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Conditioning of the nictitating membrane response of the rabbit (*Oryctolagus cuniculus*) as a function of length and degree of variation of intertrial interval*

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The study involved three experiments. The first, a parametric investigation of nictitating membrane conditioning with eight constant intertrial intervals (ITIs) between 5 and 120 sec, orthogonal to interstimulus intervals (ISIs) of 250 and 750 msec plus three temporal conditioning control groups, revealed that performance improved rapidly with increasing ITI but stabilized at relatively low ITI values. At 750-msec ISI, a decrement in performance was found at 60-sec ITI. Experiment II, using constant ITIs of 45-75 sec in 5-sec steps, at 750-msec ISI confirmed the trend toward a performance decrement around 60 sec, although the trend was weak and highly variable. Experiment III evaluated the differences in performance between constant and variable ITI, using three ITI values and three conditions of variation at each value. Findings were discussed in terms of differences in conditioning resulting from both length and degree of variation of ITI and some subtle effects which may emerge only when constant ITIs are used.

The majority of studies relating intertrial interval (ITI) and acquisition performance in classical conditioning have shown heightened performance with lengthening of the ITI. Although other theoretical formulations (e.g., Estes, 1955) predict this relationship, it has most often been taken as support for Hull's (1943) reactive inhibition construct.

Spence and Norris (1950) reported increasing conditioned eyelid response frequency with increasing ITI over intervals of 9, 15, 30, and 90 sec with human Ss and concluded that the form of the ITI function was negatively accelerated. Actually, their data reveal an initial increase in percent CRs, with a small decrease at 30 sec and a subsequent increase at 90 sec. Gormezano (1966) reported that an average ITI of 120 sec produced faster conditioning of the nictitating membrane response (NMR) of the rabbit than did an average ITI of 30 sec. More recently, however, Frey and Misfeldt (1967) found that when conditioning was accomplished in a single session, performance was poorer at an ITI of 120 sec than at several higher and lower values. Brelsford and Theios (1965) found single-session conditioning to be better at 111-sec ITI than at 300-sec, although these investigators suggested an ITI by Session Length interaction to account for their data. Mis, Andrews, and Salafia (1970) found an interaction between ITI and ISI when constant ITIs of 60 and 300 sec were used.

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Clearly, the specification of an ITI function is at best tenuous. This is especially true of the function for constant ITI values, which have rarely been employed in ITI studies, and for the conditioned NMR, since this response system has relatively recently appeared in the experimental literature (Gormezano, Schneiderman, Deaux, & Fuentes, 1962) and comparative data on many variables have yet to be obtained. Therefore, the purpose of the present series of studies was to investigate the ITI function for the NMR over a large range of constant ITI values at both optimal and nonoptimal ISI values (Experiments I and II) and to compare performance at both constant and variable (averaged) ITI values (Experiment III).

EXPERIMENT I

Method

Subjects

The Ss were 216 naive male and female New Zealand rabbits, 70 to 100 days old at the start of the experiment. They were housed in pairs and maintained on ad lib food and water. Twelve Ss were randomly assigned to each of 16 experimental groups and 8 Ss to each of three temporal control groups. Due to our policy of excluding animals that become highly agitated or acquire eye infections, 18 Ss were eliminated, leaving a total N of 198, with at least 10 in each experimental group and at least 6 in each temporal control group.

Apparatus

Four rabbits were run concurrently in a sound-attenuated room containing four separate cubicles, each serviced independently by control and recording equipment located in an

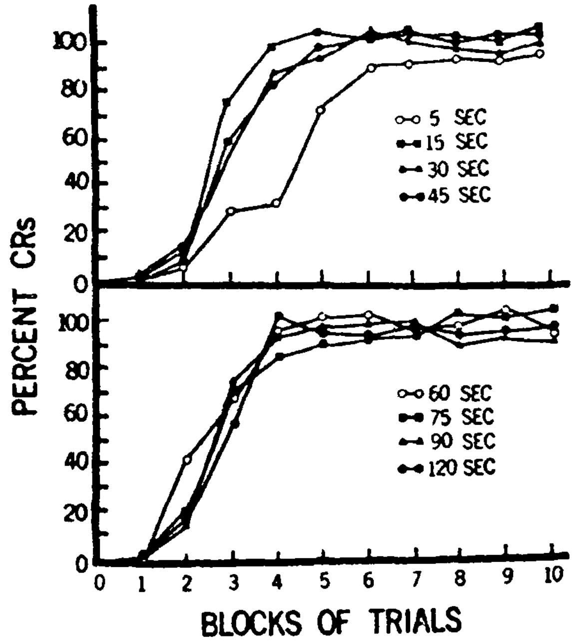

Fig. 1. Acquisition curves for rabbits conditioned at eight ITI values for the 250-msec ISI.

adjoining room. A panel in front of each S contained two impedance-matched speakers, used to present a continuous white noise for masking during the ITI, and the tone CS. A four-channel source delivered a shock US to electrodes chronically affixed to the skin about the right eye of each rabbit.

Immediately prior to each experimental session, animals were placed in Plexiglas restraining boxes. Movements of the nictitating membrane were monitored by a small photoelectric transducer mounted on each S's head by means of a muzzle-like assembly and mechanically coupled to a surgical silk suture in the membrane. Signals from the transducers were amplified and graphically recorded by a Grass Model 5D polygraph. A CR was defined as a pen deflection of at least 1 mm, occurring at least 50 msec after CS onset. Similar apparatus and procedures have been described and illustrated in detail by Gormezano (1966).

Procedure

Twenty-four hours prior to the first experimental session, Ss were prepared by having a surface anesthetic (Ophthaine) applied and then a surgical silk loop tied into the nictitating membrane of the right eye. Hair around the eye was shaved and wound clip electrodes were applied approximately 5 mm below the inferior eyelid and 5 mm posterior to the temporal canthus. Ss were then placed in the experimental cubicles, with the 66-dB SPL masking noise on, for a 15-min habituation period, after which they were randomly assigned to one cell of a 2 by 8 matrix with ISIs of 250 or 750 msec orthogonal to ITIs of 5, 15, 30, 45, 60, 75, 90, or 120 sec.

Conditioning sessions began on the day following habituation and continued, one per day, for 10 days. Each conditioning session consisted of 15 CS-US pairings at the ISI and ITI appropriate for the cell to which the animals had been assigned. The CS was a continuous 1,000-Hz tone at 85 dB SPL, and the US was a 3-mA 60-Hz shock delivered to the wound clip electrodes and overlapping the last 50 msec of CS presentation. A random block design was employed with four Ss per block replicated three times.

Three temporal control groups were run with the last block of experimental groups, at an ITI of 5, 60, or 120 sec. The temporal groups were treated in every respect like the experimental groups, except that the CS was omitted and the US was simply presented alone at the appropriate ITI.

Results and Discussion

It should be noted at the outset that the total session length for each group was dependent on the ITI value. One of the reasons for selecting 15 trials per daily session was to minimize the session length differences over groups, while still having enough daily trials to establish an ITI effect. It is possible, however, that performance differences resulted from a combination of ITI and session length differences.

Analysis of CR Frequency

Acquisition curves for the eight groups at the 250-msec ISI are presented in Fig. 1. An immediate increase in acquisition rate is seen between the 5- and 15-sec ITIs, followed by little difference in performance among the remaining ITI values. Figure 2, which depicts acquisition curves for the eight groups at the 750-msec ISI, shows a similarly rapid increase in performance from 5- to 15-sec ITI, with smaller increases up to 45 sec followed by a sharp decrement at 60 sec, approaching the performance level of the 5-sec ITI group, and then a return to asymptotic level for the remaining three ITI values. These ITI differences as well as the overall superiority of the 250-msec ISI groups are more apparent in Fig. 3, which depicts the mean number of trials to the 20th CR for the 16 experimental groups. The temporal control groups were not depicted because

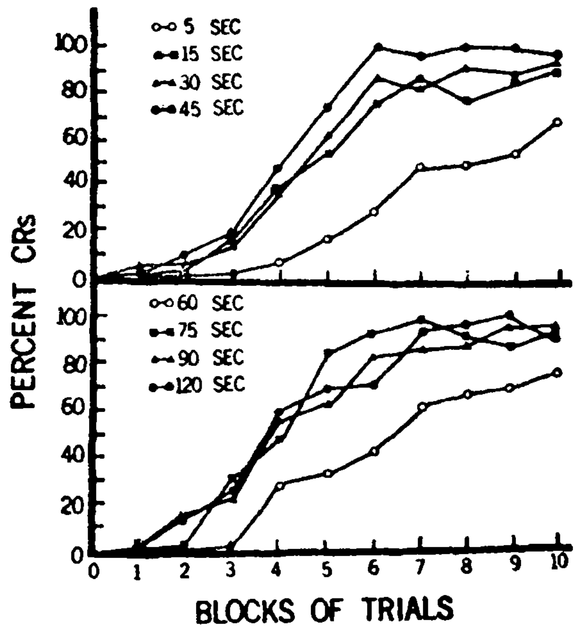

Fig. 2. Acquisition curves for rabbits conditioned at eight ITI values for the 750-msec ISI.

in no case did an animal in one of these groups achieve performance beyond a random response level.

A 2 by 8 by 10 mixed factorial analysis of variance was performed on the CR frequency data from all but the temporal control groups. This analysis revealed that conditioning at the 250-msec ISI was superior to conditioning at the 750-msec ISI ($F = 79.32$, $df = 1/161$, $p < .001$). Further, there was a significant trend for performance to vary directly with ITI ($F = 8.64$, $df = 7/161$, $p < .001$). Performance was, of course, very significantly related to increasing number of conditioning sessions ($F = 711.30$, $df = 9/1449$, $p < .001$). The analysis of variance also revealed highly significant interactions, namely, ISI by ITI ($F = 3.17$, $df = 7/161$, $p < .005$), ISI by Sessions ($F = 34.52$, $df = 9/1449$, $p < .001$), and ITI by Sessions ($F = 343$, $df = 69/1449$, $p < .001$).

The pattern of results up to this point may be summarized as follows. (1) For all ITI values, performance at the 250-msec ISI was superior to performance at the 750-msec ISI. This result was as expected (Schneiderman & Gormezano, 1964; Smith, Coleman, & Gormezano, 1969) and requires no further elaboration. (2) Prescinding for the moment from the decrement in conditioning for the 750-msec/60-sec group, it is clear that within each ISI value, performance increased with increasing ITI, although asymptotic levels were reached more rapidly with constant ITIs than had been previously reported with variable ITIs (e.g., Brelsford & Theios, 1965; Frey & Misfeldt, 1967). (3) The significant ISI by ITI interaction appears to have resulted primarily from the performance of the 750-msec/60-sec group. This is seen more clearly by multiple comparisons among treatment means which revealed that at the 250-msec ISI, the 5-sec ITI group differed significantly ($p < .01$) from all other groups, but none of the remaining groups differed significantly among themselves. However, at the 750-msec ISI, the 5-sec ITI group differed significantly ($p < .01$) from all others except the 60-sec group, while the 60-sec group differed significantly ($p < .01$) from the 45-, 75-, 90-, and 120-sec ITI groups, but not from the 5-, 15-, or 30-sec groups.

The remaining significant interactions, namely, ISI by Sessions and ITI by Sessions, were further analyzed to determine whether the differences in performance over sessions resulted from effects of the treatments on CR emergence only or on both CR emergence and subsequent performance. Since this could not be determined solely by the analysis of acquisition curves or trials to 20th CR, the procedure adopted was to compare each S to each other S in terms of a performance reference point. Thus, the block of trials in which a rabbit attained the 20th CR was arbitrarily chosen as a reference block, and the animal's performance in the three blocks immediately preceding and immediately following the reference block were recorded. This procedure was repeated for each S, in

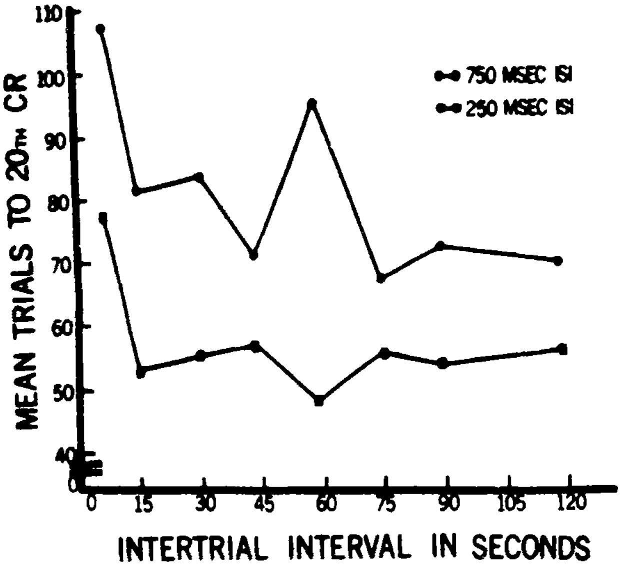

Fig. 3. Mean number of trials to the 20th CR for the 16 experimental groups.

each group, resulting in a series of acquisition curves from which the various contributions to differences could be assessed. If there was considerable overlap in these curves and no significant differences attributable to the treatments, then the differences found in the previous analyses could be ascribed to effects of treatments on CR emergence only. On the other hand, less overlap and significant differences would mean that the treatments differentially affected not only CR emergence, but also CR frequency thereafter.

A 2 by 8 by 7 mixed factorial analysis of variance was carried out on the data resulting from the above manipulations. (The data were not depicted because of the generally large degree of overlap and the fact that the trends can be seen from the analysis.) In addition to the expected trial blocks effect ($F = 1115.93$, $df = 6/918$, $p < .001$), the analysis revealed a significant ISI effect ($F = 18.81$, $df = 1/152$, $p < .001$) and an ISI by Trial Blocks interaction ($F = 6.76$, $df = 6/918$, $p < .001$), which, when considered in relation to the previous analyses, indicates that the ISI variable affects not only initial acquisition, but also subsequent performance. On the other hand, there was no significant ITI main effect or interaction, indicating that the effect of ITI is principally or entirely on CR emergence.

Analysis of CR Latency

Analysis of CR latencies generally confirmed the findings of the CR frequency analyses, and the latency results may be summarized as follows. First, for each ITI value, (1) mean latency of the first 20 CRs, (2) overall mean latency, and (3) latency variability were all found to differ significantly ($p < .01$ for all comparisons) as a function of ISI, with longer latencies and greater

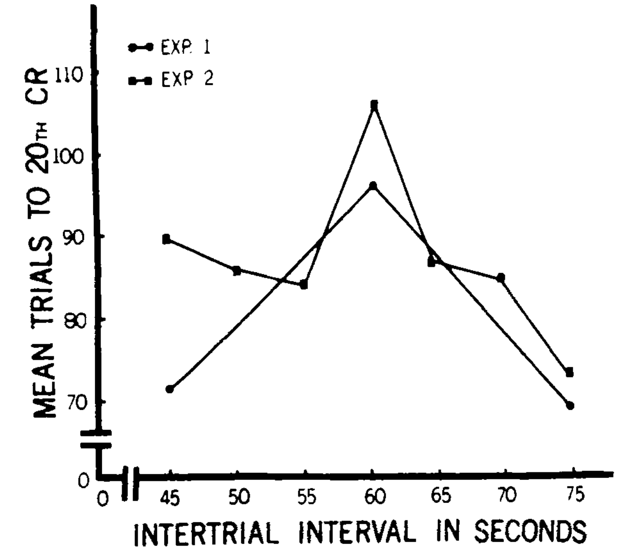

Fig. 4. Mean number of trials to the 20th CR for rabbits conditioned at seven ITIs in Experiment II with the three corresponding groups from Experiment I.

variability for the 750-msec ISI. Second, within each ISI there was a tendency for performance to be inversely related to CR latency, i.e., the better the performance, the shorter were the latencies. Individual analyses of variance of latencies at each ISI revealed that the tendency was small and nonsignificant ($F < 1$) for the 250-msec ISI groups, but differences were significant ($F = 2.58$, $df = 7/81$, $p < .05$) for the 750-msec ISI groups. Finally, for 14 out of the 16 experimental groups, there was a tendency for CR latencies to decrease as conditioning proceeded. The only exceptions were the groups in which performance measured by CR frequency was at a very low level, namely, the 5- and 60-sec ITI groups at 750-msec ISI. Thus, in general, CR latencies tended to be shorter and variability tended to be smaller as a function of whichever ISI or ITI manipulations lead to faster acquisition.

EXPERIMENT II

Although the results of Experiment I were generally consistent with the ITI literature, in showing heightened performance with increasing ITI, there were two apparent discrepancies. First, the rise in performance seemed more rapid with constant ITIs than had been previously reported with variable ITIs, and second, there was a decrement in performance at the 750-msec ISI for the 60-sec ITI group. The purpose of Experiment II was to detail the nature of the observed decrement by evaluating performance at 750-msec ISI over seven ITI values ranging from 45 to 75 sec.

Method

Subjects

The Ss were 140 rabbits obtained, housed, and fed as in Experiment I. Twenty Ss were assigned to each of seven experimental groups. Again, adhering to a strict criterion for exclusion, 23 Ss were excluded due to illness or eye infections, leaving a total of 117, ranging from 14 to 19 per group.

Apparatus and Procedure

After habituation, Ss were randomly assigned to one of seven experimental groups: 45-, 50-, 55-, 60-, 65-, 70-, or 75-sec constant ITI, at 750-msec ISI. Except for the use of these ITI values, the apparatus, conditioning parameters, and procedures were the same as those used in Experiment I.

Results and Discussion

The mean numbers of trials to the 20th CR for the seven groups are presented in Fig. 4. Also depicted are the three corresponding data points from Experiment I. Although the function relating acquisition to ITI over this narrow range of ITI values was variable, the trend of these data was in the expected direction, namely, a decrement in conditioning at the 60-sec ITI, with superior performance at both lower and higher ITI values. Unfortunately, analysis of variance of trials to the 20th CR did not reveal a significant ITI effect. Further, a 7 by 10 mixed factorial analysis of the acquisition data revealed only a significant trials effect ($F = 198.60$, $df = 9/990$, $p < .001$), but no overall ITI effect ($F = 1.24$, $df = 6/110$, $p > .05$) or ITI by Trials interaction ($F < 1$).

The reasons for the lack of significance seem to be both the relatively small size of differences and the relatively large degree of variability present across this range of ITI values. Regardless of the reasons, though, the results of Experiment II did not succeed in detailing the nature of the decrement observed in Experiment I.

EXPERIMENT III

The purpose of this experiment was to compare performance resulting from the use of constant and variable ITIs. Further, it was expected to aid in determining whether the decrements in performance found in Experiments I and II might be specifically related to the use of constant ITIs.

Method

Subjects

The Ss were 72 rabbits obtained, housed, and fed as in the previous experiments. Sixteen Ss were excluded due to illness or eye infections, leaving a total of 56, ranging from 3 to 8 Ss per group.

Apparatus and Procedure

After habituation, eight Ss were randomly assigned to each of nine groups. There were three ITI values (30, 60, and 120 sec) orthogonal to three conditions of variation of ITI, namely, constant (C), or no variation, Variable 1 (V1) in which three variations were presented in quasirandom fashion for each averaged ITI value, and Variable 2 (V2) in which five variations were presented for each averaged ITI value. In both the V1 and V2 conditions, the variations bore a constant ratio to the averaged ITI value. Thus, in the V1 condition, ITI values presented were 25, 30, or 35 sec, 40, 50, or 60 sec, and 100, 120, or 140 sec for the 30-, 60-, and 120-sec ITI conditions, respectively. In the V2 conditions, the ITI values were 20, 25, 30, 35, or 40 sec, 40, 50, 60, 70, or 80 sec, and 80, 100, 120, 140, or 160 sec for the 30-, 60-, and 120-sec ITI conditions, respectively. For all groups, the ISI was 750 msec and the experiment was run for eight daily sessions. Except for the use of these ITI values and conditions of variation, the apparatus, conditioning parameters, and procedures were the same as those used in Experiments I and II.

Results and Discussion

Due to the similarity of performance in the variable ITI groups, they were combined for purposes of comparison with the performance of the constant ITI groups. Figure 5 presents the mean number of trials to the 20th CR for the C and combined V groups at each ITI value. For the V groups, there was a trend toward improving performance up to about 60-sec ITI, followed by little apparent difference at 120 sec. This trend was reversed for the C groups. At both 30- and 120-sec ITI, performances of the C groups were slightly superior to the V groups, while at 60-sec constant ITI, a depression in performance was found similar to that found in the previous experiments in this study. A 3 by 3 by 8 mixed factorial analysis of the CR frequency data revealed a significant trials effect ($F = 155.01$, $df = 7/301$, $p < .001$) and a significant ITI by Conditions of Variation (C vs V) interaction ($F = 2.90$, $df = 4/43$, $p < .05$). None of the other effects or interactions were statistically reliable, although the ITI main effect approached significance ($F = 2.60$, $df = 2/43$, $.05 < p < .10$).

These data suggest that, ordinarily, conditioning with constant ITIs may be slightly superior to conditioning with variable ITIs. Although no temporal conditioning was found in the three control groups of Experiment I, nevertheless, it is well known that time can play a role in conditioning when constant time intervals are part of the experimental situation (Dmitriev & Kochigina, 1959). In addition, the constant ITIs seem to permit the display of apparently time-dependent phenomena such as the depression at 60-sec ITI, which has been observed in all three experiments.

At first glance, these results appear to differ from those of Prokasy and Chambliss (1960), who found no significant differences between groups conditioned at constant and at variable ITIs. These investigators, however, used human Ss and only one ITI value, namely, 25 sec. Although the differences were not significant,

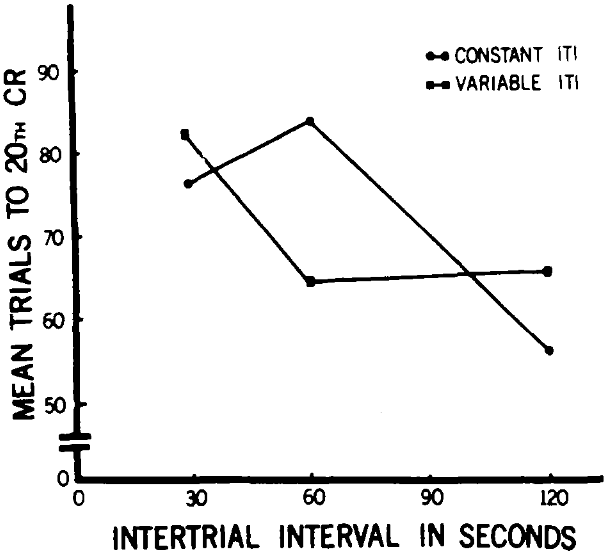

Fig. 5. Mean number of trials to the 20th CR for three groups of rabbits conditioned at constant ITIs and three combined groups conditioned at variable ITIs.

slightly more rapid conditioning occurred for their constant ITI groups, which is in agreement with the slight superiority of the 30-sec ITI group, the most comparable point in the present experiment.

GENERAL DISCUSSION

The major findings of the study were: (1) at both optimal (250-msec) and nonoptimal (750-msec) ISIs, increases in constant ITI led to increases in conditioning rate, (2) these increases occurred rapidly for short ITIs with a leveling of the effect between 15- and 45-sec ITI, depending on the ISI, (3) ITI manipulations were found to affect primarily CR emergence, while ISI manipulations affected both CR emergence and subsequent performance, (4) the use of constant ITIs seemed to permit the display of apparently time-dependent effects, which may be obscured by the use of variable ITIs, and (5) although, strictly speaking, no temporal conditioning was demonstrated, the effect of using constant ITIs seemed to be a slightly heightened acquisition rate (i.e., a temporal effect) at some ITI values.

The general finding of increased performance with increasing ITI was consistent with the bulk of ITI studies. As noted, the increases in conditioning rate occurred primarily at low ITI values with a leveling of the effect at about 15- to 45-sec ITI. Although others have reported an ITI function over larger ranges, there are a number of possible reasons for the apparent discrepancy. First, most of the studies, especially the earlier ones, involved human eyelid conditioning. A number of differences between human eyelid and rabbit nictitating membrane conditioning have already been found, and it is likely that others exist. Thus, direct comparisons across species of the effects of many variables such as ITI may be difficult. However, even in the human eyelid conditioning studies, the largest effects have tended to occur at short ITI values (see Ross & Hartman, 1965, for summary).

Furthermore, the rabbit conditioning studies which have reported ITI effects over larger ranges have tended to involve single-session conditioning (e.g., Brelsford & Theios, 1965; Frey & Misfeldt, 1967, Experiment 2). Where multiple sessions were used, few effects were found beyond relatively short ITI values. For example, Frey and Misfeldt (1967, Experiment 1) reported no significant ITI effect over seven daily sessions at ITI values of 60, 150, and 300 sec.

The other major pattern of results, namely, the depressions in performance at the nonoptimal ISI, which occurred in all three experiments seems characteristic of effects of interpolated stimuli in the ITI found by a number of researchers (e.g., Papsdorf & Kettlewell, 1968; Papsdorf, Levinthal, & Salafia, 1969; Hupka, Kwaterski, & Moore, 1970; Grevert & Moore, 1970; Leonard, Fischbein, & Monteau, 1972) and usually interpreted as consolidation disruption effects. For years, researchers have found that certain kinds of posttrial stimulation such as electroconvulsive shock, chemicals, or stimulation of certain areas of the brain can lead to memory deficits (McGaugh & Herz, 1972). In the case of rabbit nictitating membrane conditioning, investigators have found that interpolated bursts of light, white noise, or shock (US alone) seem to have similar disruptive effects if they occur at certain points in the ITI. The present results appear to support the proposal of Papsdorf and Kettlewell (1968) that the CS-US pairings, if they occur reliably at certain critical intervals after a trial, may also disrupt consolidation of the events of that trial.

If the apparent similarity in the results of the present study and those of studies involving interpolated stimuli is more than a superficial resemblance, then certain issues must be clarified. The first is how learning takes place when the CS-US pairing acts as a disruption. The answer probably resides in the assumption that a CS-US presentation occurring at a critical point has less disruption effect than a US-alone or other interpolated stimulus, because the CS-US pairing sets up new neural activity to persist into the next interval. Although generally unsympathetic to a consolidation interpretation for their findings, Leonard et al (1972) indicated that with such an assumption, a consolidation explanation could more readily account for their data.

Another reasonable question is why no decrement in conditioning was found at the optimal (250-msec) ISI. Although decrements have been found when optimal ISIs were used (e.g., Hupka et al, 1970), they have been found more often and have been more pronounced with nonoptimal ISIs (Snyder & Papsdorf, 1968). Since there were no specifically interpolated disruptors in the present study, it seems reasonable to expect that if a decrement caused by CS-US pairing were present at the optimal ISI, it would be relatively small or imperceptible.

Finally, it is reasonable to question whether the use of constant ITIs could have determined the effect, by the learning of some form of time discrimination (e.g., Prokasy, 1965), quite aside from any notions of consolidation. However, the mechanism by which the discrimination of time intervals could yield the findings of the present study is obscure, especially in light of the lack of conditioning in the temporal control groups in Experiment I. Also, the pattern of results emerging from the interpolated stimulus literature suggests that: (1) the disruptive effects appear to result from retroactive rather than from proactive processes (Papsdorf et al, 1969), (2) the time of maximal disruptive effect of interpolated stimuli may be a function of such variables as US intensity and duration (Papsdorf et al, 1969; Mis et al, 1970), and (3) as mentioned, occurrence and size of the effects may be a function of length of ISI. Thus, although there are a number of discrepancies in the literature and further research is needed, there do seem to be some rough relationships among conditioning parameters and the occurrence and degree of disruption.

The use of a consolidation disruption interpretation to account for the depressions in conditioning observed in the three experiments of the present study is admittedly post hoc. It would seem that the best way to determine with confidence the validity of such an explanation would be to monitor posttrial neural activity and then present specific stimuli at times determined by such activity. We are presently undertaking pilot studies in this direction at the Fairfield Laboratory.

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