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The effect of a retention interval on habituation of the neophobic response

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In three experiments, water-deprived rats were preexposed to a novel saccharin solution. The neophobic response to this flavor was then assessed in a choice test involving saccharin and water, administered either immediately or 24 h after preexposure. Subjects displayed a significantly greater preference for saccharin at the 24-h test than at the immediate test (Experiments 2 and 3). This "incubation" effect was eliminated if the subjects were more water-deprived at the delayed test than at the immediate test (Experiment 1), and enhanced if the amount of saccharin consumed during preexposure was increased (Experiment 3). Possible ways in which current theories of habituation might be amended in order to accommodate this finding are discussed.

Thirsty rats presented with a novel flavored solution will reject it in favor of one that is familiar—a phenomenon known as neophobia. Continued exposure to the novel solution eventually results in an attenuation of the neophobic reaction, an effect usually taken to be an instance of habituation (see, e.g., Domjan, 1975). The experiments to be reported here concern the effects of interposing a retention interval between initial exposure to a novel flavor and a subsequent test of the extent to which neophobia has been attenuated.

A characteristic of habituation (it is sometimes taken to be a defining feature; see Thompson & Spencer, 1966) is that a habituated response will show spontaneous recovery when a retention interval intervenes between habituation training and a test session in which the critical stimulus is re-presented (see, e.g., Davis, 1970). Evidence for a recovery of the habituated neophobic response to a flavor is available only at very long retention intervals. Domjan (1977) reports perfect retention for up to 30 days, with a loss appearing only in subjects tested after an interval of 75 days; Kaye, Gambini, and Mackintosh (1988), who tested rats either 4 or 48 h after initial exposure to a novel flavor, found no effect of the retention interval on habituation. In contrast, an experiment by Green and Parker (1975, Experiment 1; see also Bond and Westbrook, 1982; Nachman & Jones, 1974) suggests that the effects of an exposure trial may "incubate" rather than suffer a loss over a retention interval. Thirsty rats were exposed to a saccharin solution for 10 min, and then different groups were tested for their choice between saccharin and unflavored water either immediately or after various intervals ranging from 45 min to 24 h. The neophobic response was found to *decrease* as the retention interval was increased.

The effect demonstrated by Green and Parker (1975), challenging as it does our expectation of spontaneous recovery, deserves careful examination to ensure that possible artifacts have been eliminated. One feature of the procedure used by Green and Parker (1975; see also Bond & Westbrook, 1982) was that the subjects tested at the longer intervals were more deprived than those tested at shorter intervals (no fluid was offered between the initial exposure trial and the test trial). This confounding of retention interval with deprivation level is acceptable only if we can share the authors' assumption that the effect of the latter is solely to increase the absolute level of consumption, and not to influence choice. It is quite possible, however, that preference for saccharin in animals given a choice between saccharin and water might be influenced by the subjects' state of deprivation—water-deprived rats tend to eat little, a state of affairs that might encourage the intake of sweet-tasting substances (see, e.g., Grice & Davis, 1957; Verplanck & Hayes, 1953). The consequence would be an apparent increase in the extent to which the initial habituation training had produced an attenuation of neophobia after the longer retention interval. Our first experiment was designed to assess this possible interpretation of the results.

EXPERIMENT 1

One aim in Experiment 1 was to replicate the incubation effect reported by Green and Parker (1975). Accordingly, two groups of rats were given preexposure to a saccharin solution. Habituation of neophobia to this stimulus was assessed by means of a choice test (the alternatives being saccharin and water) administered shortly after the preexposure trial for Group P-I (preexposed, immediate test), or 24 h later for Group P-D (preexposed, delayed test). On the basis of the previously published results, we might expect the preference for saccharin to be greater

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in Group P-D than in Group P-I. In order to demonstrate that the increased level of deprivation experienced by Group P-D was not in itself enough to change preference in this way, a second pair of groups was included. These, N-I and N-D (nonpreexposed, immediate or delayed test, respectively) were treated in exactly the same way as Groups P-I and P-D, except that they received water rather than saccharin during the initial preexposure phase.

Method

Subjects and Apparatus. The subjects were 32 male Lister rats with a mean free-feeding weight of 454 g (range: 395-505 g). Before the start of the experiment proper, they were housed in pairs in cages of opaque plastic (34 cm long, 22 cm wide, and 19 cm high) with wood shavings as bedding. Food was always freely available in these cages. Tap water was supplied from bottles with stainless steel ball-bearing-tipped spouts. These cages were kept in the colony room, which was brightly lit from 0800 to 2000 each day.

After the initial water-deprivation stage, the animals were singly housed in cages (35 cm long, 22 cm wide, and 19 cm high) with grid floors. The cages were equipped with two adjacent trays, from both of which fluid could be delivered through spouts of the type described above. The front of the two trays was filled with food; just before each fluid presentation the food was removed, and it was replaced immediately afterwards. During experimental sessions, fluid was delivered from calibrated 50-ml centrifuge tubes, equipped with the same drinking spouts as the water bottles. The amount consumed was recorded to the nearest 0.5 ml.

Procedure. A schedule of water deprivation was established over the 5 days before the start of the experiment proper. The water bottles were removed at 1800 on the 1st day, and on each subsequent day they were presented for a fixed period of time beginning at 1400. This time period was 4 h on the 1st day, 2 h on the 2nd, 1 h on the 3rd, and 30 min on the final 2 days. Throughout the course of the experiment, the subjects continued to receive free access to water for 30 min at 1400, unless stated otherwise. The experiment proper began on the following day, Day 1. All subjects received access to 5 ml of water for 15 min at 1000, in order to accustom them to drinking during the experimental sessions. On Day 2, the animals were divided into four groups. At 1000, Groups P-I and P-D received access to 5 ml of a solution of sodium saccharin (2 g/l) for 15 min. Groups N-I and N-D received access to the same volume of water. At 1100 on the same day, Groups P-I and N-I were given a 15-min choice test, in which they had free access to a saccharin solution and to water. Bottles containing the two fluids were presented simultaneously, counterbalanced across the two tray positions. Groups P-D and N-D remained undisturbed (they received no supplementary water at 1400) until Day 3, when at 1100 they received a choice test identical to that given to the I groups.

Results and Discussion

Figure 1 shows for each group the mean volume of each fluid (water and the saccharin solution) consumed on the test session. It is apparent that the incubation effect reported by Green and Parker (1975) was not replicated here. Group P-D was no more ready to consume saccharin than was Group P-I. Indeed a preference score of the sort reported by Green and Parker (1975) would reveal a shift away from saccharin in Group P-D, as a consequence of their increased tendency to drink water in the test. This effect of the retention interval is not a consequence of any change in habituation to the saccharin, since the nonpreexposed subjects showed exactly the same pattern of results as did the preexposed subjects. Evidently one effect of an increased level of deprivation is to increase the amount of water consumed in a choice test when the alternatives are water and saccharin.

Statistical analysis of the test data was conducted using difference scores, computed for each animal by subtracting the amount of water drunk from the amount of saccharin drunk. An analysis of variance with preexposure condition (preexposed or nonpreexposed) and retention interval (immediate or delayed) as factors yielded a significant effect of the latter [$F(1,28) = 6.01$, $p < .05$], but no effect of preexposure and no significant interaction ($Fs < 1$).

At first sight, the results of Experiment 1 allow a clear answer to one of the questions addressed. The effect of

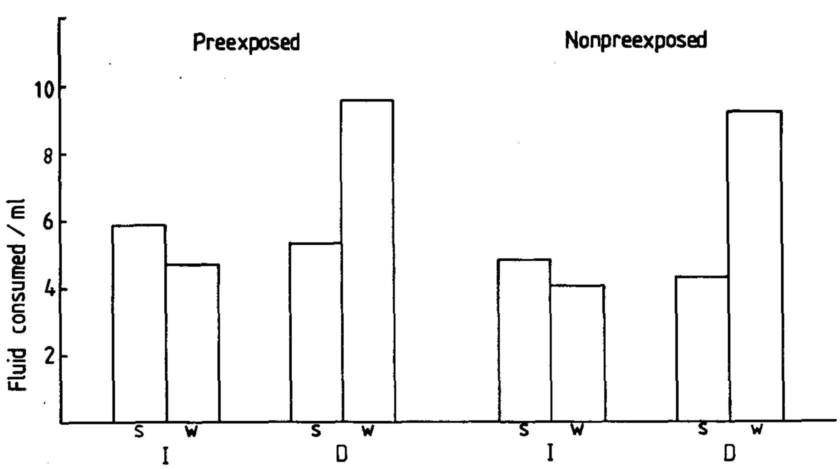

Figure 1. Mean consumption of saccharin (s) and water (w) by preexposed and nonpreexposed groups tested either immediately (I) or after a delay (D) during the test session of Experiment 1.

increasing deprivation is not to increase the relative amount of saccharin consumed on the choice test; rather, the reverse effect is observed. Accordingly, the incubation of habituation reported by Green and Parker (1975) cannot be an artifact of increased deprivation in the delayed test groups. Unfortunately, however, Experiment 1 revealed no sign of an incubation effect in spite of the fact that our design and procedure were as close to those of Green and Parker (1975) as we could arrange. Preexposed subjects showed an increased preference for water as the delay interval was increased, just as did the nonpreexposed subjects. The experiments to be reported next, therefore, represent the attempt to determine what conditions must be met if the incubation effect is to be demonstrated.

EXPERIMENT 2

The results of Experiment 1 suggest that increasing levels of water deprivation increase the likelihood that rats will consume water rather than saccharin in a choice test. Such an effect would act to obscure the incubation effect that Experiment 1 was intended to reveal in the preexposed subjects. In Experiment 2, therefore, we attempted to eliminate any difference in deprivation level between I and D groups. Such a difference arose in Experiment 1 because the I groups had access to 5 ml of fluid immediately before the test and had access to water for 30 min on the preceding afternoon. The D groups, in contrast, received no water in the afternoon preceding the test nor any fluid immediately before it. In Experiment 2, therefore, we used the same procedures as were used in Experiment 1, except that the D groups received water at 1400 on the day before the test (i.e., on the afternoon of Day 2) and were given 5 ml of water on Day 3 just before their choice test.

Method

Subjects and Apparatus. The subjects were 32 male Lister rats with a mean free-feeding weight of 458 g (range: 345-545 g). The apparatus was the same as in Experiment 1.

All aspects of the procedure that are not specified were identical to those of Experiment 1. Water deprivation was introduced over a 5-day period as in that experiment. On the next day, intended to be Day 1 of the experiment, all animals were given 5 ml of water at 1000, but in error were given no access to water at 1400. Accordingly, the experiment proper was not begun until the next day. All subjects received 5 ml of water at 1000 on Day 1; at 1400, all received access to water for 30 min. Preexposure occurred at 1000 on Day 2. Half of the subjects, Groups P-I and P-D, received access to 5 ml of saccharin solution, whereas the remainder, Groups N-I and N-D, received access to 5 ml of water. In order to maximize the chance of seeing an incubation effect, the immediate choice test was brought forward and administered immediately after the preexposure session: After the preexposed fluid had been removed, the food was not returned to the food trays, and immediately Groups P-I and N-I were given a choice test, which was conducted exactly as that of Experiment 1. Groups P-D and N-D received access to water for 30 min at 1400 on Day 2. At 1000 on Day 3, these groups received access to 5 ml of water for 15 min, immediately after which they received a choice test identical to that given to Groups P-I and N-I.

Results and Discussion

Figure 2 shows the amount of water and of saccharin consumed by each group during the test session. Looking first at the nonpreexposed groups, there are no obvious differences between those given the immediate and those given a delayed test. There was no dramatic increase in preference for water in Group N-D as was seen in the corresponding group in Experiment 1, confirming our assumption that the effect seen in the previous study was a consequence of deprivation level. It may be noted that in Experiment 2 both Group N-I and Group N-D consumed more water than saccharin (unlike Group N-I in Experiment 1). We do not know the reason for this ef-

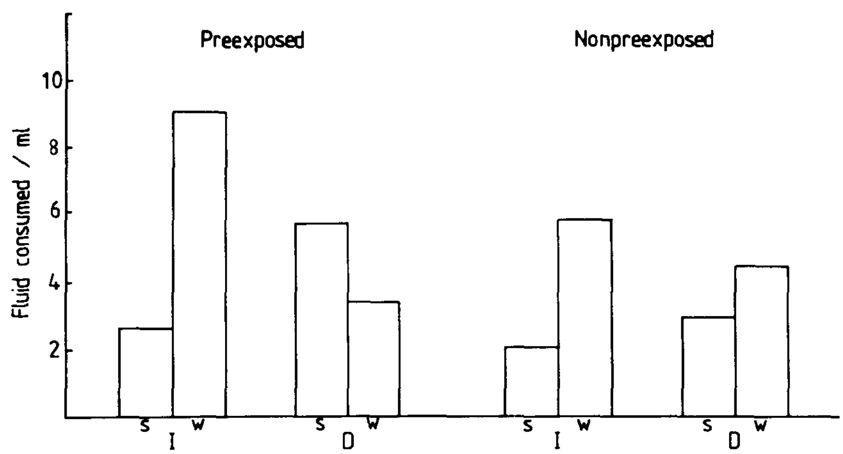

Figure 2. Mean consumption of saccharin (s) and water (w) by preexposed and nonpreexposed groups tested either immediately (I) or after a delay (D) during the test session of Experiment 2.

fect; perhaps it reflects the fact that in Experiment 2 the overall level of deprivation might have been somewhat higher because of the restricted access to water allowed on the day before Day 1. Alternatively, it may be a consequence of the fact that in Experiment 2 the "immediate" test followed preexposure more closely than it did in Experiment 1; the interval from presentation of the training trial to the onset of the test trial was 15 min rather than the 60 min of Experiment 1. Whatever its source, the same preference for water was seen in the test results for Group P-I, making all the more striking the reversal of preference shown by Group P-D. The latter subjects consumed more saccharin than water.

A factorial analysis of variance was conducted on the difference scores as in Experiment 1. This revealed a significant effect of retention interval [$F(1,28) = 13.06$, $p < .01$], no significant main effect of whether or not the subjects had been preexposed to saccharin ($F < 1$), and a significant interaction between these two factors [$F(1,28) = 4.42$, $p < .05$]. This interaction appeared to reflect the fact that only in the P groups was the preference shown modified by the length of the retention interval. This interpretation was confirmed by an analysis of simple main effects, which revealed that Group P-D showed a significantly greater preference for saccharin than did Group P-I [$F(1,28) = 16.34$, $p < .001$]. Group N-D, however, showed no more preference for saccharin than Group N-I [$F(1,28) = 1.14$]. We have thus been able to demonstrate with this experimental procedure—which was admittedly rather different from that used by Green and Parker (1975)—a result that is consistent with the suggestion that the habituation of neophobia may be subject to incubation.

EXPERIMENT 3

The apparent incubation effect demonstrated in Experiment 2, although similar to that reported by Green and Parker (1975), is substantially smaller; Green and Parker's subjects given the delayed test consumed almost four times as much saccharin as water. One factor governing the size of the preference shown in the test appears to be the amount of saccharin consumed during preexposure. Bond and Westbrook (1982) explicitly investigated this factor by giving different groups of subjects access to a saccharin solution for either 1 or 6 min. Neither group showed much evidence of habituation when given an immediate test, but habituation was more clearly apparent in a delayed test for the subjects allowed the longer period of initial exposure. Subjects given exposure for only 1 min drank on the average 1.5 ml; those given exposure for 6 min drank a mean of 6.6 ml. The latter volume is admittedly only a little greater than the quantity (5 ml) consumed in initial exposure in our experiments. Nonetheless, the pattern of results reported by Bond and Westbrook (1982) encouraged us to hope that the effect of the retention interval might be made more readily apparent if the extent of initial exposure was increased.

Experiment 3 included four groups of subjects trained and tested just as in Experiment 2, except that the preexposed groups received 15 ml rather than 5 ml of saccharin during exposure. Nonpreexposed groups received 15 ml of water at this stage. Subjects given the delayed test were given access to water as in Experiment 2, to ensure that their state of deprivation on test would be much the same as that experienced by those given the immediate test.

Method

The subjects were 32 male Lister rats with a mean free-feeding weight of 441 g (range: 390–515 g). The apparatus was the same as in Experiment 2.

All aspects of the procedure that are not specified were identical to those of Experiment 2. On Day 1, all subjects received controlled access to 5 ml of water at 1100; at 1400, they all received access to water for 30 min. Preexposure occurred at 1100 on Day 2. Groups P-I and P-D received access to 15 ml of saccharin solution, whereas Groups N-I and N-D received access to 15 ml of water. Groups P-I and N-I were given a choice test immediately; Groups P-D and N-D received access to water for 30 min at 1400. At 1100 on Day 3, Groups P-D and N-D received access to 15 ml of water for 15 min, immediately after which they received a choice test. The choice tests were administered exactly as in Experiment 2.

Results and Discussion

The results of Experiment 3 are shown in Figure 3. The preexposed groups showed an incubation effect similar to, but rather more marked than, that observed in Experiment 2: Group P-I preferred water over saccharin, whereas Group P-D, tested after a delay, preferred saccharin to water. The nonpreexposed groups also showed a slight increase in preference for saccharin over water over the delay—Group N-I was indifferent, whereas Group N-D preferred saccharin to water—but the effect was much less than that seen in the P groups. This description of the data was confirmed by a factorial analysis of variance conducted on the difference scores as in Experiment 1. This revealed a significant main effect of retention interval [$F(1,28) = 50.16$, $p < .01$], as well as a significant interaction of this factor with whether or not the subjects had been preexposed to saccharin [$F(1,28) = 15.54$, $p < .01$]. The main effect of preexposure was not significant ($F < 1$). The significant interaction between preexposure and retention interval was consistent with the presence of an incubation effect; this interpretation was supported by an analysis of simple main effects, which revealed that Group P-D showed a significantly greater preference for saccharin than did Group P-I [$F(1,28) = 60.77$, $p < .001$]. Preference for saccharin was also significantly greater in Group N-D than in Group N-I [$F(1,28) = 6.95$, $p < .05$], suggesting that in this experiment (for reasons that remain obscure; no such effect was evident in Experiment 2) retention interval enhanced saccharin preference even in the absence of preexposure. But the presence of the criti-

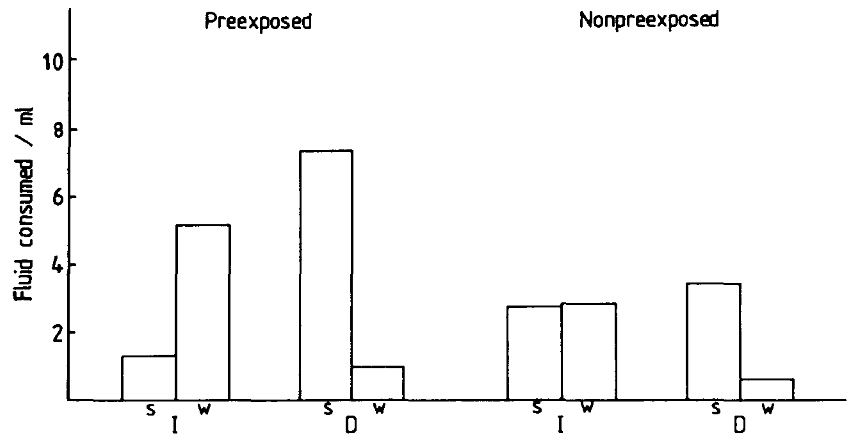

Figure 3. Mean consumption of saccharin (s) and water (w) by preexposed and nonpreexposed groups tested either immediately (I) or after a delay (D) during the test session of Experiment 3.

cal incubation effect was confirmed by the observation that saccharin preference was significantly greater in Group P-D than in Group N-D [$F(1,28) = 7.34$].

The results of Experiment 3 thus replicated the incubation effect observed in Experiment 2: Preference for saccharin increased over a delay to a significantly greater extent in the preexposed than in the nonpreexposed groups. Although cross-experiment comparisons must be treated with caution, the incubation effect appeared to be more substantial in Experiment 3, in which the amount of saccharin consumed during preexposure was increased. This is consistent with the data reported by Bond and Westbrook (1982), who found that the size of their incubation effect was dependent on the duration of preexposure (and hence on the amount consumed during preexposure). Bond and Westbrook (1982) explain the effect of the amount consumed in terms of Wagner's (1976) associative account of habituation, arguing that prolonged initial exposure promotes the formation of context-stimulus links on which habituation in part depends. It should be pointed out, however, that any theory of habituation is entitled to assume that the magnitude of habituation will depend on the degree of initial exposure, and that the chances of seeing an incubation effect may be enhanced when a substantial amount of habituation training has been given.

GENERAL DISCUSSION

After some effort, we have been able to reproduce the effect that Green and Parker (1975) refer to as incubation in a habituation preparation. Rats given exposure to a novel saccharin solution will show habituation of neophobia (drinking more of it than control subjects not given preexposure) when tested 24 h later; but when they are tested immediately after preexposure, there is no sign of any attenuation of neophobia. This effect was present in our Experiment 3 but not in Experiment 1, and only to a lesser extent in Experiment 2. We have identified two features that appear to be critical in producing the effect.

First, it is important that subjects tested after the 24-h retention interval should not be substantially more deprived than those tested after the short retention interval. An increase in deprivation will selectively increase a rat's tending to consume water rather than saccharin (compare the two nonpreexposed groups of Experiment 1); an increased tendency to drink water would act to obscure any increase in habituation of neophobia to saccharin that occurs over the retention interval. Second, it is necessary to give subjects extensive exposure to the novel flavor on the habituation training trial; although some sign of the incubation effect was seen in Experiment 2 when subjects received 5 ml of saccharin during preexposure, the effect was much more marked for subjects in Experiment 3 that received 15 ml in preexposure (see also Bond & Westbrook, 1982). Presumably habituation, when it finally becomes evident (i.e., after 24 h in these experiments) will be greater the more extensive the initial habituation training.

This last point allows us to offer an explanation for why Green and Parker (1975) were able to demonstrate incubation in spite of the fact that they allowed deprivation levels to increase for subjects tested after long retention intervals. In Green and Parker's preexposure procedure, subjects were not given a fixed amount of saccharin but were allowed free access for 10 min. Green and Parker do not report how much was consumed during this time, but it might well have been enough to ensure a habituation effect so profound as to outweigh, at the long retention interval, the opposing effect induced by the increase in deprivation. Whatever the merits of this speculation, the critical point for our present purposes is that the incubation effect initially demonstrated by Green and Parker (1975) is not to be explained away as some artifact of deprivation; accordingly, some place must be found for it in our current theories of habituation, which, as we have already noted, are more inclined to assume that the effects of exposure are likely to dissipate with time rather than show incubation.

Green and Parker (1975) explained their results in terms of the special properties of consolidation in gustatory memory. Presentation of a taste, they suggested, begins a slow process of encoding, with up to 45 min being needed for taste information to be established in a form that can be utilized. This suggestion was not incorporated into any formal theory of habituation, but it can readily be accommodated by comparator theories of the sort proposed by Sokolov (e.g., 1963). According to these theories, exposure to a stimulus allows the formation of a representation (a "neuronal model") of that event. Habituation occurs to the extent that there is a match between this model and a subsequent stimulus presentation. Now if the process of encoding proposed by Green and Parker (1975) can be equated with the formation of a more exact model of the stimulus, then the outcome would be that habituation would be improved by a retention interval. The problem with this argument, of course, is that its initial assumption is entirely ad hoc; it could be proposed, with equal plausibility, that detailed features of a stimulus are initially represented in the model and that they tend to be lost with time.

A similar objection can be made to attempts to adjust Wagner's (1976, 1981) model to deal with incubation phenomena. According to this theory, habituation has two components. The unconditioned response will be rendered less likely when a representation of the stimulus is active in short-term memory as a consequence of the recent presentation of the stimulus. The second source of habituation derives from the fact that associative links may be formed between the representation of the stimulus and the cues that define the context in which it occurs. Presentation of these cues will be able to activate a representation of the stimulus even after a long retention interval, and this associatively primed state will interfere with processing of the stimulus itself and ensure a diminution in the unconditioned response. If it is assumed, first, that the development of effective context-stimulus associations requires a period for consolidation to occur, and second, that the associative mechanism is much more powerful than the nonassociative mechanism for habituation, then the observed results can be accommodated. But the arbitrary nature of these assumptions makes the explanation less than satisfactory.

According to the S-R theory of habituation developed by Groves and Thompson (1970), repeated or prolonged presentation of a stimulus (S) produces a decline in the effectiveness of the pathway connecting the mechanism responsible for detecting S to the mechanism responsible for emitting the response (R). One way in which this simple theory might be elaborated in order to deal with the incubation effect makes use of the notion of arousal. Groves and Thompson (1970) suppose that, in addition to its effect on the S-R pathway, the presentation of the stimulus will engender a general state of arousal that will dissipate with time. The first presentation of a novel stimulus like saccharin may be regarded as an arousing event. A test for habituation given shortly after this presentation may therefore underestimate the extent of habituation—the S may have only a weak tendency to elicit the R, but this tendency will be amplified by the heightened level of arousal. If the test is delayed until the arousal has dissipated, however, this amplification of responding will not occur, and it will appear as though habituation has increased. This argument assumes that arousal, although enhancing the neophobic reaction to saccharin, has no effect on water consumption. However, two-process theory asserts that arousal will enhance the neophobic response to *any* stimulus, and if the reduction in arousal that occurs over a retention interval were to increase consumption of water as well as of saccharin, there would be no grounds for expecting saccharin preference to change over the delay. In order to explain our results, therefore, two-process theory must allow that arousal selectively alters saccharin consumption. Luckily, this is not necessarily an unreasonable assumption. It seems quite likely that a well-habituated stimulus like water will be far less sensitive to the effects of arousal than will a relatively novel substance like saccharin. If this is the case, then our data are perfectly consistent with the predictions of two-process theory.

An alternative interpretation that also makes use of the notion of arousal comes when we consider the incubation effect demonstrated by Kamin (1957) for avoidance learning. This effect, poor performance after a short retention interval but an improvement as the interval is increased, has been attributed by some (e.g., Klein & Spear, 1970) to changes in the effectiveness of a retrieval process. Immediately after initial conditioning, the subjects are assumed to be temporarily in a different state from that present during initial training. They are thus unable to retrieve what they originally learned. But having reverted to their original state after a retention interval, they are again able to retrieve the relevant information. The parallel with "state-dependent learning" (Spear, Klein, & Riley, 1971) will be apparent. Clearly an exactly analogous argument could be applied to the present incubation effect, the state in question being that of the arousal that occurs as a consequence of stimulus presentation, and the information that must be retrieved being whatever is supposed to be acquired during the initial habituation trial. But the possibility of a rather simpler interpretation should be acknowledged at this point. Habituation will suffer generalization decrement; that is, the UR will tend to return if the test stimulus is changed to some extent from that used in training. Now there are a variety of reasons why a test flavor presented immediately after initial training should be perceived as being different from the stimulus presented in training—reasons that will not apply when this test occurs after a longer interval. For example, initial presentation of a novel flavor could put the animal into a state of arousal. At the immediate test, the animal may still be in this state of arousal; moreover, the direct sensory aftereffects of the stimulation may persist. Neither of these things will be true at the delayed test. As a result, there will be more generalization decrement on the immediate test than on the delayed test, making habituation more likely to be evident in the latter case than in the former.

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