

Performance of the nictitating membrane CR following CS-US interval shifts

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The present study assessed the effects of CS-US interval shifts upon the performance of the rabbit's nictitating membrane conditioned response. The results showed that gradual daily reductions of the CS-US interval from 250 to 50 msec did not decrement the asymptotic performance rate. Moreover, the high performance rates found on trials utilizing 100- and 50-msec CS-US intervals were sustained even though these intervals do not allow for the regular occurrence of an anticipatory CR. When simultaneous CS and US presentations were given, decreases in conditioned responding developed. Finally, the reacquisition of the membrane CR was immediate, despite the decremental effects of prior backward and simultaneous CS and US presentations upon CR maintenance performance. The results were evaluated with regard to theories addressing response timing requirements of conditioned responses.

Evidence shows that the temporal shifting of the CS-US interval following the development of a conditioned response (CR) disrupts subsequent performance. Larger CS-US interval shifts produce more disruption than smaller shifts (Coleman & Gormezano, 1971; Prokasy & Papsdorf, 1965). In addition, an abrupt change in the CS-US interval attenuates responding to a greater extent than gradual shifting procedures (Coleman & Gormezano, 1971; Prokasy, Ebel, & Thompson, 1963). The theoretical implications of these findings address the timing requirements for CR occurrence. In this regard, the response-shaping hypothesis (Boneau, 1958; Ebel & Prokasy, 1963) has offered that CR development requires a response-produced change in the sensory characteristics of the US. For example, if the US is an aversive corneal air puff, the occurrence of an eye blink CR just prior to the onset of the US guarantees the effective reduction in the noxious properties of the sensory event. Therefore, the response-shaping hypothesis predicts that CR timing characteristics are controlled by the availability of CR overlap upon the occurrence of the US in a temporal dimension. More recently, CR timing characteristics have been considered within a position (Sears, Baker, & Frey, 1979) that acknowledges the role of innate neuronal organization in CR development. In this approach, CSs are viewed as signals that have information value regarding both US probability and temporal distance. The occurrence of the CR

prior to the onset of the US depends upon the amount of time required to execute motor reflexive chains and the ability of the CS to command the activity of these chains.

The present study offers evidence regarding the fate of the CR when decreases of the CS-US interval are carried to the point at which the CS and US have simultaneous onsets. Of particular interest to theories addressing response timing is whether a CR can be maintained at very short intervals that do not allow for CR acquisition. In rabbit nictitating membrane conditioning, CS-US intervals of 100 msec and less tend to be ineffective for CR acquisition, with the amount of decrement increasing as the CS-US interval approaches simultaneity over this restricted range (Smith, Coleman, & Gormezano, 1969).

METHOD

Subjects

Twelve male and female rabbits (*Oryctolagus cuniculus*), 90-100 days old and weighing approximately 2 kg, were employed in the study.

Apparatus

The procedures for recording nictitating membrane responding have been given by Gormezano (1966). Bromage and Scavio (1978) detail variations from the original description utilized in the present work. Basically, Plexiglas boxes, accommodating the size of the rabbit, were used to restrict head and body movements during the conditioning sessions. Nictitating membrane responses were recorded by means of Conrac microtorque potentiometers, which convert physical movements into linear voltage changes. The rotary stem of the potentiometer was connected to the nictitating membrane by means of silk thread

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that terminated in a small wire hook. The hook was placed in a loop of surgical thread sutured in the right nictitating membrane. Finally, the outputs of the potentiometer were relayed to the analog-to-digital converter of a PDP-12 computer that was responsible for data recording and stimulus presentations in the experiment.

The CS was a 250-msec, 1,000-Hz, 86-dB (re 20 $\mu\text{N}/\text{m}^2$) tone superimposed on a 72-dB white-noise background. The US was a 50-msec, 4-mA, 60-Hz shock delivered through stainless steel electrodes embedded 15 mm apart, 15 mm behind the right eye.

Procedure

The loop of suturing thread was placed in the rabbits' nictitating membranes 48 h after their arrival in the laboratory. Then, six rabbits were assigned to each of two groups, designated "gradual" and "extinction." At 24 h following membrane preparation, each group received a 40-min session, during which the rabbits were housed in the conditioning chambers without stimulus presentations. On the next day, Stage 1 training was initiated and required both groups to receive 72 CS-US pairings daily for 3 successive days. A 250-msec CS-US interval was employed during Stage 1 acquisition of the membrane CR. In Stage 2, the gradual group received 72 CS-US pairings daily for 4 successive days. On each day, the CS-US interval was systematically decreased by 50 msec, beginning with a 200-msec CS-US interval for Day 1 of Stage 2 and ending with a 50-msec CS-US interval on Day 4 of Stage 2. The extinction group received 72 US-CS (backward) pairings on each of the 4 days of Stage 2. The temporal separation between the US and the CS on the backward trials was held constant at 250 msec. It was expected (Ayres, Mahoney, & Proulx, 1976) that the backward pairings would produce CR performance decrements analogous to extinction outcomes. In Stage 3, both the extinction and the gradual groups received 72 simultaneous deliveries (0-msec CS-US interval) daily on each of 5 successive days. Finally, in Stage 4, both groups received 72 CS-US presentations utilizing the original 250-msec CS-US interval. These reacquisition trials were confined to one daily session given upon the conclusion of Stage 3.

Since very short CS-US intervals and simultaneous CS and US deliveries do not allow for the observation of anticipatory CR occurrences, CR frequency and latency were monitored on test trials given in each training session for the gradual and extinction groups. The test trials were administered on every 10th trial, for a total of 8 test trials each session. Each test trial consisted of a CS-alone presentation. Nictitating membrane extension of at least 1 mm occurring during the 250-msec duration of the test trial CS was scored as a CR. Within each daily session, the intertrial intervals were randomized at values of 50 and 70 sec, with a mean of 60 sec.

RESULTS

Stage 1

As can be seen in the first panel of Figure 1, both gradual and extinction groups, receiving acquisition training at a 250-msec CS-US interval, reached asymptotic CR probabilities on Day 3. An analysis of variance performed upon percentage of membrane CRs on the test trials revealed no reliable group difference on the final Stage 1 day.

Stage 2

The second panel of Figure 1 displays the performance on the test trials of Stage 2 for the gradual and extinc-

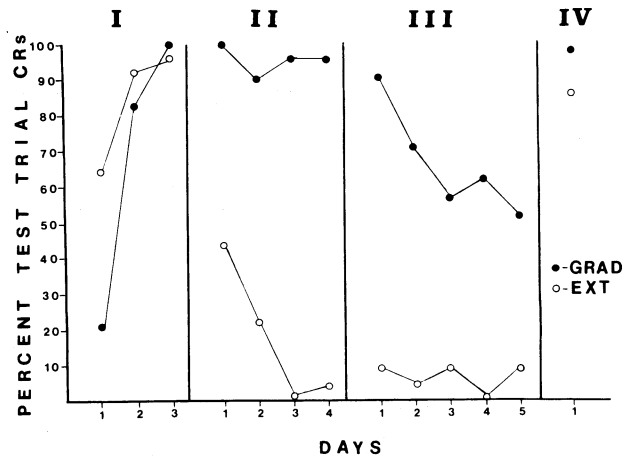


Figure 1. Percentage of test trial membrane CRs for the gradual (Grad) and extinction (Ext) groups over the four stages of the experiment. The stages are indicated by Roman numerals.

tion groups. The gradual group maintained asymptotic CR performance rates throughout Stage 2, even though the CS-US interval was decreased by 50 msec daily from its initial value of 200 msec on Day 1 of Stage 2. In contrast, the extinction group suffered a rapid decrement in CR performance as a result of the backward pairings given on each Stage 2 day. An analysis of variance performed for both groups upon percentage of test trial CRs in each training session revealed a significant Group by Days interaction [$F(3,30) = 7.27$, $p < .01$]. This interaction was further evaluated by individual analysis of variance tests applied to each group upon percentage test trial CR performance over the Stage 2 days. The extinction group analysis yielded a significant days effect [$F(3,15) = 10.20$, $p < .01$], with no comparable significant outcome found for the gradual group. Therefore, the data analyses support the conclusion that the gradual group did not undergo a CR decrement as the CS-US interval was decreased, whereas the extinction group exhibited large performance losses upon the introduction of backward pairings of the CS and US.

Stage 3

The performance of the gradual and extinction groups over the 5 days of Stage 3 when simultaneous CS and US presentations were given are shown in the third panel of Figure 1. The gradual group exhibited reductions over the course of Stage 3. The extinction group continued to maintain the extremely low levels of responding that were initially observed at the conclusion of Stage 2. Therefore, simultaneous CS and US presentations, accorded to the gradual and extinction groups, produced no excitatory influences upon CR performance. An analysis of variance upon the percentage of membrane CRs for the gradual and extinction groups on the daily test trials of Stage 3 revealed a significant group difference [$F(1,10) = 29.77$, $p < .01$].

This result supports the observation regarding the performance advantage of the gradual group relative to the extinction group in Stage 3. In addition, the individual test trial performances of the gradual and extinction groups were submitted to analysis of variance tests. For the gradual group, a significant days effect [$F(4,20) = 2.95, p < .05$] was obtained, and this corroborates the observed attenuation in CR performance. For the extinction group, no significant effects were obtained; this is indicative of the continued low, constant rate of conditioned responding over Stage 3.

Stage 4

In Stage 4, the gradual and extinction groups received reacquisition CS-US pairings at a temporal interval of 250 msec. As the fourth panel in Figure 1 illustrates, both groups showed strong CR performance rebounds with the restoration of the asymptotic response levels. An analysis of variance performed upon the percentage of test trial CRs for the gradual and extinction groups on the reacquisition day revealed no reliable differences in responding. However, the magnitude of the reacquisition effect was gauged in separate analysis of variance tests for the gradual and extinction groups which compared the CR performance rate on the last day of Stage 3 to the rate on the Stage 4 reacquisition day. Significant day differences were obtained both for the gradual [$F(1,5) = 12.10, p < .01$] and extinction [$F(1,5) = 32.75, p < .01$] groups. These analyses confirm the pronounced reacquisition of the membrane CR in the single Stage 4 session.

CR Latency

As a further means to address the response timing characteristics of the membrane CR, onset latencies were calculated for the gradual group. (CR onset latency refers to the temporal distance from CS initiation to CR evocation.) Table 1 displays the mean CR latencies for the gradual group on the daily test trials following the development of asymptotic CR performance on Day 3 of Stage 1. For reference, the CS-US intervals employed on the successive training days are also indicated. As the table reveals, CR latency during Stage 2 remained stable despite the daily decreases in the CS-US interval from 200 to 50 msec. Most interestingly, the mean CR latency on Days 3 and 4 of Stage 2 are appreciably longer than the CS-US interval values on those days. An analysis of variance upon mean CR latency over the daily Stage 2 test trials did not reveal significant effects. This result is consistent with the observation of stable CR latencies accompanying the asymptotic performance levels over the Stage 2 days for the gradual group. In Stage 3, which required simultaneous CS and US deliveries, CR latencies on the test trials show greater variability relative to the range expressed in Stage 2. However, the variability in CR

Table 1
Mean CR Latency (Milliseconds) Over the Test Trials on the Training Days Following CR Acquisition for the Gradual Group

Day	Stage 1		Stage 2		Stage 3		Stage 4	
	L	I	L	I	L	I	L	I
1			140	200	131	0	138	250
2			129	150	128	0		
3	164	250	130	100	80	0		
4			133	50	109	0		
5					98	0		

Note—L = mean CR latency; I = CS-US interval.

latency could not be confirmed to be reliable by an analysis of variance test. Finally, on the Stage 4 reacquisition day, the mean CR latency returned to a value associated with the high performance rates found in Stage 2.

DISCUSSION

The major findings of this study may be briefly summarized. Following the development of asymptotic CR performance, gradual daily reductions in the CS-US interval from 250 to 50 msec did not affect conditioned responding. In addition, the mean CR latencies were found to exceed CS-US interval values of 100 and 50 msec. However, simultaneous CS and US presentations produced performance decrements. Finally, reacquisition of the membrane CR was rapid and complete despite the decremental effects of backward and simultaneous CS and US presentations.

The results of the present experiment are not entirely consistent with either a response-shaping or an evolutionary account of CR timing characteristics. The principal difficulty for the response-shaping hypothesis involves the observation of high CR performance levels even though the mean CR latencies were longer than the corresponding CS-US interval values. According to the response-shaping position (Ebel & Prokasy, 1963), the onset of the CR is required to precede the US delivery so that the sensory consequences of the US can be effectively modified. The evolutionary approach (Sears et al., 1979) is vulnerable to a similar criticism. This account emphasizes the unique timing information present in stimulus conditions and its resulting influence on response adaptiveness. On those trials that allowed for CR latency to exceed the CS-US interval, adaptive mechanisms should have produced performance deficits.

The present data also suggest that a distinction may have to be made between CS-US intervals that are effective for CR acquisition and intervals that simply allow for CR maintenance. Previous evidence (Smith et al., 1969) has established that CS-US intervals of 100 and 50 msec are not favorable for membrane CR formation. However, in the present experiment, the 100- and 50-msec CS-US intervals successfully maintained the membrane CR in daily sessions. Simultaneous CS-US presentations, also known to be inimical to CR acquisition (Smith et al., 1969), were confirmed in the present work to be insufficient for CR maintenance. Therefore, the lower limits for CS-US intervals controlling CR acquisition and maintenance may have differential values, with the maintenance value more closely approaching the simultaneous CS and US presentation condition.

Finally, the rapid reacquisition of the membrane CR despite the imposition of CS and US contingencies detrimental to CR performance demonstrates the remarkable resiliency of associative information. The reacquisition result implies that an under-

lying associative connection must remain intact despite variations in the CS and US contingency relationships.

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