EFFECTS OF STIMULUS INTENSITY AND INTERTRIAL INTERVAL ON HABITUATION OF THE HEAD - SHAKE RESPONSE IN THE RAT

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ABSTRACT

EFFECTS OF STIMULUS INTENSITY AND INTERTRIAL INTERVAL ON HABITUATION OF THE HEAD-SHAKE RESPONSE IN THE RAT

By

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The present investigation was concerned with the effects of stimulus intensity and intertrial interval on habituation (response decrement due to repeated stimulation) of the head-shake response in the laboratory rat. The head-shake response is best described as a rapid rotation of the head about the front-to-rear axis, and is elicited by directing a stream of pressurized air into the ear.

Fifteen male Holtzman rats, 85 days of age, were used in a 3 x 5 within-subjects factorial design. Each subject was given one session corresponding to each possible combination of each intertrial interval and stimulus intensity resulting in 15 experimental sessions. Intertrial intervals were 1, 10 and 100 sec.; stimulus intensities were 0.5, 1, 2, 10, and 100 mm. of alcohol in a manometer. Each of the sessions consisted of ten 15-sec. trials using the air stimulus at the appropriate intertrial interval and stimulus intensity for that session,

followed by a 30 min. retention interval, and finally terminating after 5 more trials using the same intertrial interval and intensity as the first 10 trials. This design allowed for the analysis of retention of habituation as well as the course of habituation across trials within a session.

Both independent variables had major effects on habituation of the head-shake response. With respect to intensity, the greater the stimulus intensity the higher the initial head-shake response level, the greater the amount of habituation, the higher the asymptotic response level, and the slower the rate of decrement. Stimulus intensity did not appear to affect appreciably the 30-min. retention of habituation. For intertrial interval, the results showed that shorter intervals were associated with a greater amount of decrement and a lower asymptotic response level. On the other hand, intertrial interval did not affect the rate of habituation or the retention of habituation.

The general conclusion of the study was that habituation of the head-shake response in the rat appeared to be due to both a short-term decremental effect, that occurred within single stimulus presentations and took approximately 100 sec. to recover completely, and a longer-term across-trial decrement that showed only 70-80 per cent recovery after a 30 min. retention interval. This conclusion was interpreted within the context of a broad multiprocess conception of the phenomenon of habituation.

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By

Henry R. Askew

A THESIS

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To

Linda Lee,

my wife and therapist

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

Habituation is commonly defined in terms of response decrement due to repeated stimulation. This definition has features of those offered by Harris (1943), Thorpe (1956), Thompson and Spencer (1966) and Ratner and Denny (1970) in their major reviews of the topic of habituation. The broad generality of habituation across species and across different response systems in single species (Harris, 1943) serves to point out the probable importance of the phenomenon for living organisms.

Thompson and Spencer (1966) propose a number of specific characteristics of habituation. They state that these characteristics "may consequently serve as the detailed operational definition of habituation. . . ." Their list of characteristics is as follows:

1. "Given that a particular stimulus elicits a response, repeated applications of the stimulus result in decreased response (habituation). . . The decrease is usually a negative exponential function of the number of stimulus presentations."

2. "If the stimulus is withheld, the response tends to recover over time (spontaneous recovery)."

3. "If repeated series of habituation training and spontaneous recovery are given, habituation becomes sucessively more rapid (this might be called potentiation of habituation)."

4. "Other things being equal, the more rapid the frequency of stimulation, the more rapid and/or more pronounced is habituation."

5. "The weaker the stimulus, the more rapid and/or more pronounced is habituation. Strong stimuli may yield no significant habituation."

6. "The effects of habituation training may proceed beyond the zero or asymptotic response level."

7. "Habituation of response to a given stimulus exhibits stimulus generalization to other stimuli."

8. "Presentation of another (usually strong) stimulus results in recovery of the habituated response (dishabituation)."

9. "Upon repeated application of the dishabituatory stimulus, the amount of dishabituation produced habituates (this might be called habituation of dishabituation)."

Although Thompson and Spencer's (1966) list serves as a fine summary of the major phenomena and variables associated with habituation, a close examination of the literature points out many cases where several of the characteristics do not hold. For example, failures to find dishabituation (Brown, 1965; Clark, 1960; Collins, 1967), habituation of dishabituation (Wolda, 1961), potentiation of habituation (Askew *et al*., 1969; Brown, 1965), and below-zero habituation (Gardner, 1968) have recently been reported. In addition, not only do different response systems appear to differ in terms of several of these phenomena, but some of the concepts used in the list need further definition to be at all useful. This is especially true for those concepts relating to the variables such as the amount and rate of habituation. It appears, therefore, that Thompson and Spencer's

(1966) list of characteristics represents an oversimplification of a very complicated picture.

The present study will be concerned with specifying more clearly many dependent variables such as rate, amount and retention of habituation and investigating, with a well established experimental situation, the effects of two variables whose general importance for habituation are accepted but require detailed analysis in terms of each dependent variable. Specifically, the variables are stimulus intensity and intertrial interval. First, the dependant variables to be analyzed will be considered and then the effects of stimulus intensity and ITI on habituation will be reviewed.

Analysis of Dependent Variables

The language used to describe differences in habituation phenomena has been carefully considered with the result that different authors often mean different things when talking about dependent variables such as the amount and rate of habituation. Consequently, in the present study habituation phenomena will be measured and compared in terms of several standard dependent variables. Figure 1 gives an example of an habituation and a recovery session for purposes of illustrating those aspects of the situation to which the dependent variables refer.

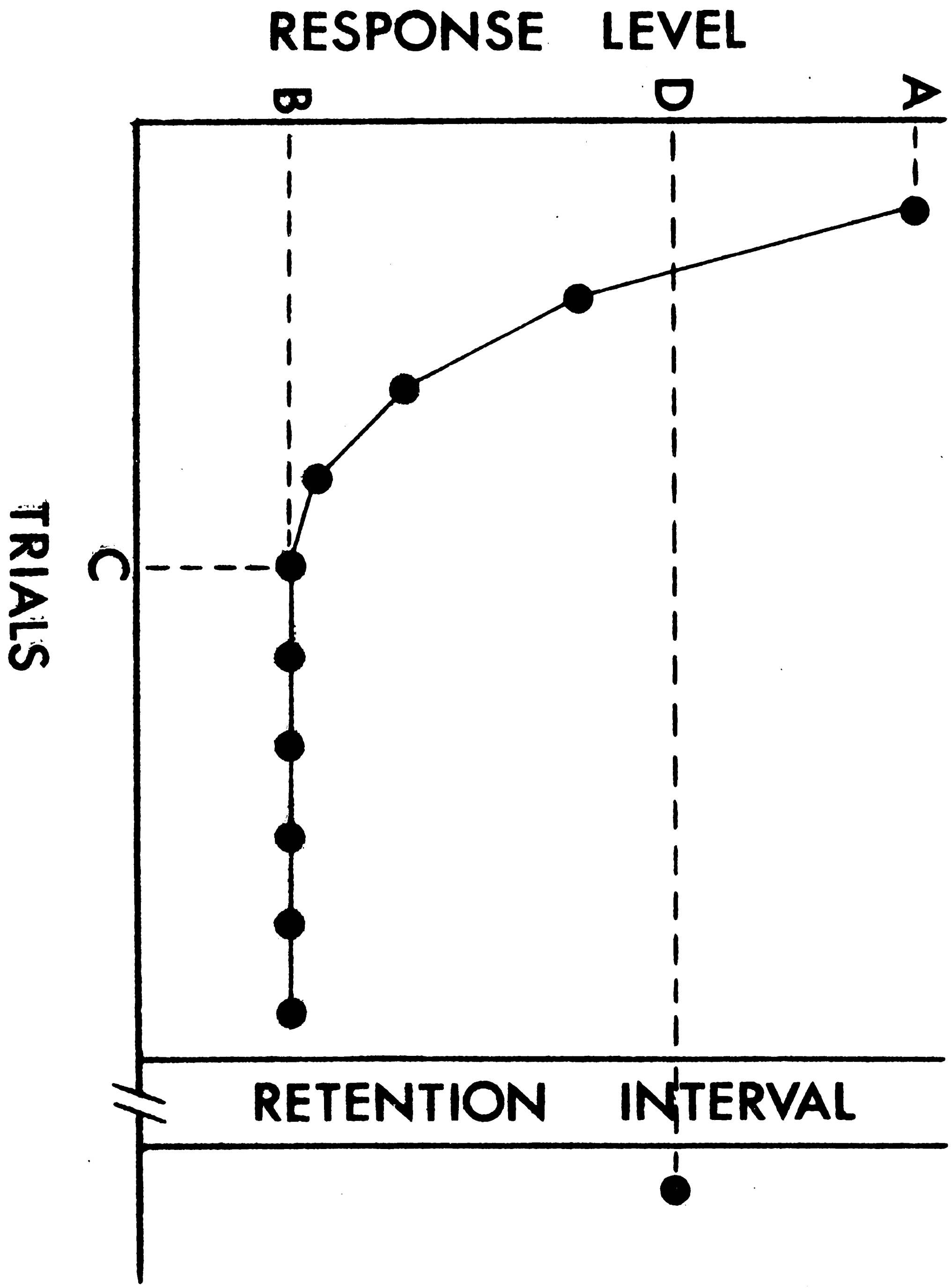

Figure 1.--Schematic representation of typical habituation and recovery sessions (see text for explanation).

First, the _initial response level_ will refer to the level of responding on the first stimulus presentation (A on Figure 1). Similarly, the _terminal response level_ will refer to the level of responding on the final stimulus presentation of the habituation session (B on Figure 1). The _amount of decrement_ will be defined as the difference between the initial and terminal response levels (A minus B on Figure 1). As a measure of the relative amount of decrement the _percent decrement_ will be defined as the percentage of the initial response level which decreases (B divided by A on Figure 1). The other measure that is useful here is how fast the decrement occurs. The _rate of decrement_ will be defined as the number of trials or the amount of time necessary before the response level falls to its asymptotic response level (C on Figure 1). In addition, the _amount of retention_ of habituation refers to the difference between the initial response level on the original session and the initial response level on some later session (A minus D on Figure 1). The _amount of recovery_ is defined as the difference between the terminal response level on the original session and the initial response level on a later session (D minus B on Figure 1). Finally, the _percent recovery_ will be defined as the percent of the decrement which recovers by some later session (D minus B divided by A minus B in Figure 1).

These concepts will be utilized in reviewing and drawing generalizations from the literature associated with the effects of stimulus intensity and intertrial interval on habituation, as well as being used with the results of the present study. A survey of the habituation literature reveals that most investigators fail to look at multiple dependent variables in spite of obtaining results that are often quite complicated. In addition, terminology is often carelessly used with little consistency across investigators. Therefore, the standard dependent variables will be used to describe the results of the studies reviewed in the present study regardless of whether the authors dealt with these aspects of their data.

Effects of Stimulus Intensity and Intertrial Interval

Virtually all authors who have dealt with habituation have observed that intensity and ITI are major variables that affect the phenomenon (e.g. Thompson and Spencer, 1966; Harris, 1943; Ratner and Denny, in press). The specific effects of these variables have not, however, been precisely spelled out. The reason for this lack of precision will become apparent in the following reviews of the literature.

Stimulus Intensity

This section summarizes some of the more comprehensive and systematic experiments on the effects of stimulus intensity on the amount and rate of habituation, the initial and terminal response levels, and the retention of habituation over a rest period.

Kuenzer (1958) investigated the habituation of the withdrawal response in earthworms to electrical stimuli as a function of stimulus intensity. He reports that the greater the intensity of the stimulus the greater the initial response level, the greater the amount of decrement, and the slower the rate of decrement to a zero asymptotic response level. In addition, this study appears to be the only one that attempted to look at the retention of habituation. Kuenzer found that after 24 hours recovery was complete for the weaker stimulation but recovery for the strong stimulation was only on the order of 75 per cent.

In a study by Miller and Murray (1966) the stimulus conditions necessary for elicitation of an "immobility" response (pause in ongoing drinking behavior) in guinea pigs were investigated. Two groups of animals were given either a 47 or 77-db. tone as the habituation stimulus. The authors report that the 77-db. group had an initial response level and an amount of decrement that were significantly greater than the lower intensity group. The rate of decrement to a zero response level was approximately the same for both groups.

Davis and Wagner (1968) looked at the effects of auditory tone intensity on habituation of startle responses in rats. Initial and terminal response level were directly related to the intensity of the tone over a range of 96-db. to 120-db. Although data directly relevant to the amount and rate of habituation were not presented in their study, a personal communication with Davis revealed that when 108-db. and 120-db. tones were compared, there did not appear to be a significant difference in the amount and rate of habituation.

Dunlop, Webster and Rodger (1966) examined amplitude changes in evoked potentials at the cochlear nucleus, inferior colliculus and medial geniculate body of unanesthetized cats to auditory stimuli. At all three locations initial and terminal response level were a direct function of stimulus intensity and significant decrement resulted for all intensities. In the cochlear nucleus and inferior colliculus there were no significant relationships between intensity and amount and rate of decrement. At the medial geniculate, however, the higher intensities produced a greater amount of habituation although there did not appear to be any difference in the time taken for the response rate to reach asymptote.

When intensity of electrical stimulation was varied, Thompson and Spencer (1966) report that the amount of habituation of a hindlimb flexion reflex in the spinal cat was greater the weaker the stimulation. Their strongest stimulus yielded no habituation. Looking at only those intensities that habituated, it appeared that the weaker stimulus showed a slower rate of decrement. It should be noted, however, that Thompson and Spencer used a percent of initial response level score which makes their results somewhat difficult to integrate with the rest of the literature.

With respect to research with humans, Prechtl (1957) investigated habituation of the head-turning response to mechanical stimuli on the face of human babies. He concludes that the response decreases to a zero level in fewer trials when a weak stimulus is used than when the stimulus is strong. Unfortunately, information on the other dependent variables is lacking in this study.

Wolfensberger and O'Conner (1965) looked at possible differences in GSR latency, amplitude and duration and EEG alpha block duration for two light intensities. Using a within-subjects design, each of these two intensities were given 12 times within the session. Although presentation of the actual data is sketchy, a complete presentation of the statistical analyses indicated that while the more intense stimulus produced a higher initial level on all four of the measures, there was no evidence that the rate and amount of decrement were different for the two (i.e., the Intensity x Repetition interaction was nonsignificant for all dependent variables).

In another study measuring components of the orienting reflex, Uno and Grings (1965) used five intensities of an auditory stimulus to investigate the effects of intensity on habituation of skin conductance, skin potential, heart rate, digital blood volume and digital pulse amplitude in humans. The design was also within-subjects with each intensity value being given five times during the session. All of the dependent variables showed a differential initial level of responding over the different intensities, although there appeared to be a large ceiling effect for the three higher intensities. In terms of the other dependent variables it appeared that higher intensities showed a higher terminal response level and a smaller amount of habituation. There did not appear to be any great difference in the rate of decrement.

It is apparent that the effects of stimulus intensity on habituation are not as simple as Thompson and Spencer (1966) suggest. The initial response level is almost always greater for higher intensities. Likewise, when the asymptotic response level reached is greater than zero (or base rate), higher intensities typically decrement to a higher asymptote. On the other hand, amount of habituation is sometimes reported to be greater, sometimes less and sometimes no different for different intensities. For rate of habituation, although most found no difference, two studies reported that weaker stimuli habituate at a faster rate and one study found that the weaker stimulus took longer to habituate. The need for more work on intensity in different stimulus-response systems is obvious.

Intertrial Interval

This section is intended to summarize what is presently known about the effects of ITI on the amount of habituation, the rate of habituation, the terminal response level reached, and the retention of habituation over a rest period.

Barrass (1961) investigated the effects of ITI on several aspects of sexual behavior of male insects (*Mormoniella vitripennis*). Nonreceptive females were presented to the males at ITIs of one-half min. to thirty minutes. Although an adequate statistical analysis is lacking it appears that sexual behavior decreased by a greater amount and to a lower asymptote the shorter the ITI. There did not appear to be a great difference in the rate of habituation between the different ITI conditions.

Prosser and Hunter (1936) compared habituation of a reflexive startle leg response in the rat when the click stimulus was repeated at intervals of 2, 5, or 15 sec. Habituation to a zero level occurred at a more rapid rate for the 2 and 5 sec. conditions than for the 15 sec. ITI. Since all conditions decreased to a zero level there was no difference in the amount of habituation.

In a study of cochlear nucleus evoked potential habituation in unanesthetized cats to an auditory stimulus by Webster, Dunlop, Simons and Aitkin (1965) it was found that habituation took place only to auditory stimuli with ITIs of .1 and 1 sec. When the ITIs were 5, 10, or 20 sec. no habituation occurred. In a follow-up study, Simons, Dunlop, Webster and Aitkin (1966) presented 80 db. click stimuli at ITIs of 1, 5, or 10 sec. to unanesthetized cats. Evoked potentials were recorded at the medial geniculate body and the inferior colliculus as well as the cochlear nucleus. At the cochlear nucleus only slight habituation occurred across the three conditions, although the three conditions were not significantly different. On the other hand, both at the inferior colliculus and the medial geniculate body a large decrement in the amplitude of evoked potentials occurred across all ITI conditions with the 1 sec. ITI producing a significantly greater amount of decrement than the longer ITIs. There did not appear to be a difference in the rate with which the decrement took place. Finally, a study by Cook, Ellinwood and Wilson (1968) substantiates these conclusions. The greater the rate of stimulation (1/10 sec., 2/sec. or 5/sec.) the greater the amount of decrement in the evoked potential response at the primary auditory cortex and the lower the asymptotic level reached. Rate of habituation, defined by the authors as the number of trials necessary for asymptote to be reached, showed no differences for the three ITIs.

In a somewhat different procedure, Brown (1965) looked at the effect of intersession interval on habituation and retention of habituation of post-rotational nystagmus in cats. Each session consisted of 10 trials with a fixed 580 sec. ITI. Different groups were given four repeated sessions at either a 1, 2, 4, 7 or 14 day intersession interval. Following the fourth session a fifth and sixth session were given 14 and 28 days later to measure retention of habituation. There were no differences between the conditions in the amount and rate of across-session decrement. However, when retention of across-session decrement was investigated there was a significantly greater amount of retention for the longer intersession intervals.

Bartoshuk (1962a) presented independent groups of 1-4 day old human neonates with forty 1 sec. 85 db. click stimuli with a fixed ITI of either 15, 30, or 60 sec. Equal amounts and rates of decrement were found for each of the conditions. However, in a follow-up study, Bartoshuk (1962b) compared a 6 with a 60 sec. ITI and found there was a greater amount of decrement for the 6 sec. condition, indicating that the negative finding in the first study was most likely the result of using too small a range of ITI values.

In a study of the head turning response in the human baby, Prechtl (1957) reports that within the range of one-half to 3 sec., habituation to the mechanical stimulus on the cheek was more rapid (took fewer trials to reach a zero level) the shorter the ITI. Due to the fact that the response level decreases to a zero level there was no difference in the amount of habituation.

In an unusual study of habituation of the GSR to a tone, Winokur, Stewart, Stern, and Pfeiffer (1962) examined the trial by trial course of the decrement with a variable 30, 60, and 90 sec. ITI. The authors note that the decrement on any trial (after the first three) was a function of the length of the preceding interval. If the previous interval was longer than the next interval, a decrease would occur. If, on the other hand, the preceding interval was shorter, some recovery of GSR amplitude occurred. The findings of this study agree with the notion that shorter ITIs produce a greater amount of habituation.

Schaub (1965) also looked at the effect of ITI on habituation of the GSR in human subjects. He varied the length of a fixed ITI between 30, 60, and 180 sec. for three groups of Ss. He also compared a fixed ITI of 70 sec. with a variable ITI with a mean of 70 sec. With respect to the fixed ITI experiment Schaub reports that only the 60 and 30 sec. ITI groups showed any evidence of habituation. For the 180 sec. group Schaub reported that the GSR amplitude actually increased rather than decreased. This finding appeared to be reliable and can be classed with studies by Franzisket (1963) and Kimble and Ray (1965) where this temporal conditioning or sensitization also occurred. A detailed discussion of this temporal conditioning effect and habituation can be found in Ratner and Denny (1970).

In Schaub's (1965) second experiment, only a slight and nonsignificant difference between the fixed and variable ITI groups resulted. Within the variable ITI group the three ITIs of 30, 60, and 120 sec. were plotted separately revealing a significant difference due to the interval since the last stimulus presentation. Thus, if the time since the last presentation was 120 sec. the mean GSR tended to be significantly higher than if the time since the last presentation was either 30 or 60 sec. These latter two values did not appear to differ. This study offers partial support to the Winekur _et al_. (1962) study previously reviewed.

Several generalizations emerge from this review of studies dealing with the variable of intertrial interval. First, studies from a number of species yield evidence that shorter ITIs result in a greater amount of decrement to a lower terminal response level than longer ITIs. On the other hand, these same studies also show that there is a very little difference, if any, between the effect of the different ITIs on the rates with which the response rate

falls to asymptote. However, two studies do not fit this pattern (Prosser and Hunter, 1936; and Prechtl, 1957). In both cases the difference between the effects of the different ITIs was in terms of the number of trials necessary for the response rate to reach a zero level. In other words, there was a difference in the rate of habituation and no difference in the amount of habituation. Possible explanations for these discrepancies will be dealt with in a later section.

Statement of the Problem

The experimental situation that is used in the present study is the head-shake response (HSR) in the rat elicited by a stream of pressurized air directed into the ear. Previous work by Askew, Leibrecht and Ratner (1969) and Leibrecht and Askew (in press) have established the advantages of this experimental situation for studying habituation. Briefly, the HSR can be easily elicited, easily identified, has a low base rate, can be adequately characterized by frequency of occurrence alone, is highly reliable, and occurs in a wide variety of species.

Specifically, the present study will use a within-subjects factorial design to investigate the effects of stimulus intensity and ITI on habituation of the HSR. The fact that there are no appreciable carry-over effects after 24 hours (Askew et al. 1969), coupled with the large but

reliable individual differences in the HSR lead to the within-subjects design as the most efficient and powerful approach.

METHOD

Subjects

The Ss were 15 male Holtzman albino rats 85 days of age. All Ss had been reared in group cages, had been fed and watered ad lib, and were experimentally naive. The Ss were received in the laboratory 15 days prior to the onset of the experiment and were housed in group cages under conditions of constant illumination and temperature until the experiment was completed.

Apparatus

Movement of the animals was restricted by placing them upon an elevated 2 x 6.5 in. platform (constructed of one-fourth in. hardware cloth) 29 in. above the floor. Hanging downward and sloping outward at an angle of 10° from the edges of the platform were sections of galvanized sheet metal, forming a "collar" 10 in. long to discourage escape attempts. The base of the wooden column which supported the platform was mounted on a lazy susan ball bearing so that the entire test stand could be rotated in either direction.

The test stimulus consisted of pressurized air from a Silent Giant aquarium pump (Model 120) delivered through a hand-held rubber tube with an inside diameter of 1 mm. Two adjustable valves were placed in the tube such that the air pressure at the end of the tube could be precisely regulated. Pressure was measured by placing the end of the tube 1 mm. from the end of an open manometer with an inside diameter of 1.5 mm. The manometer contained enough alcohol to form 12 cm. columns on both sides. This system resulted in a range of possible intensities varying from a zero to a 14 cm. deflection in the column of alcohol. It should be noted that a low-frequency, low-intensity "humming" sound was produced by the pump and carried through the tube, providing a complex air-tone stimulus.

Electromechanical relays and timers were used to time intervals and operate signal lights. Head-shake responses were recorded on a Gerbrands event recorder.

Procedure

The HSR was elicited by moving the air stimulus back and forth across the center of the left ear of the rat at an approximate rate of three cycles per sec. The distance of the tube from the ear was three-eighths to one-half inch and the locus of stimulation was approximately three-eighths inch wide. Whenever _S_ moved its head an appreciable distance during stimulation, _E_ moved his hand accordingly to keep the stimulus directly in _S_'s ear. If _S_ turned around on the stand, _E_ rotated the stand until _S_ was again in the proper orientation, at which time the normal stimulus pattern was resumed. E practiced during previous experiments (Asket et al., 1969; Leibrecht and Askew, in press) and became relatively proficient in maintaining the correct ear to test stimulus relationship for all but the most drastic movements on the part of S. (Distributed practice for an hour or two is probably sufficient to reliably deliver the stimulus).

Prior to the onset of the experimental conditions Ss were given a pretest to determine their reactions to the experimental situation. The pretest consisted of five 15 sec. trials with the most intense stimulus (100 mm.) and the shortest intertrial interval (1 sec.). These values were used because they appeared to produce the strongest competing responses of any of the conditions. If a subject showed vigorous escape behavior such as repeatedly jumping off the stand or constantly turning around on the stand it was rejected. A total of three animals were rejected; two for repeatedly climbing off the stand and the other for a repeated wiping of the stimulated ear with its paw.

The variables of ITI and stimulus intensity were manipulated in a 3 x 5 within-subjects factorial design. The ITIs of 1, 10 and 100 sec. were combined with stimulus intensities of 0.5, 1, 2, 10, and 100 mm. of alcohol such that for each subject on each test-retest pair of sessions all trials were given with the same ITI and intensity.

Therefore, each subject was given one pair of sessions corresponding to each of the 15 different combinations of the two independent variables. The interval between the 15 pairs of sessions was 24 hr. with each subject being given the 15 experimental pairs of sessions in a randomly determined order.

Each pair of sessions began with S being placed on the stand and being allowed 5 min. to adapt to the stand. S was then given 10 trials and was returned to its home cage 4 to 6 ft. away from the test stand. After spending 25 min. in its home cage S was returned to the stand for the retest session, given another 5 min. adaptation period without stimulation and then given 5 additional trials with the same ITI and intensity as was used for the preceding test session. This test session-30 min. rest-retest session design was used to investigate retention of habituation.

Twenty-four hours after the completion of the last of the 15 experimental pairs of sessions, each subject was given a base rate control session consisting of 10 trials with a 10 sec. ITI and a zero stimulus intensity. The tube was moved back and forth next to the ear, as in preceding sessions, but the air stream was directed away from the head. This procedure resulted in the auditory and visual components of the stimulus without the mechanical component. HRSs were recorded on this control session as on any other session.

Electromechanical relays and timers operated signal lights which indicated to E when the stimulus onset and offset was to occur. E held a small microswitch in his left hand which was used to record HSRs on the Gerbrands event recorder. The electromechanical equipment was mounted in a sound attenuating box which, coupled with a background white noise level of 75 db., made the sound from the equipment virtually inaudible.

Scoring of the data was done by placing a transparent plastic template over each trial recorded on the event recorder paper. As well as showing deflections corresponding to HRSs the record also indicated on another channel the points of stimulus onset and offset. The template divided the 15 sec. stimulus presentation into five 3-sec. time periods and the data were then recorded on data sheets as the number of HSRs occurring during each 3-sec. time period on each trial.

RESULTS

The data analyses consisted of scoring each subject's performance on each session in terms of the several dependent variables that were discussed in the introduction. Then each of the dependent variables was statistically analyzed using a 3-way single observation per cell repeated measures analysis of variance (Winer, 1962, p. 290) with fixed factors of ITI and Intensity and a random factor corresponding to Subjects. For tests of the main fixed effects, the double interaction with Subjects was used as the error term. Similarly, the triple interaction was used to test the ITI x Intensity interaction. Since there was no within-cell variance estimate the Subjects effect and interactions involving Subjects could not be tested.

Preliminary inspection of the homogeneity of covariance assumption showed that it was not appreciably violated. On the other hand, the assumptions of homogeneity of variance and normality were violated for most of the dependent variables although the magnitude of the violations could generally be classified as moderate to mild (Boneau, 1960). However, since an *N* of 15 is of moderate size and since all cells in the analyses have equal *N*s it appeared that violations

of these assumptions would not greatly affect the true probability of making a type I error (Boneau, 1960; Hays, 1963). To be on the safe side, however, a conservative strategy of using a reduced level of significance was followed. An additional factor contributing to the need to lower the level of significance was the procedure of handling several dependent variables separately. This is a problem because with each dependent variable analyzed (after the first) the true overall alpha level becomes higher than that specified for each test. Due to these two considerations, a level of significance of .005 will be used throughout.

Before dealing with effects of intensity and ITI on across-trial decrement several general findings must be examined. Averaging across all intensities and ITIs there was a significant amount of decrement (t=7.3, df = 14, p<.005), amount of recovery (t = 9.7, df = 14, p<.005), and amount of retention (t = 6.00, df = 14, p<.005) over the 30 min. intersession interval. The relative amount of decrement (percent decrement) was approximately 41 per cent and the relative amount of recovery (percent recovery) was approximately 75 per cent. When the amount and rate of decrement on the five retest trials (trials 11-15) were compared with the same measures from trials 1-5, there were no significant differences (t = 2.58, df = 14, p>.005 and t = 1.50, df = 14, p>.005) indicating that there were no reliable "savings" effects in spite of the fact that the response level started significantly lower on trial 11 than it was on trial 1.

Effects of Stimulus Intensity on Across-Trial Decrement

Figure 2 gives the mean number of HSRs per trial as a function of trial number and stimulus intensity for the 10 test trials and the 5 retest trials. This figure is presented for descriptive purposes only with the actual statistical analysis being carried out on several dependent variables that characterize different aspects of the picture shown in Figure 2. The major results of the analyses of variance of seven dependent variables are shown in Table 1. It should be noted at this point that the base rate condition was not included in the analyses of variance since it was not given in a random order with the other conditions and only one intertrial interval was used for the control session. It should also be noted that the Eta^2 statistic is presented in the table. Eta^2 is calculated by dividing the sum of squares for the effect being tested by the total sum of squares. Hence, this statistic represents that proportion of the total variance in each analysis of variance which is accounted for by that particular effect. This statistic should be interpreted carefully, however, since it is closely related to the number of other effects being tested and the ranges of values of the independent variables employed in this particular study.

TABLE 1--Means for across-trial decrement as a function of stimulus intensity.

	Base Rate	0.5	1	2	10	100	F	P(4/56)	Eta^2
Initial level on trial 1 (#HSRs)	.30	.27	1.36	2.91	4.47	4.64	71.45	<.001	.569
Terminal level on trial 10 (#HSRs)	.20	.24	.62	1.53	2.04	1.91	44.15	<.001	.361
Amount of across-trial decrement (#HSRs)	.07	.02	.73	1.38	2.42	2.73	27.72	<.001	.317
Percent decrement	26.7	16.7	42.2	44.5	50.0	54.3	10.02	<.001	.124
Rate of across-trial decrement (# trials)	1.27	1.22	2.20	2.96	3.73	3.67	16.02	<.001	.187
Amount of retention (HSRs)	.27	-.07	.29	.49	.73	1.00	6.79	<.001	.089
Amount of recovery (#HSRs)	-.07	.09	.44	.89	1.69	1.73	14.45	<.001	.196
Percent recovery	86.7	86.7	80.1	73.8	67.1	69.4	<1	NS	

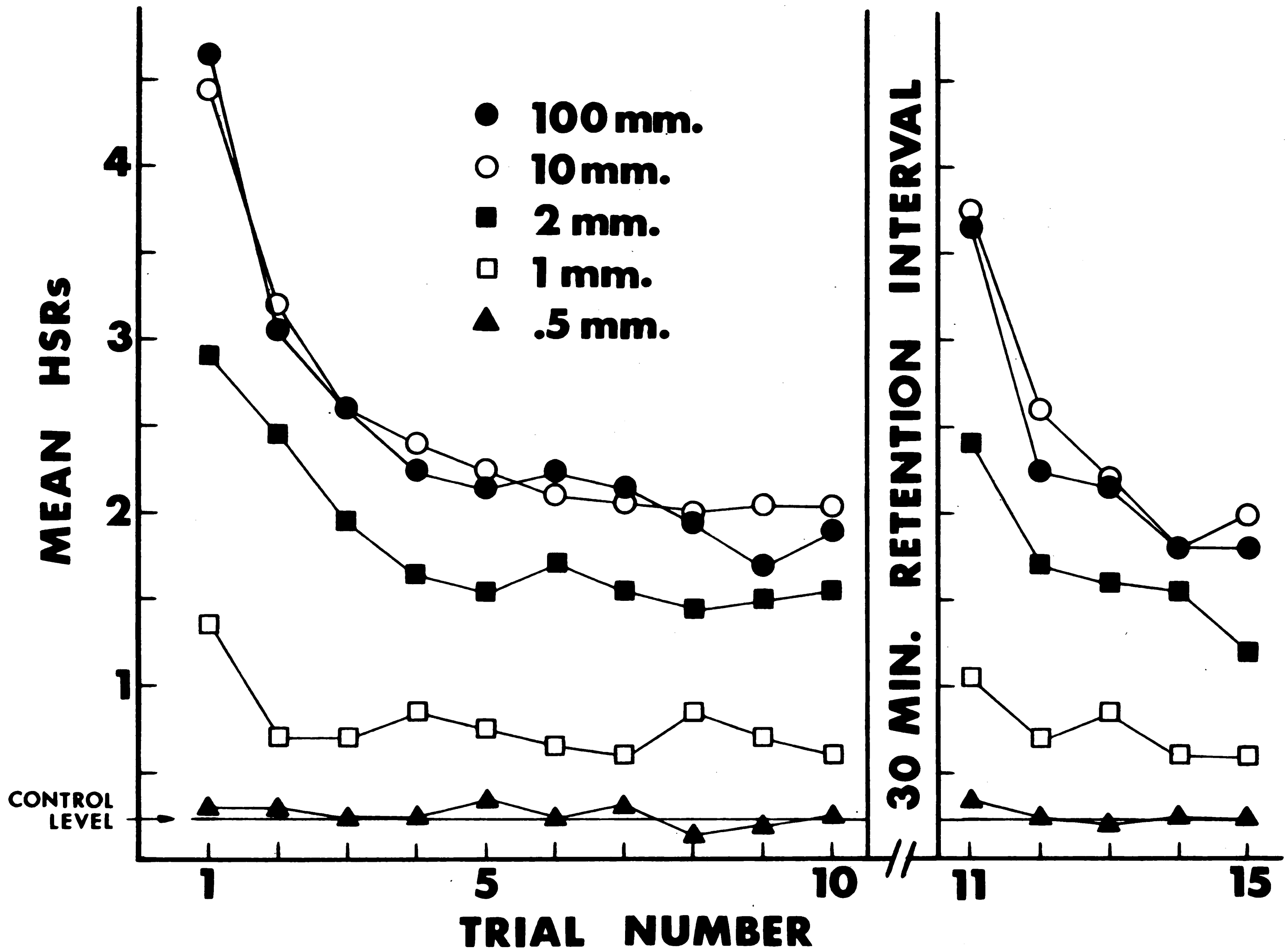

Figure 2.--Mean number of HSRs per trial as a function of trial number and stimulus intensity for the 10 test trials and the 5 retest trials.

Of interest first is the <u>initial HSR level</u>, which consisted of the number of HSRs on trial 1. The results indicated that the initial HSR levels differed significantly. Inspection of Figure 2 shows that the greater the intensity of the stimulus the higher the initial level of responding. As can also be seen from this figure, the range of intensities employed appeared to cover the effective range of the intensity variable with the lowest intensity (0.5 mm.) approximately equal to the control level and an apparent "ceiling" being reached at the higher intensities with only a slight increment in response level resulting from increasing the intensity from 10 to 100 mm. Figure 3 gives the initial HSR level (number of head-shake responses on trial 1) as a function of stimulus intensity for the 15 individual subjects. The mean curve is also shown on the figure. Individual curves were plotted to determine whether, the relationship between intensity and initial HSR level is truely incremental within subjects, or whether it is merely a result of an all-or-none within subject response system with a simply a greater proportion of subjects responding as a function of greater intensity. Inspection of this figure showed that most subjects did, in fact, show increased responding with increased intensity. The mean curve does, therefore, accurately characterize performance of individual <u>S</u>s.

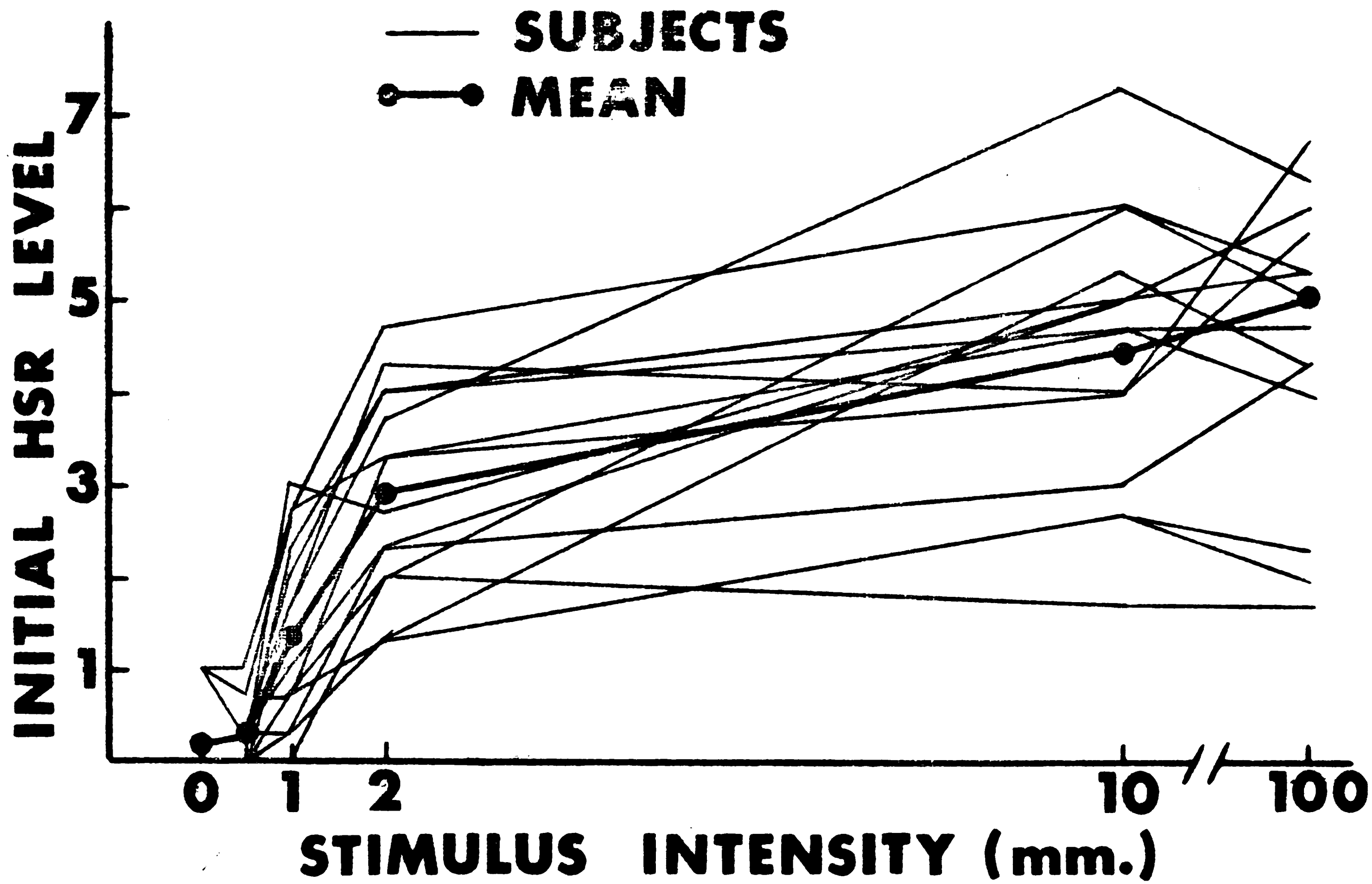

Figure 3.--Initial HSR level as a function of stimulus intensity for the 15 individual subjects.

In terms of across-trial decrement, the terminal HSR level on trial 10 was subtracted from the initial HSR level on trial 1 yielding a measure of the amount of across-trial decrement which was highly significant as a function of stimulus intensity. The greater the stimulus intensity the greater the amount of decrement. There was also a significant difference among intensities in the percent decrement with the higher intensities resulting in a greater relative decrease. However, inspection of the means in Table 1 and the curves in Figure 2 indicated that the difference may be the result of the 0.5 mm. condition failing to show any decrement and therefore obtaining a mean percent decrement score that was much lower than the other conditions. A Duncan multiple range test on these five means showed that while the 0.5 mm. condition differed significantly from all other conditions, the other four intensities did not differ significantly from each other. In other words, for those four intensity conditions that showed appreciable decrement, there did not appear to be a major difference in the relative amounts of decrement that occurred. Finally, inspection of the terminal HSR level on trial 10 showed that it is greater than base rate for all but the least intense stimulus. As shown in Table 1, the terminal HSR levels were significantly different for the different intensities.

Another aspect of this situation that needs to be to be analyzed is the rate of across-trial decrement. The need for a separate rate measure is evident when one considers the possibility that different conditions may be equal in initial level, amount of decrement and terminal level but still be very different insofar as they may differ in the rate with which the HSR level reaches asymptote. As a measure of the rate of across-trial decrement the trial number on which the HSR level first became equal to or less than the asymptotic response level was used. Asymptotic response level was defined as the terminal HSR level on trial 10. Therefore, a score of 3 on the rate of decrement measure indicated that trial 3 was the first trial where the HSR level first was less than or equal to the terminal HSR level. Hence, the smaller the decrement score the faster the rate of decrement. As shown in Table 1, the intensity conditions differed significantly in terms of the number of trials necessary to reach asymptote. The more intense the stimulus the greater number of trials it took to reach asymptote (or the slower the rate of across-trial decrement).

Another aspect of the effects of stimulus intensity on across-trial decrement concerns retention of the decrement over the 30 min. intersession interval between the test and retest sessions. The results of statistical analyses of three measures of retention are given in Table 1. From these analyses we see that the greater the stimulus

intensity the greater the amount of retention defined as the difference between the HSR level on trial 1 and the HSR level on trial 11 (the first trial after the retention interval). Secondly, there was significant difference across the different intensities in the amount of recovery defined as the difference in the HSR levels on trials 10 and 11 (immediately preceding and following the intersession retention interval). Finally, there was no significant difference between the intensities with respect to the percent recovery of across-trial decrement. This measure is simply the amount of recovery of decrement divided by the total amount of decrement.

Summary

As can be seen in Figure 2, associated with an increase in the intensity of the air stimulus were an increase in the initial HSR level, an increase in the amount of across-trial decrement, an increase in the terminal HSR level, and a decrease in the rate of across-trial decrement. In addition, an increase in intensity was also significantly related to an increase in the amounts of retention and recovery of the decrement although the percent of the original decrement recovered showed no change.

Effects of Intertrial Interval on Across-Trial Decrement

Figure 4 gives the mean number of HSRs per trial as a function of trial number and intertrial interval. As

in the previous section the statistical analysis was carried out on several dependent variables which represent different aspects of the picture shown in Figure 4. The major results of the statistical analyses are shown in Table 2.

First, there was no significant difference in the initial HSR level as a function of the three ITI values. This result is to be expected since these different conditions could not express themselves until after the first trial had been completed. Thus, it can be concluded that the groups did not differ before the variable of ITI was introduced.

With respect to across-trial decrement, there was a significant difference in the amount of across-trial decrement (number of HSRs on trial 1 minus the number on trial 10) as a function of ITI. The relationship consisted of a significantly greater amount of decrement the shorter the ITI. Since there was no difference in the initial HSR level on trial 1 and there was a significant difference in the amount of across-trial decrement, it was expected that the terminal HSR level would be different for the three ITIs. As can be seen in Table 2 this was the case. In addition, although there was a tendency for a greater percent decrement to be associated with shorter ITis, this result was not quite significant.

Although there was a highly significant difference in the amount of across-trial decrement there was no

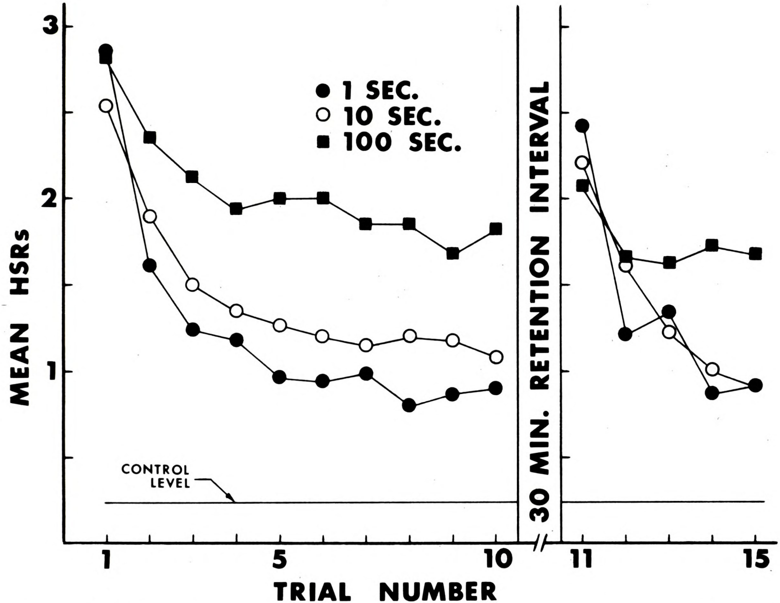

Figure 4.--Mean number of HSRs per trial as a function of trial number and intertrial interval for the 10 test trials and the 5 retest trials.

TABLE 2--Means for across-trial decrement as a function of intertrial interval.

	1	10	100	F	P(2/28)	Eta^2
Initial level on trial 1 (#HSRs)	2.84	2.53	2.81	2.48	NS	-
Amount of across-trial decrement (#HSRs)	1.93	1.45	.99	23.35	<.001	.046
Percent decrement	50.4	41.3	32.9	5.11	NS	-
Terminal level on trial 10 (#HSRs)	.91	1.08	1.83	31.44	<.001	.111
Rate of across-trial decrement (#trials)	2.65	2.89	2.72	1	NS	-
Amount of retention (#HSRs)	.41	.32	.73	2.69	NS	-
Response level on trial 11 (#HSRs)	2.43	2.21	2.08	3.52	NS	-
Amount of recovery (#HSRs)	1.52	1.13	.25	39.50	<.001	.127
Percent recovery	81.1	84.8	60.4	4.09	NS	-

significant difference in the rate of across-trial decrement. This result can be seen upon careful inspection of Figure 4: there does not, in fact, appear to be major difference in the number of trials necessary for the HSR level to reach the different asymptotes.

Turning to the retention of across-trial decrement, there was no significant difference in the amount of retention of across-trial decrement (defined as the difference between the HSR levels on trials 1 and 11). Coupled with the previously reported finding of no difference in the initial HSR level on trial 1, this result indicates that while the different ITIs caused large differences in the amount of across-trial decrement, recovery occurred to approximately the same level for all three conditions. An analysis of the HSR level on trial 11 did not, in fact, show a significant difference between ITIs. These findings were also reflected in the highly significant difference in the amount of recovery. With respect to percent recovery, although there was a trend favoring a greater percent recovery for the shorter ITIs, this result did not quite reach significance at the .005 level.

Summary

The results showed that the shorter the ITI the greater the amount of decrement and the lower the asymptotic level of responding. There was, however, no difference in the rate with which the decrement occurred. In spite of large

differences for the different ITIs in the amount of decrement, the HSR level appeared to recover to approximately the same level after a 30 min. intersession interval.

Interactions between Stimulus Intensity and ITI

Only the Intensity x ITI interaction for the amount of recovery was significant (F = 4.18, df = 4/56, $p < .005$). This interaction was the result of the failure of intensity to affect the amount of recovery for the 100 sec. ITI condition. All intensities showed only slight amounts of recovery for the 100 sec. condition, while there were large differences in the amount of recovery as a function of intensity for the two shorter ITIs. The Intensity x ITI interactions for all of the other dependent variables associated with across-trial decrement were not significant.

Effects of Stimulus Intensity on Within-Trial Decrement

The previous sections have dealt with the decrement that occurred across the 15 trials. In the case of within-trial decrement, the concern is with the decrement in responding which occurred during the course of single 15 sec. presentations of the air stimulus. Specifically, the analysis of within-trial decrement parelleled that of across-trial decrement with the major difference being that trials 1 and 2 were treated as if they were test-retest sessions. The aim of this analysis was to look at the amount and rate

of decrement on trial 1, and the retention of the within-trial decrement as measured by the responsiveness on trial 2. For purposes of looking at within-trial decrement, the 15 sec. trials were divided into five 3-sec. time periods and the number of HSRs within each of these time periods served as the raw data.

Figure 5 shows the mean number of HSRs per 3-sec. time period as a function of intensity for several representative trials. By treating trial 1 as if it were a typical habituation session several dependent variables can be examined. As before, the results of the statistical analyses are shown in Table 3. The difference in the HSR rate previously observed across the whole of trial 1 is also apparent on time period 1 of trial 1. As can be seen the difference in the <u>initial HSR level</u> on time period 1 of trial 1 among intensities was highly significant. Similarly, significant differences in the <u>amount of within-trial decrement</u> (the difference in HSR level between time periods 1 and 5 of trial 1), the <u>terminal HSR level</u> on time period 5 of trial 1, and <u>rate of within-trial decrement</u> (number of 3-sec. time periods necessary before the HSR level first reaches the terminal HSR level) also occurred. All of these differences paralleled those found with across-trial decrement: i.e., associated with an increase in stimulus intensity was an increase in the terminal HSR level, an increase in the amount of within-trial decrement, and a decrease in the rate of within-trial decrement.

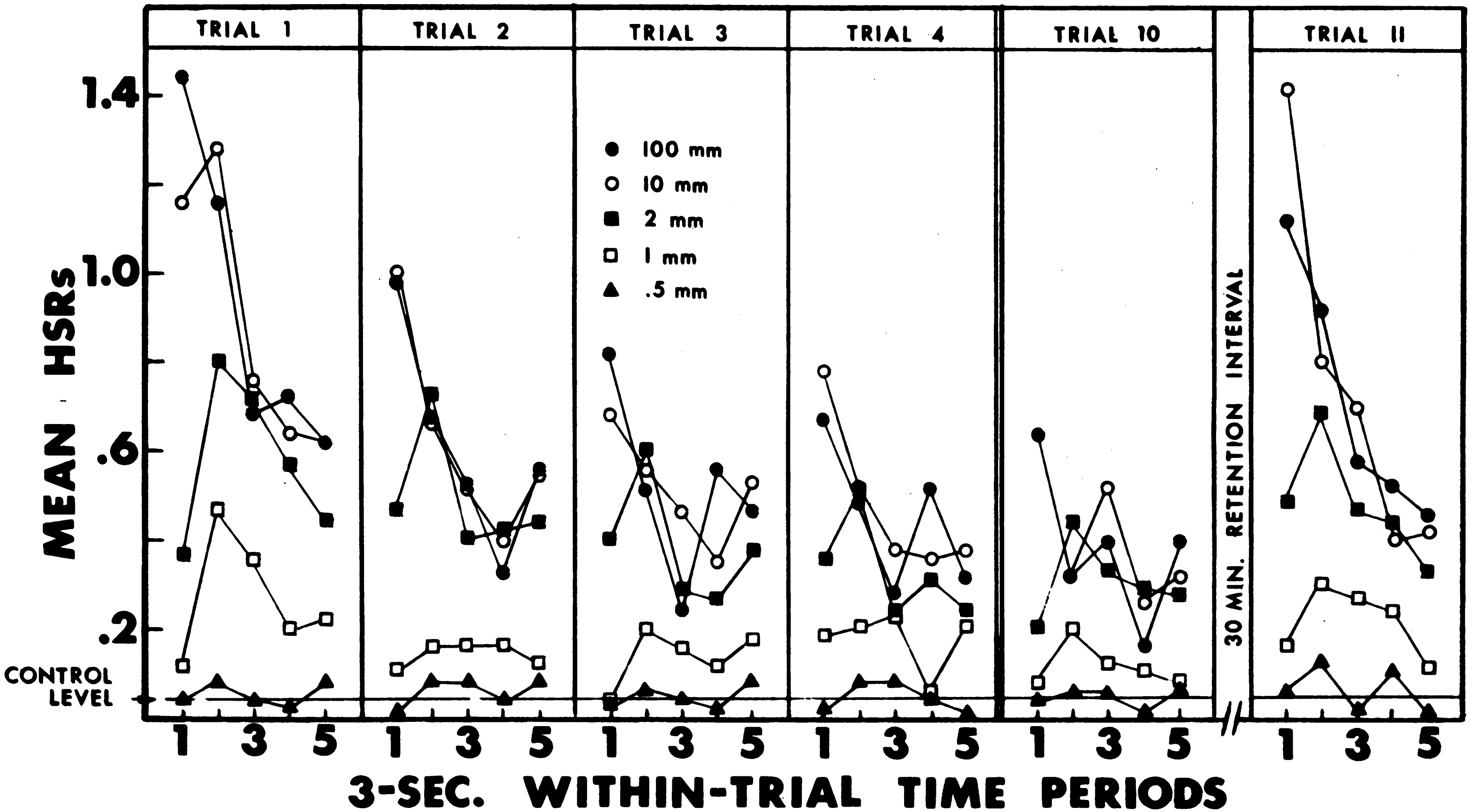

Figure 5.--Mean number of HSRs per 3-sec. time period as a function of stimulus intensity for several representative trials.

TABLE 3--Means for within-trial decrement as a function of stimulus intensity.

	Base Rate	Intensity (mm.) 0.5	1	2	10	100	F	P(4/56)	Eta^2
Initial level on time-period 1 (#HSRs)	0	.04	.11	.38	1.16	1.44	25.96	<.001	.383
Amount of within-trial decrement (#HSRs)	0	-.04	-.11	-.07	.53	.82	8.18	<.001	.154
Terminal level on time-period 5 (#HSRs)	0	.08	.22	.22	.62	.62	6.97	<.001	.125
Rate of within-trial decrement (#time periods)	1.0	1.04	1.09	1.36	2.07	2.18	15.45	<.001	.200
Amount of between-trial retention (#HSRs)	-.07	.04	0	-.09	.09	.47	3.10	NS	-
Amount of between-trial recovery (#HSRs)	.07	-.09	-.11	.02	.44	.36	4.24	<.005	.074

One unexpected finding here was the shape of the within-trial decremental functions for the 1 and 2 mm. intensity conditions. Maximum HSR levels occurred not on the first 3-sec. time period but on time period 2. This finding appeared to be highly reliable by virtue of the fact that it continued to occur on all of the trials shown in Figure 5. Equally interesting is why this shape did not occur for the more intense 10 and 100 mm. conditions. A plausible explanation in terms of competing responses will be dealt with in a later section.

Another aspect of this analysis is the amount of retention of within-trial decrement from trial 1 to trial 2. First, as shown in Table 3 there was no significant difference in the <u>amount of between-trial retention</u> (defined as the difference in HSR level between time period 1 of trials 1 and 2). On the other hand, when the <u>amount of between-trial recovery</u> (defined as the difference between the terminal HSR level on time period 5 of trial 1 and the initial HSR level on time period 1 of trial 2) was examined, the greater stimulus intensities resulted in a greater amount of recovery. The failure to find a significant difference in the amount of retention may simply reflect the inappropriateness of the dependent variable used given the differing shapes of the curves for different intensities rather than a true difference.

Summary

The effects of stimulus intensity on within-trial decrement were essentially the same as on across-trial decrement with the higher intensities being associated with a higher initial HSR level, higher terminal HSR level, greater amount of decrement and a slower rate of decrement. Also, in both cases higher intensity was associated with a greater amount of recovery. However, two differences between within-trial and across-trial decrement as a function of intensity resulted. First, higher intensities resulted in a significantly greater amount of retention for the across-trial decrement, and although the trend was in this direction for the within-trial decrement, this result was not statistically significant. And second, the interaction between intensity and shape of the habituation function only occurred for within-trial decrement.

Effects of Intertrial Interval on the Retention of Within-Trial Decrement

Figure 6 presents the mean number of HSRs per 3-sec. time period as a function of intertrial interval for several trials. Of major interest here was an analysis of retention of within-trial decrement as a function of the different ITIs. As before, trials 1 and 2 are being treated as if they were test-retest sessions and the recovery of within-trial decrement is being investigated for recovery

intervals of varying lengths corresponding to the three ITIs. The major results of the statistical analyses are shown in Table 4.

TABLE 4--Means for the retention of within-trial decrement as a function of intertrial interval.

	ITI (Sec.) 1	10	100	F	P(2/28)
Amount of between trial retention (#HSRs)	.25	.11	-.05	3.20	NS
Amount of between-trial recovery (#HSRs)	-.01	.19	.20	1.13	NS

Although there was clearly no significant effect of ITI on the <u>amount of between-trial recovery</u> there was a slight trend for a greater <u>amount of between-trial retention</u> although this trend was also not significant. Looking beyond the first two trials on Figure 6, however, this trend becomes more reliable. It appeared that with a 100 sec. ITI there was considerable between-trial recovery with the initial HSR level on each trial being relatively high. With respect to the 1 and 10 sec. ITIs, large amounts of recovery between trials did not appear to take place. The significant difference between ITIs in across-trial decrement appears then to be a function of differential between-trial recovery, with different response levels on the beginning of each trial, but falling to the same terminal level by the end of each trial.

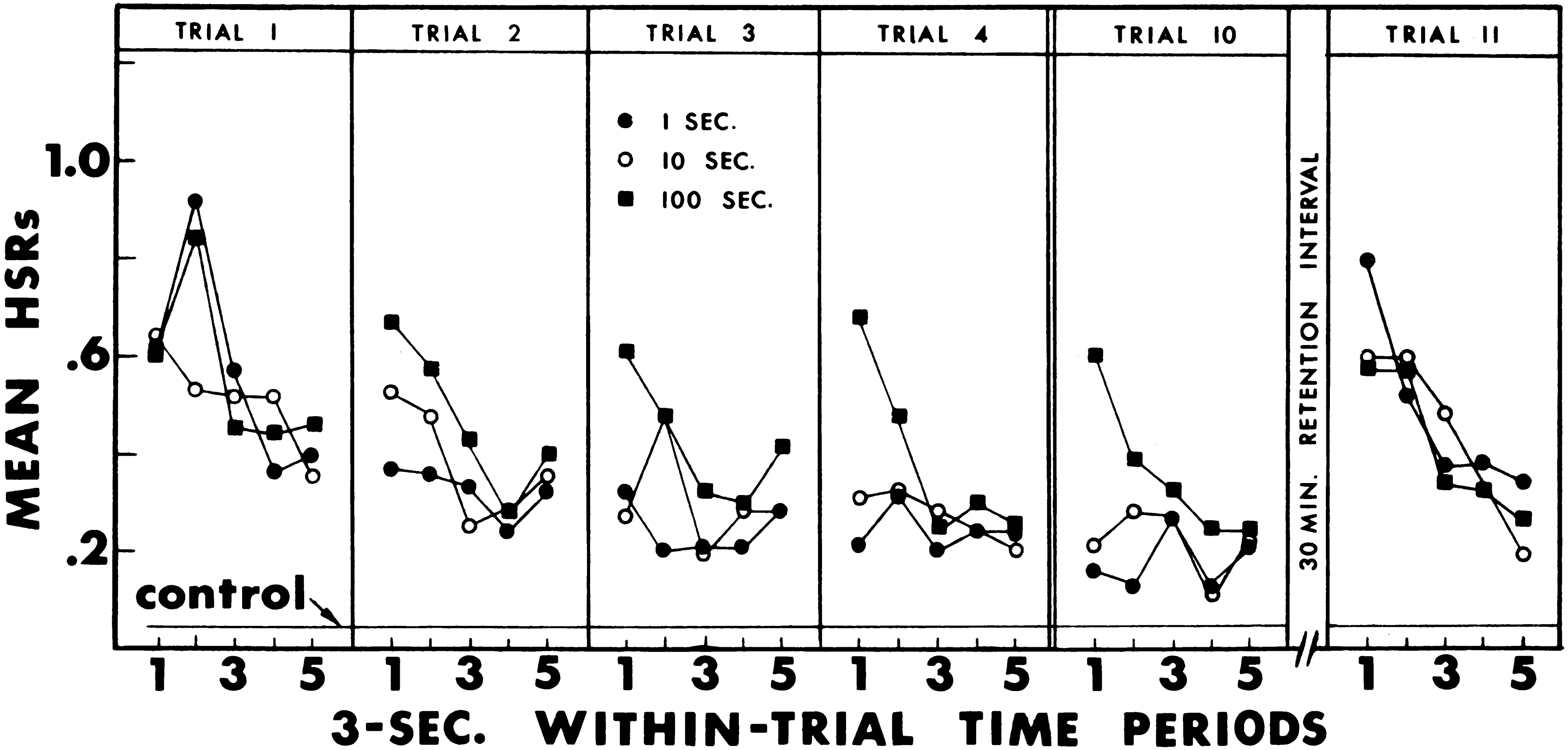

Figure 6.--Mean number of HSRs per 3-sec. time period as a function of intertrial interval for several representative trials.

Summary

The different ITIs appeared to differ with respect to the degree to which recovery occurred during the interval, with a large amount of recovery occurring for the 100 sec. condition and much less for the 10 and 1 sec. conditions. Apparently, a good deal of the decrement that occurred within single trials was relatively short-term, recovering rather quickly after termination of the stimulus.

Interactions between Stimulus Intensity and ITI

There were no significant Stimulus intensity x ITI interactions for any of the dependent variables associated with within-trial decrement and between-trial recovery.

DISCUSSION

The greater the stimulus intensity in the present study the greater the initial HSR level. This result agrees well with previous studies (e.g. Kuenzer, 1958; Miller and Murray, 1966; Dunlop et al., 1966; Davis and Wagner, 1968) and supports the general finding that increasing the intensity of a stimulus typically increases the eliciting value of that stimulus. A related finding here is the different shapes of the within-trial habituation functions for the different intensities that were observed in the present study. This result appears to be explained by postulating an interaction between stimulus intensity and the response hierarchy such that with increasing intensities, the response tendency to shake the head becomes proportionally stronger than competing response tendencies. A likely candidate for such a competing response would be turning the head and orienting toward the air stimulus. Animals were frequently observed to make this response during the early part of the stimulus presentation, but, unfortunately, no data were available to assess the possibility that the frequency of

of this response differed as a function of stimulus intensity. Regardless of the specific nature of such a competing response, its effect would be to increase latency and thereby reduce the frequency of the HSR during the first few seconds of the trial.

The finding of a greater amount of decrement with more intense stimuli in the present study agrees with studies by Kuenzer (1958), Miller and Murray (1966) and Dunlop et al. (1966). It disagrees with studies by Uno and Grings (1965) and Thompson and Spencer (1966) who obtained the opposite result. A possible explanation for these differences is in terms of the dependence of the amount of decrement measure on the initial response level such that if there is some sort of "ceiling" imposed on the initial response level at the beginning of the session, and if the usual differences in terminal level occurred, there would be a greater amount of habituation for the less intense stimuli. Although Thompson and Spencer (1966) do not present enough information to evaluate this possibility, Uno and Grings (1966) findings indicate that there does, in fact, appear to be a ceiling on the initial level such that large increases in intensity did not result in increases in initial response level. This argument is speculative, however, and more studies manipulating intensity will be required before it can be properly evaluated.

Turning to the rate of across-trial decrement, the finding in the present study of a faster rate with weaker stimuli agrees with findings by Kuenzer (1958) and Prechtl (1957). However, most of the studies reviewed found no differences in the rate of decrement. Examination of the differences between previous studies that did and did not report differences in the rate of decrement seems to implicate the terminal level. Specifically, in the two studies that did find differences in rate, decrement for all intensities occurred to a zero level. On the other hand, where the decrement did not occur to a zero level the different intensities showed different terminal response levels and no differences in the amount of time it takes the response level to reach asymptote. The only exception to this pattern is that found in the present study where there were differences in asymptote and also differences in the rate of decrement. The results of this study may be partially reconciled with the rest of the literature if the nature of actual rate of decrement measure employed is examined. Specifically, if a subject did not show any decrement from trial 1 to trial 10 a rate score of 1 was given, indicating that the subject was as low or lower than the terminal HSR level on trial 1. The effect of this strategy was that the rate of decrement scores for the two lower intensity conditions were very low. Looking just at the three higher intensity conditions where the decrement resulted for all subjects, it does not,

in fact, appear that the rate of decrement changes very much as a consequence of intensity. The difference in rate, then, may be in large part a result of differential proportions of subjects showing decrement with different intensities rather than a rate difference among subjects that showed decrement.

A major conclusion that can be drawn from the preceding discussion is that the effects of stimulus intensity on habituation are not as simple as Thompson and Spencer (1966) imply. There are frequent differences among studies in the way intensity affects the initial response level, terminal level, and the amount and rate of decrement. It is the contention of the present author that these complexities are due to differences in the nature of the different stimulus-response systems employed, and in particular differences in how intensity affects the initial and terminal levels.

Turning to the other major independent variable, the effects of intertrial interval on the amount of across-trial habituation, the rate of across-trial decrement and the terminal HSR level are in line with the major portion of the literature. Specifically, shorter ITIs resulted in a greater amount of decrement and a lower terminal HSR level but there was no difference in the rate of decrement. Only the studies by Prosser and Hunter (1936) and Prechtl (1957) do not fit this pattern. In both cases the difference

between the different ITIs was in terms of the number of trials necessary for the response rate to reach a zero response level, resulting in a difference in the rate of habituation and no difference in the amount of habituation. These two studies do not necessarily contradict the previously discussed generalizations about the effects of ITI if it is assumed that where habituation precedes to a zero level this constitutes some sort of "floor" effect such that of necessity there is no difference in the amount of habituation. In addition, the difference in the rate of habituation can be similarly explained by postulating a relationship between the observed response that is habituating and the underlying decremental processes such that the response disappears before the underlying processes have reached asymptote. Therefore, if one could measure the decrement within some part of the nervous system it might be found that the same relationship between ITI and rate and amount of habituation holds for these exceptional studies but the stimulus-response system is such that after a few presentations it does not accurately reflect underlying decremental phenomena which are still occurring.

Two processes appear to be necessary to account for the effects of ITI on habituation of the head-shake response in the rat. First, the difference in asymptotes reached between the different ITIs appears to be the result of allowing greater recovery from the effects of the preceding

trials the longer the time between trials. Evidence for such a short-term decremental process in the present study is seen when the within-trial functions for the different ITIs across the entire session were examined. As was observed, the 100 sec. ITI HSR level showed almost complete between-trial recovery from trial to trial (with accompanying within-trial decrement). The shorter ITIs, on the other hand, showed little evidence of between-trial recovery after the first two trials. This general explanation of the difference in asymptotes that occurs with different ITIs being due to the failure of short ITIs to allow appreciable recovery of short-term decremental processes was first suggested by Winokur et al. (1962) and it does appear to satisfactorally explain the results of previous studies dealing with ITI as well as the results of the present study.

A second, longer-term decremental process also has to be postulated to completely explain the effects of ITI in the present study. Evidence for the existance of such a longer-term effect is shown by the significant retention of habituation across the 30 min. intersession interval. Further support comes from a previous study of habituation of the HSR by Leibrecht and Askew (In press) where across-trial decrement was significantly retained for an interval of at least six hours. The finding in the present study that all three ITIs recovered to approximately the same

level after the 30 min. intersession interval indicates that the variable of ITI did not appreciably affect the course of this longer-term decremental process.

In summary, the difference in asymptote for the three ITI conditions in the present study appeared to be due to the compounding of short-term and longer-term decremental processes for the short ITIs. For the longer ITI, the short-term processes were given additional time to dissipate from trial to trial with the result that the response level never fell as low as it did for the short ITIs. This view predicts that given a substantial rest period the compounded short-term decremental processes for the short ITI conditions should completely dissipate and the short and long ITI conditions should recover to approximately the same response level. This is precisely what occurred in the present study.

It should be noted that the 2-process explanation of the effects of ITI utilized in the present study is similar in form to Hull's 2-process inhibition theory of extinction (Kimble, 1961, p. 305). They are similar in that both attempt to explain observed decremental phenomena in terms of the interaction of short-term and long-term decremental processes. On two major counts, however, Hull's theory has little relevance to the present study. First, with the failure to find retention of habituation of the HSR in the rat for intersession intervals of 24 hr. by

Askew et al. (1969) and Leibrecht and Askew (In press) a relatively permanent conditioning effect such as postulated by Hull can be quickly ruled out. Secondly, results by Leibrecht (1969) indicate that habituation of the HSR was very resistant to dishabituation and what dishabituation that did occur appeared to be the result of a superimposed process of sensitization. This finding is not what would be expected if the mechanism underlying habituation of the HSR was inhibition.

A multiprocess interpretation of habituation phenomena such as is employed in the present study is not new. Hinde (1960) presents evidence that habituation of the mobbing response in chaffinches to an owl model is the result of the interaction of both long-term and short-term incremental and decremental effects. A multiprocess interpretation also appears to be supported by a consideration of the variability among different portions of the habituation literature, particularly in terms of the relative permanence of decremental phenomena and underlying physiological mechanisms involved. It is, for example, an over-simplification to argue that habituation of the OR, which appears to be best explained on the basis of central inhibition of afferent input, is the result of the same underlying process as that occurring in Thompson and Spencer's (1966) spinal cat preparation, where centrally mediated inhibition cannot be involved. Similarly, there is really no reason to believe that the repeated application of a

particular stimulus cannot activate several underlying decremental processes ranging from sensory adaptation, to some sort of altered synaptic transmission in the afferent CNS, to centrally mediated inhibition of sensory input, to effector fatigue simultaneously in a given individual organism.

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