Response-independent habituation of the orienting response in the preweanling rat

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The effect of pattern of stimulus presentation on habituation of the cardiac component of the orienting response to an auditory stimulus was investigated in four experiments. The duration of stimulus presentation was held constant, but some animals were given six 10-sec stimulus presentations and others were given a single 60-sec stimulus. During the first 10 sec of the auditory stimulus, heart rate (HR) decreased approximately 40 beats per minute (bpm) in both groups, but during subsequent 10-sec epochs, the changes in HR were markedly different in the two groups. For those animals given a single 60-sec stimulus, the cardiac orienting response did not habituate; that is, HR either continued to decrease or remained approximately 40 bpm below baseline. In contrast, those animals given six 10-sec stimulus presentations showed smaller decreases in HR with each successive stimulus presentation, and after approximately four presentations, no detectable change in HR was observed. Despite these dramatic differences in habituation of the cardiac component of the orienting response, neither group oriented to the auditory stimulus when it was presented again following a short retention interval. Moreover, with increasing retention intervals, both groups showed the same forgetting function (reappearance of the orienting response). The implications of these findings for theories of the orienting response as well as theories of habituation are discussed.

The ability to modify the responses elicited by environmental stimulation is essential for an animal's survival. Habituation, a decrement in response magnitude or frequency not attributable to fatigue or sensory adaptation (e.g., Thompson & Spencer, 1966), is perhaps the most common mechanism through which animals change their responses to repeatedly experienced stimuli. The process of habituation appears to be ubiquitous throughout the animal kingdom and has been extensively studied both phylogenetically and ontogenetically. Habituation of visual fixation, for example, has dominated research on the development of learning and memory in the human infant (e.g., Bornstein, 1985; Kaplan, Werner, & Rudy, 1990). In addition, habituation has been extensively studied in a number of invertebrate species (e.g., Rankin & Carew, 1988; Wood, 1988), and much of our knowledge of the cellular bases of learning and memory has relied upon habituation of the gill-withdrawal response in *Aplysia* (e.g., Carew, 1984).

In studies on habituation, it is important to distinguish between habituation of the observed response and the inferred theoretical process thought to produce that decrement (e.g., Peeke & Petrinovich, 1984; Thompson, Groves, Teyler, & Roemer, 1973). In some situations, these may be dissociated. A study by Davis (1970) on habituation of

the startle response in adult rats to intense acoustic stimuli illustrates this dissociation. In that study, animals were repeatedly exposed to a 120-dB white-noise burst, and the magnitude of the whole-body startle response was measured. A 2-sec interval separated each stimulus presentation for subjects in one group, whereas a 16-sec interval separated stimulus presentations for those in another group. Habituation of the startle response was found to be a function of interstimulus interval: the shorter the interval, the more the response habituated. However, when animals in these two conditions were subsequently tested after a 1-min interval, those in the 16-sec condition were found to be less responsive (i.e., exhibited more habituation) than the animals in the 2-sec condition. Results like these demonstrate that the underlying process responsible for habituation may not always be accurately reflected in the observed response (see also Borszcz, Cranney, & Leaton, 1989).

In comparative and developmental research, the orienting response has been widely used as an index of attention and sensory information processing (e.g., Graham, Anthony, & Zeigler, 1983; Haroutunian & Campbell, 1981). The orienting response is elicited by novel stimuli of low to moderate intensity and consists of autonomic, central, and behavioral reactions. A defining characteristic of the orienting response is that it habituates relatively rapidly (e.g., Graham, 1979). Perhaps the most well-developed and widely used theoretical interpretation of habituation of the orienting response is Sokolov's stimulus-comparator hypothesis (Sokolov, 1963). From the Sokolovian perspective, presentation of a novel innocuous stimulus elicits an orienting response and initiates the formation of a neuronal model of that stimulus. On subsequent ex-

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posures to the eliciting stimulus, a comparison is made between the neuronal model and the physical stimulus. When this comparison does not result in a match between the two, an orienting response is elicited and additional attributes of the stimulus are encoded. This process recurs each time the stimulus is presented until the neuronal model matches the sensory stimulus. At that time, presentation of the eliciting stimulus will not elicit an orienting response. Although not all of Sokolov's specific ideas about the orienting response and habituation have been supported by subsequent research, his general conceptual model of a stimulus-comparator process has been incorporated into many contemporary theories (e.g., Cohen, 1973; Wagner, 1976).

A comparison of the results of two recent studies from our laboratory suggests that the stimulus-presentation procedure can have a dramatic effect on habituation of the bradycardic orienting response in preweanling rats to a novel auditory stimulus. In a study on long-term retention of habituation, repeatedly presenting a 10-sec auditory stimulus at 1-min intervals resulted in relatively rapid habituation (Richardson & Campbell, 1991b). The initial stimulus presentation elicited a cardiac deceleration of approximately 40 beats per minute (bpm), but after just three or four stimulus presentations, little or no responding was observed. In contrast, in another study in which the same auditory stimulus, a pulsating 1600-Hz tone, was presented as a single uninterrupted stimulus for 300 sec, the cardiac deceleration was larger and showed little tendency to habituate (Hayne, Richardson, & Campbell, *in press*). During the last 30 sec of the 300-sec stimulus, for example, heart rate was still 60 bpm below the prestimulus baseline.

EXPERIMENT 1

The purpose of the first experiment was to compare the cardiac response in preweanling rats to 60 sec of auditory stimulation, presented either as a single uninterrupted stimulus or as six 10-sec trials separated by 1-min intervals. If the combined results of our earlier studies (i.e., Hayne et al., *in press*; Richardson & Campbell, 1991b) are replicable, then markedly different rates of habituation to these two patterns of stimulus presentation should be obtained.

Method

Subjects. Twenty-four experimentally naive Sprague-Dawley rats born in the Psychology Department's vivarium at Princeton University were used as subjects. The animals were 16 ± 1 days old at the time of test. Birth was counted as Day 0. On Day 2, all litters were culled to 8 animals each. No more than 2 animals from any single litter were included in the same group. The animals were housed in $48 \times 25.5 \times 20.5$ cm polycarbonate rodent cages with their dam and littermates. All animals had ad-lib access to food and water and were maintained on a 16:8-h light:dark cycle (lights on at 7:30 a.m.). All testing was conducted during the light portion of the cycle.

Apparatus. Testing was performed in a clear Plexiglas chamber ($28 \times 20.5 \times 46$ cm). This chamber was located inside a single-wall Industrial Acoustics sound-attenuating chamber (IAC). Dim

illumination was provided by a small incandescent night-light located on one side of the IAC. A small window in the door of the IAC permitted observation of the animal.

Sensory stimulus. An 80-dB (as measured on Scale C of a Simpson sound-level meter), 1600-Hz pure tone was used to elicit the orienting response. This stimulus pulsed at a rate of 2/sec with a rise/fall time of 250 msec. This tone was generated by a Coulbourn Instruments precision signal generator, amplified by a Realistic audio amplifier (Model SA-10), and presented by a 4-in. speaker (Jensen) located inside the IAC. For one group the tone was 10 sec in duration, and for another group it was 60 sec in duration. Those subjects exposed to the shorter stimulus received six 10-sec trials separated by 1-min interstimulus intervals (ISIs), whereas those subjects exposed to the longer stimulus received a single 60-sec trial. Thus total time of stimulus exposure was the same in the two conditions.

Heart rate recording procedure. To record heart rate (HR), two transcutaneous stainless steel electrodes (25 ga, approximately 1.5 cm in length) shaped like safety pins were used. These electrodes were acutely implanted just prior to test (this took 10-15 sec). One electrode was placed ventrally by the urogenital region, and the other was placed dorsally at the nape of the neck. The electrodes and attached leads (32-ga Teflon-coated wire, Alpha) did not appear to interfere appreciably with the subjects' behavior.

Cardiac potentials obtained through these electrodes were amplified by a Grass preamplifier (Model P15). The R-spike activated a Schmitt trigger (Coulbourn Instruments), and its output was detected by a microcomputer that recorded the interbeat interval (IBI) to the nearest millisecond. The microcomputer controlled all timing sequences and data collection. The cardiac signal was continuously displayed on an oscilloscope (Hitachi Model V-212).

Treatment of cardiac data. IBIs were measured to the nearest millisecond for all subjects during a 5-sec prestimulus period and during the stimulus. The IBI data were converted to a bpm measure for analysis. To measure the HR orienting response, the mean HR during the prestimulus was subtracted from the mean HR during the stimulus. The orienting response is indicated by lower HRs during the stimulus period (resulting in a negative difference score).

Test procedures. All animals were allowed to adapt to the test environment for 15 min prior to presentation of the auditory stimulus. One group of subjects was then exposed to a single 60-sec auditory stimulus, and a second group was given six trials, each 10 sec in duration. Each trial was separated from the next by a 60-sec ISI.

Results

In all cases in which repeated trials were included as a factor in an analysis of variance (ANOVA), the reported probability values were adjusted by the Greenhouse-Geisser method. All post-hoc pairwise comparisons were conducted with the Newman-Keuls procedure ($p < .05$).

The mean change in HR in 16-day-old rats to 60 sec of auditory stimulation presented either as six 10-sec stimuli or as one uninterrupted 60-sec stimulus is shown in Figure 1. The cardiac decelerations in the two groups were equivalent during the first 10 sec of the auditory stimulus but diverged dramatically during the subsequent 50 sec of stimulus presentation. The magnitude of the orienting response of those subjects given six 10-sec stimuli decreased rapidly with each successive 10-sec period, returning to baseline by about the fourth trial. In contrast, the HRs of those subjects given a single 60-sec stimulus continued to decline throughout the entire stimulus period.

A mixed-design ANOVA confirmed these interpretations of the results. This analysis yielded a significant effect of

Figure 1. Mean change in heart rate (in beats per minute) in 16-day-old rats to 60 sec of auditory stimulation. Half of the animals were given a single 60-sec stimulus presentation (filled symbols), whereas the other half received six 10-sec presentations, each separated by 1 min (open symbols).

stimulus duration [$F(1,22) = 20.27, p < .01$]. Although the effect of block was not significant ($F < 1.0$), the interaction of stimulus duration and block was significant [$F(5,110) = 19.26, p < .01$]. Those subjects given a single 60-sec stimulus exhibited a significantly larger cardiac response than animals given six 10-sec stimuli on every block except the first.

As expected, the two groups did not differ on basal HR (estimated by the 5-sec period preceding stimulus presentation; $F < 1.0$). The mean HR for the subjects given the single extended stimulus presentation was 547 bpm, and that for the subjects given six 10-sec stimuli was 546 bpm. A repeated trials ANOVA was performed on the prestimulus HRs for those subjects given six stimulus exposures. This analysis did not yield a significant effect of trial [$F(5,55) = 1.57, p > .10$], indicating that HR had returned to baseline prior to the onset of each successive trial.

Discussion

The results of this experiment confirm the previously reported findings that were obtained in two separate studies. When 60 sec of auditory stimulation are presented in six temporally separated 10-sec epochs, the autonomic component of the orienting response (bradycardia) habituates rapidly. Conversely, when the 60 sec of auditory stimulation is presented as a single uninterrupted stimulus, HR continues to decelerate throughout the entire period, suggesting that the encoding process is not complete and that a central representation of the stimulus is yet to be established. To the extent that HR deceleration is a representative measure of the orienting response, these results suggest that it may be the onset and/or offset of stimulation and not the total time of stimulus presentation that triggers the formation of a central representation of that stimulus. That is, stimulus onsets and offsets may be a more effective means of establishing a neural template than prolonged, continuous stimulation.

Although only preweanlings were tested in this experiment, it should be recognized that a similar phenomenon occurs in the adult rat, albeit with slightly different temporal parameters (cf. results obtained with young adult rats by Hayne et al., in press, and Richardson & Campbell, 1991b). The absolute effects of temporal duration may change over age, but young adults exposed to a single uninterrupted auditory stimulus will exhibit a more persistent cardiac response than will same-age subjects given the same total amount of stimulus exposure in several temporally spaced trials.

EXPERIMENTS 2A AND 2B

The purpose of the following experiments was to assess the characteristics of the central representation established by the two stimulus-presentation procedures utilized in the previous experiment. To the extent that formation of a neural representation of a sensory stimulus is proportional to habituation of the orienting response, as might be predicted by stimulus-comparator models and the onset-offset process described above, magnitude of the orienting response to a subsequent presentation of the stimulus should be much greater in the group receiving 60 sec of uninterrupted stimulation than in the group receiving six 10-sec stimuli.

In each of the next two experiments, animals were initially given either a single 60-sec stimulus or six 10-sec stimuli separated by 1-min ISIs. Fifteen minutes after this limited stimulus presentation, the animals were given either four 10-sec stimuli (Experiment 2A) or one 60-sec stimulus (Experiment 2B). If habituation of the orienting response reflects the formation of a neuronal model of the eliciting stimulus, then animals in the 60-sec condition should respond to the auditory stimulus when it is re-presented but animals in the repeated 10-sec condition should not. The purpose of the two different test procedures was to determine if habituation to the temporal characteristics of the eliciting stimulus had occurred. If, for example, animals given six 10-sec stimuli did not initially display the cardiac orienting response to the 60-sec test stimulus but did begin to respond when the test stimulus exceeded the 10-sec duration of the original stimulus, it would indicate that the central representation included information concerning stimulus duration as well as the physical characteristics of the auditory stimulus.

Method

Subjects. In each experiment, 20 experimentally naive Sprague-Dawley rats born in the Psychology Department's vivarium at Princeton University were used as subjects. All of the animals were 16 ± 1 days old at the time of test. All housing and maintenance were the same as in Experiment 1.

Procedures. The same apparatus, auditory stimulus, and general procedures used in Experiment 1 were employed in both experiments with the following exceptions: 15 min after the initial stimulus-presentation procedures, all animals were either given four 10-sec exposures to the auditory stimulus with 60-sec ISIs (Experi-

ment 2A) or a single 60-sec uninterrupted stimulus (Experiment 2B). During the 15-min intersession interval, all animals were left undisturbed in the test environment.

Results

Experiment 2A. The left panel of Figure 2 shows the initial cardiac orienting response to the two patterns of stimulus presentation. As in Experiment 1, the onset of the 1600-Hz auditory stimulus elicited a rapid decrease in HR during the first 10 sec in both groups. This cardiac response persisted in those subjects in the 60-sec condition but habituated rapidly in those animals given six temporally separate 10-sec stimulus presentations.

A mixed-design ANOVA of these data yielded a significant effect of stimulus duration [$F(1,18) = 7.86$, $p < .02$], of block [$F(5,90) = 3.49$, $p < .02$], and of the interaction of the two [$F(5,90) = 4.02$, $p < .01$]. Those animals given the single 60-sec stimulus exposure exhibited a significantly larger cardiac response than those given six 10-sec trials on every block except for the first.

The two groups of animals did not differ in terms of basal HR ($F < 1.0$). The mean HR for those animals given a single 60-sec stimulus exposure was 516 bpm, whereas that for the animals given six 10-sec trials was 518 bpm. Furthermore, basal HR did not change as a function of trials in those subjects repeatedly exposed to the 10-sec auditory stimulus [$F(5,45) = 1.57$, $p > .10$].

The cardiac response to the 1600-Hz auditory stimulus when presented 15 min after completion of the initial stimulus presentations is shown in the right panel of Figure 2. The decrease in HR elicited by the first 10-sec stimulus was nearly identical in the two groups and averaged only 5 bpm. Analysis of these data did not yield any significant effects (largest $F = 1.94$, $p > .10$).

Experiment 2B. The left panel of Figure 3 shows the cardiac response to 60 sec of auditory stimulation, presented either as a single uninterrupted stimulus or as six temporally spaced 10-sec stimuli. As in the previous experiments, the HR deceleration elicited by the auditory stimulus habituates rapidly when the stimulus is presented

Figure 2. Mean change in heart rate (in beats per minute) to 60 sec of auditory stimulation presented either in a single trial (filled symbols) or in six 10-sec trials (open symbols) and subsequent responsiveness to the same stimulus after a 15-min retention interval (left and right panels, respectively).

Figure 3. Mean change in heart rate (in beats per minute) to 60 sec of auditory stimulation presented either in a single trial (filled symbols) or in six 10-sec trials (open symbols) and subsequent responsiveness to the same stimulus after a 15-min retention interval (left and right panels, respectively).

in six 10-sec blocks but does not habituate when elicited by an uninterrupted stimulus. A mixed-design ANOVA on these data yielded a significant effect of stimulus duration [$F(1,18) = 6.60$, $p < .02$] but no effect of block [$F(5,90) = 1.47$, $p > .10$]. The interaction of stimulus duration and block was significant, however [$F(5,90) = 5.83$, $p < .01$]. Those animals given the single 60-sec stimulus exhibited a larger cardiac response than those given six 10-sec trials on the fourth, fifth, and sixth blocks.

The two groups of animals did not differ in terms of basal HR ($F < 1.0$). The mean HR for those animals given a single 60-sec stimulus exposure was 514 bpm, whereas that for the animals given six 10-sec trials was 506 bpm. Furthermore, basal HR did not change as a function of trials in those subjects repeatedly exposed to the auditory stimulus [$F(5,45) = 2.57$, $p > .08$].

The right panel of Figure 3 shows the cardiac response to an uninterrupted 60-sec test stimulus presented 15 min after completion of the initial stimulus presentations. The auditory stimulus did not elicit a significant decrease in HR in either group, indicating that both groups had habituated to the stimulus even though there had been no evidence of habituation in the first phase of the experiment in the group receiving 60 sec of uninterrupted auditory stimulation.

There is some suggestion in Figure 3 that animals initially given six 10-sec stimulus presentations responded slightly more to the uninterrupted 60-sec test stimulus than did those animals initially given the single 60-sec stimulus, especially during the third block. If correct, these data would suggest that information about the duration of the eliciting stimulus was encoded during the initial stimulus series, and when that difference was detected an orienting response was elicited. To examine this possibility, separate repeated measures ANOVAs were conducted on each group's response in the second session. Both of these ANOVAs yielded F s < 1.0 . Moreover, a detailed inspection of the data revealed that the aberrant point seen in Figure 3 was due to a single animal whose HR decreased

nearly 75 bpm from the second to the third block. These results do not support the suggestion that the preweanlings had incorporated temporal information into their central representation of the eliciting stimulus.

Discussion

In Experiments 2A and 2B, a 60-sec auditory stimulus elicited dramatically different patterns of cardiac deceleration, a manifestation of the orienting response, in preweanling rats depending upon the temporal characteristics of the stimulus presentation. As in Experiment 1, presentation of successive 10-sec stimuli produced rapid habituation of the orienting response. In contrast, the HR response to the uninterrupted 60-sec auditory stimulus did not habituate, even partially, throughout the entire stimulus period. More importantly, when these animals were tested 15 min after the initial stimulus-presentation sequence, neither group showed an orienting response (cardiac deceleration) to either temporal pattern of stimulus presentation. This indicates that cessation of attention to an ongoing stimulus, as measured by termination of the cardiac orienting response to that stimulus, is not critical for establishing a central representation of that stimulus. These results suggest that cessation of orienting to a stimulus may not always reliably index the establishment of a neural template of that stimulus.

EXPERIMENT 3

The purpose of this experiment was to further confirm the dissociation between cessation of orienting to a stimulus and the formation of a central representation of that stimulus. In Experiments 2A and 2B, only one interval between the initial stimulus-presentation sequence and the test sequence was investigated, and it is possible that differences in the strength of the central representation established by the two types of stimulus presentation might have been masked by a ceiling effect at the short interval used in these experiments. To explore this possibility, preweanling animals were given the same temporal patterns of stimulus presentation used in Experiments 1 and 2 and then tested for habituation to the auditory stimulus either 20, 60, 240, or 1,440 min after their initial habituation session. These intervals were chosen based upon the results of a recent study on long-term retention of habituation of the orienting response (Richardson & Campbell, 1991b). In that study, it was found that retention of habituation decreased rapidly over this period in preweanling rats.

Method

Subjects. Eighty experimentally naive Sprague-Dawley rats born in the Psychology Department's vivarium at Princeton University were used as subjects. All of the animals were 16 ± 1 days old at the time of test. All housing and maintenance were the same as in Experiment 1.

Procedures. The same apparatus, auditory stimulus, and general procedures used in Experiment 1 were employed in this experiment. Following the initial stimulus-presentation sequence consisting either

of six 10-sec stimuli or one 60-sec stimulus, separate groups of animals were tested for retention of habituation to the auditory stimulus either 20, 60, 240, or 1,440 min after the initial stimulus-presentation sequence. The second stimulus session consisted of four 10-sec stimulus presentations as in Experiment 2A. During the intersession interval, all animals were returned to their home cages. The animals were returned to the test environment and allowed to adapt for 15 min prior to stimulus presentation at all four intervals.

Results and Discussion

The left panel of Figure 4 shows the initial cardiac response to the two stimulus-presentation procedures. These results replicate those obtained in Experiments 1-2. The cardiac response in the animals given six 10-sec auditory stimuli habituated rapidly, whereas that in the animals given a single 60-sec stimulus did not. The data from the four subsequently formed groups were collapsed to obtain these functions.

A mixed-design ANOVA on these data yielded a significant effect of stimulus duration [$F(1,78) = 29.91$, $p < .01$] and an effect of block [$F(5,390) = 11.30$, $p < .01$]. The interaction of stimulus duration and block was significant as well [$F(5,390) = 17.94$, $p < .01$]. Those animals given the single 60-sec stimulus presentation exhibited a larger cardiac response than those given six 10-sec trials on every block except the first.

Animals in the two stimulus-presentation conditions did not differ in terms of basal HR ($F < 1.0$). The mean HR for those animals given a single 60-sec stimulus presentation was 528 bpm, whereas that for the animals given six 10-sec trials was 525 bpm. Furthermore, basal HR did not change as a function of trial in those subjects repeatedly exposed to the auditory stimulus [$F(5,180) < 1.0$].

The cardiac response to the auditory stimulus following the four retention intervals is shown in the right panel of Figure 4. Only the response to the first 10-sec test stimulus, in which the response is maximal, is presented. There were no group differences in retention of habituation at any of the four intervals tested. Twenty minutes

Figure 4. Mean change in heart rate (in beats per minute) to 60 sec of auditory stimulation presented either in a single trial (filled symbols) or in six 10-sec trials (open symbols) and subsequent responsiveness to the same stimulus after various retention intervals (left and right panels, respectively).

after the initial stimulus-presentation procedure, neither group responded, and with increasingly longer retention intervals, the magnitude of the HR orienting response increased systematically and equivalently in both groups. These findings confirm those obtained in Experiments 2A and 2B and clearly demonstrate that animals can form a central representation of an auditory stimulus without exhibiting habituation of the cardiac component of the orienting response.

A 2×4 ANOVA (stimulus duration $\times$ retention interval) on the cardiac response to the first stimulus presentation of the second session supported these interpretations. Although the effect of retention interval was significant [$F(3,72) = 5.68, p < .01$], neither the effect of stimulus duration nor the interaction of stimulus duration and retention interval were significant (both $F_s < 1.0$). Although the animals exhibited loss of habituation over the 24-h interval, the initial stimulus-presentation procedure did not influence subsequent responsiveness at any interval.

GENERAL DISCUSSION

In all four experiments of the present study, habituation of the cardiac component of the orienting response was found to be more dependent on the *pattern* of stimulus presentation than on the total *duration* of stimulus exposure. The cardiac response of preweanling rats to a single uninterrupted 60-sec auditory stimulus showed no signs of habituating at any time during the entire 60-sec period (see also Hayne et al., in press). In contrast, when 60 sec of auditory stimulation was presented in six 10-sec blocks, the orienting response habituated rapidly, usually within four trials (see also Richardson & Campbell, 1991b).

Although most studies of habituation involve iterated stimulus presentations, there is substantial precedent for studying habituation using a single prolonged stimulus exposure. Moreover, this usage conforms with Peeke's (1984) expanded definition of habituation: "Habituation is the relatively permanent waning of response readiness as a result of repeated or *constant* stimulation" (p. 398, emphasis added). Tests of habituation of exploratory behavior in an open field have generally involved measuring a decrement in responding within a single prolonged exposure to a novel environment (e.g., Feigley, Parsons, Hamilton, & Spear, 1972). Similarly, studies of habituation of more naturalistic responses in birds and fish commonly involve a single prolonged stimulus presentation (e.g., Gallup, 1977; Peeke & Veno, 1973).

The mechanism(s) responsible for the persistent cardiac response to a 60-sec uninterrupted auditory stimulus in preweanlings remains to be resolved. One possibility is that discrete onset and offset of stimulation may be an important determinant of habituation being expressed. Regardless of the precise mechanism responsible for the observed differences in habituation of the cardiac component of the orienting response to the two patterns of stimulus presentation, the results are difficult to incorporate into contemporary analyses of the orienting response. For example,

from the Sokolovian perspective, habituation of the orienting response is a reflection of the formation of a neuronal model of the eliciting stimulus. Animals failing to exhibit signs of habituation would not be expected to have developed a central representation of the eliciting stimulus. In the present study, however, it is clear that the animals' habituation of the cardiac orienting response did not accurately reflect the formation of a neuronal model of the auditory stimulus.

One possible interpretation of these results is that they reflect a form of "latent habituation." Like the classic studies on "latent learning" (Tolman, 1932), the present study reveals a situation in which the subject's performance does not accurately reflect what it has learned. In the present instance, the response (cardiac deceleration) is elicited but learning (habituation) is not expressed, although it is co-occurring.

Although it has not been described as such, the process of latent habituation appears to underlie the findings obtained in a number of studies. For example, the startle response to intense auditory stimuli habituates relatively slowly. This effect has generally been assumed to reflect the inverse relation between stimulus intensity and rate of habituation. Borszcz et al. (1989), however, proposed a quite different interpretation for the typically slow habituation of the startle response to intense stimuli. These authors suggested that repeated presentations of an intense auditory stimulus conditioned fear to the test chamber and that the conditioned fear sensitized the animal to subsequent auditory stimuli. The resulting sensitization was hypothesized to amplify the startle response and mask the co-occurring habituation of the startle response. Borszcz et al. were able to show that habituation to the startle stimulus could be observed when conditioned fear to the test chamber was reduced by any one of a number of techniques (e.g., extinction).

A similar result is seen when a novel, innocuous tone is presented to a preweanling rat either 30 sec or 15 min after it has been placed in an unfamiliar environment, has been shocked, or has experienced a change in the environmental context. When the novel tone is presented 30 sec after any of these conditions, the orienting response does not occur, but when the same stimulus is presented to independent groups 15 min after any of the above conditions, the typical orienting response is seen (see Richardson, Siegel, & Campbell, 1988; Sakers, Richardson, & Campbell, 1990). More important, however, are the results of a recent study showing that animals in the 30-sec group encoded a neuronal model of the stimulus equivalent to that of animals in the 15-min condition (Richardson & Campbell, 1991a). Latent habituation was shown with the same technique used in the present study: When the stimulus was re-presented after a 15-min interval, subjects in both conditions exhibited complete habituation of the orienting response even though animals in the 30-sec group had not initially oriented to the auditory stimulus.

From the present results, it is clear that habituation of the cardiac component of the orienting response does not

always reliably reflect the central process of habituation. Although the cardiac responses of preweanling rats given a single 60-sec auditory stimulus did not habituate, they formed a central representation of the eliciting stimulus comparable to that of animals given six 10-sec tones who had fully habituated to the stimulus. These results are not predicted, or explained, by any current theory of the orienting response (e.g., Ohman, 1979).

The dual-process theory of habituation (Groves & Thompson, 1970) may provide an explanation for these results. According to this model, presentation of a novel stimulus produces *both* habituation and sensitization. Habituation causes a decrement in responding, whereas sensitization amplifies response magnitude. Although sensitization and other states of arousal are usually thought to be reflected by an increase in HR, there are a number of studies that have reported a marked bradycardic response to fearful, or arousing, stimuli (e.g., Jacobsen, 1979). Within this context, it is possible that presentation of a prolonged, uninterrupted stimulus produces more sensitization than does presentation of several briefer, temporally spaced stimuli (cf. Patterson & Petrinovich, 1979). In this regard, it may not be a coincidence that HR decelerations to potentially arousing stimuli have been reported primarily in studies that involved prolonged presentation of the stimulus (e.g., Jacobsen, 1979; Smith & Worth, 1980). In any case, the results of the present study agree with several others that have shown a dissociation between the central process of habituation and decrements in overt responding (e.g., Davis, 1970; Rankin & Carew, 1987). It is clear that determination of the generality of "latent habituation" and the mechanism(s) responsible for producing it is critical for our understanding of both habituation and the orienting response.

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