated exposure to the stimulus. There is some disagreement about the conditions in which the return of an habituated response (dishabituation) might be expected. But any theory can allow that a change in the stimulus could produce this effect (the match will no longer be perfect) as could stimulation that produces an increase in the animal’s general level of arousal (dual-process theory specifically postulates a process of sensitization). The processes just mentioned as being possible sources of dishabituation are likely to be at work in some of the experimental procedures described in this chapter. For example, one effect of presenting a familiar light in a quite novel context might be to make the stimulus impinge rather differently on the
animal, ensuring a mismatch and the recovery of the OR evident in Hall and Channell's (1985) study. Alternatively, the novelty of the new context might produce an arousing effect generating a relatively high level of responding even though the underlying state of habituation remains. Hall and Schachtman (1987) favored an explanation of this latter sort in accounting for the effects of a retention interval. The level of the OR, they suggested, will depend on both the state of habituation of the specific stimulus and the extent to which the context in which that stimulus is presented is generally arousing. One effect of a long retention interval may be to restore the arousing properties of the previously experienced context, allowing the OR to reappear in spite of the fact that the underlying tendency to make the response is weak. This analysis allows us to make a first step in explaining why the level of the overt OR and the conditionability of the stimulus should sometimes fail to correlate. The effects produced by changes in arousal on the overt OR could act to obscure the perfect correlation between the conditionability of a stimulus and the underlying state of habituation of the OR.

Although this first step may seem encouraging, it is difficult to make further progress along these lines. The interpretation that emerges from our analysis in terms of habituation is that a stimulus will lose conditionability and the ability to evoke the OR as repeated exposure produces an increasingly better formed representation. But how can this account accommodate the effects of the predictive accuracy of the stimulus? It seems necessary to assume that, in some way, varying the consequences of the stimulus from one trial to the next interferes with the process of representation formation. It may indeed be possible to construct a learning mechanism that would allow this, but none is readily available. The learning process postulated in the Pearce–Hall (1980) model, on the other hand, can handle the effects of predictive accuracy with great ease.

The obvious solution is to allow that the vigor of the OR depends on two sets of mechanisms; one set concerned with representation formation and habituation, a second with what the stimulus in question predicts. This suggestion is not novel; it matches exactly the elaboration offered by Liddell (1950) in his discussion of the Pavlovian orienting reflex. Presentation of a novel stimulus, Liddell suggested, will elicit not only Pavlov’s “what-is-it?” reflex but also a “what-happens-next?” reflex. The first of these will be subject to the influence of habituation and will decline as the animal becomes familiar with the stimulus, forms an accurate representation of it, or whatever. The second will be evoked when the consequences of the stimulus are uncertain.

The behavioral OR shown by the rats in our experiments can be presumed to reflect the state of both these “reflexes.” The initial loss of the response produced by presenting the light on its own will occur both because of habituation and because the animal is able to learn what happens next

6. STIMULUS SIGNIFICANCE

(nothing). Each of these changes will contribute to the observed behavior. But once habituation has occurred there is no reason to suppose that the “what-is-it?” reflex will play a further role and changes in the OR (and in conditionability) will depend on the predictive accuracy of the stimulus.

Physiological Analysis

If the OR we study is determined by the action of two separate mechanisms then it might prove possible to distinguish between them by means of a physiological intervention. A recent experiment of ours encourages this view. The aim of this study was to examine the impact of lesions of the serotoninergic (5-HT) pathways in the brain on the OR elicited by a light when it was associatively neutral, and when it had taken part in conditioning. In order to produce the lesions a group of rats was injected intracerebroventricularly with 5,7-dihydroxytryptamine. After recovering from the surgery the rats with the lesion, Group S, and a control group, Group C, received repeated nonreinforced presentations of the light for a number of sessions. Throughout this habituation stage, there was no evidence that the OR was performed more vigorously in Group S than Group C.

This outcome is important because it contrasts with our findings from a later stage of the experiment. Very briefly, both groups first received serial conditioning in which the light was paired with a tone that signalled food. Conditioning trials were then given in which the light was paired directly with food, followed by extinction trials with the light being again presented by itself. For the present discussion, it is of most interest to focus on the results of this final stage since it is of similar design to the initial stage. The effects of the extinction sessions on both magazine activity (right-hand panel) and the OR (left-hand panel) are shown in Fig. 6.8.

Both groups behaved similarly as far as magazine activity is concerned, which suggests that the lesions had little impact on the performance of the CR. Looking next at the results with the OR, we can see that for Group C the pattern of responding is consistent with the notion that the predictive accuracy of the light influences this activity. There was an increase in the OR during the initial sessions of extinction, when the light will be an inaccurate predictor of its consequences; but the OR became less frequent during the later sessions, when the light will be an accurate predictor of nothing. Of considerable importance is the finding that Group S shows a similar pattern, except that it was amplified during the intermediate stages of extinction.

The results thus demonstrate that the OR is facilitated by damage to the

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4 We are grateful to George A. Foster, Maria Cox, and Paul Wilson for their assistance with this experiment.
5-HT pathways, but only in special circumstances. When the light is novel then this damage does not facilitate the OR. But when the light is first presented in extinction, and it is presumably an inaccurate predictor of its consequence, then the OR is enhanced. Admittedly, these are preliminary findings, but they do suggest that we are correct in assuming that there are two systems responsible for determining the strength of the OR. One of these systems is effective when the light is first presented, it is presumably concerned with the construction of an internal representation of the light, and its operation is not disrupted by damage to the 5-HT pathways. The other system appears to be concerned with ensuring that attention is directed to stimuli that have proved inaccurate predictors of their consequences, and the effectiveness of this system does seem to be influenced by lesions of the 5-HT pathways.

A report by Grastyan (1961) provides a rather different line of evidence that is consistent with this distinction. Grastyan found that when a stimulus was first presented for conditioning, it elicited a desynchronization of hippocampal rhythms. This desynchronization was replaced during the early stages of conditioning by hippocampal theta activity, which disappeared once conditioning had become stable. At this point the stimulus was employed in a discrimination and this resulted in the restoration of theta activity. Perhaps the initial desynchronization of hippocampal rhythms reflects the activity of a process that is concerned with constructing an internal representation of the stimulus, whereas the theta activity could be related to a different process that is engaged whenever a stimulus has proved to be an inaccurate predictor of its consequences.

DETERMINANTS OF CONDITIONABILITY

Our reconsideration of the sources of the OR leads to the following conclusions. Experience that allows an animal to learn that the consequences of a stimulus are predictable will lead to a decline in the attention paid to that stimulus. This loss of attention can be tracked by measuring changes in the OR, provided we make allowances for changes in the OR produced by the habituation process and by factors that control the animal's level of arousal. To this extent the OR is not a perfect index of the effect of predictive accuracy on attention; but its not bad. What remains is to reconsider the second aspect of our original theory—that which equates the level of the OR with conditionability.

The critical observation here is that the decline in the OR produced by exposure to a stimulus does not show context specificity whereas latent inhibition (lost associability) does. This is not to be explained away by saying that in this case the OR is again an imperfect measure of attention. Our theory that makes attention depend on predictive accuracy has no reason to expect that lost attention should be restored merely because the same stimulus occurs in a different place. The theory says that attention should remain weak and this is just what the behavior shows, provided the context is familiar.\(^9\)

The conclusion to which we are drawn, therefore, is that some factor other than a recovery in attention is responsible for the failure of latent inhibition to transfer across contexts. The nature of this factor, however, remains a matter for debate. One possibility suggested by Wagner's (1976, 1981) theorizing is that latent inhibition might depend not only on what the stimulus predicts but also on the extent to which it is itself predicted. During preexposure the context will come to signal the occurrence of the stimulus making it less effective as a CS. A change of context will eliminate this effect (but see Hall & Chennell, 1985; Hall & Minor, 1984).

A more intriguing possibility is suggested by certain studies of human learning and memory that indicate that semantic memory (including forms of associative learning) may depend for effective retrieval on contextual cues, whereas recognition memory does not. An instance is provided by the work of Godden and Baddeley (1975, 1980). They found that the ability of divers to recall a list of words learned either under water or on the beach was much better when the test took place in the same context as had been used for original learning. But the ability to recognize a word as coming from the original list was not influenced by the change of context. Given this perspective, it is not surprising that the habituated state of the OR should transfer across contexts. The task required of the animal in this case is essentially that of recognizing the light as being the same as that experienced previously. But the failure of latent inhibition to transfer fully from one context to another

\(^9\)It may be added that the failure of an habituated response to return with a change in context is not unique to the procedure used by Hall and Chennell (1985). In a review of the literature on this topic Hall (1993) found that, provided the test context was not itself novel and conditions were such as to eliminate stimulus generalization decrement, habituation reliably transfers from one context to another.
perhaps implies that some associative learning is involved in the effect because appropriate contextual cues are necessary for what was learned in preexposure to influence subsequent conditioning.

There are a number of possible ways in which associations formed during preexposure might contribute to latent inhibition, provided the context is not changed. Associations among the component parts of the stimulus (McLaren, Kaye, & Mackintosh, 1989) might retard further learning about these stimulus elements. Or the process whereby an animal might learn that a stimulus is followed by no event might be construed as being associative and a possible source of interference in subsequent conditioning (e.g., Bouton, 1989). But for our purposes here it is unnecessary to attempt to decide in favor of one suggestion rather than another. All we need note is that there is good reason to conclude that there is a context-dependent process that contributes to the latent inhibition effect. Once this has been acknowledged it becomes possible to explain why conditionability and the OR should not be perfectly correlated. We are, however, still able to use the OR as an index of the attentional component of the latent inhibition effect.

CONCLUSIONS

We have examined in this chapter the following, conveniently simple, assertions about the relation between various aspects of attention and learning. The predictive accuracy of a stimulus, we suggested, will determine the attention paid to it; the amount of attention will determine how readily that stimulus can enter into associations subsequently; and the behavioral OR can be used as an index of this form of attention and thus of conditionability. Of course, things are not that simple. It emerges that predictive accuracy is not the sole determinant of the OR—that, in particular, the processes of habituation play an important part in determining its frequency of occurrence. And it turns out that the attention paid to a stimulus is not the sole determinant of its associability. Associations formed during preexposure (including those formed during the nonreinforced preexposure of the latent inhibition procedure) can hinder subsequent learning about the stimulus.

Having made these qualifications, however, the set of propositions with which we started remains largely intact. We may still say that predictive accuracy determines the strength of a form of attention that is an important component of conditionability and that, provided the effects of certain other factors are taken into account, the behavioral OR can be used as a useful index of attention.

In deriving these conclusions we have made use of the findings and theories generated by the study of habituation. Work on this topic (much of it done with human subjects; see e.g., Siddle, 1983) has tended to develop independently of that done on conditioning and associative learning (but see Wagner, 1976). However, the experimental phenomena at the heart of our analysis can also be seen as experiments on habituation, even though we have approached them from the point of view of associative learning theory. We hope that by appreciating this we have made some progress towards arranging a fruitful union between the two lines of work.

We think, also, that as well as drawing on the analysis of habituation offered by others we may be able to contribute to it. There is no doubt that the traditional orienting reflex is a complex event with potentially separable components influenced by different factors (see Graham, this volume). A full analysis of habituation will require us to be able to identify these components and the factors that control them. Our contribution is that we have helped to isolate an investigatory "what-happens-next?" component and to show that the predictive accuracy of the stimulus is critical in determining its occurrence.

REFERENCES


