

*TIMING OF AVOIDANCE RESPONSES BY RATS*¹MYRNA E. LIBBY² AND RUSSELL M. CHURCH

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Three rats were trained on an unsignalled shuttlebox-avoidance task under three response-shock intervals (10, 20, and 40 sec). Under all conditions, subjects developed excellent temporal gradients of avoidance; that is, response rate was an increasing function of time since last response. Although the response rate at any given interval of time after the previous response was inversely related to the response-shock interval, there was an underlying similarity in the temporal gradients for the three intervals. In all cases, response rate relative to the maximum response rate was approximately equal to the proportion of the interval that had elapsed. This suggests that rats in unsignalled avoidance are estimating time from response completion, and that the units of the estimate are proportional parts of the response-shock interval.

The unsignalled avoidance procedure consists of presenting shocks to a subject at a constant rate determined by the shock-shock (S-S) interval, unless the animal makes the designated avoidance response. If the response is made, a second schedule of shock presentation determined by the response-shock (R-S) interval becomes effective. Subsequent responses each reset the R-S timer, allowing continued postponement or avoidance of shock.

The asymptotic performance of animals in the unsignalled avoidance procedure often suggests that they are timing the interval. For example, Anger (1963) showed that the conditional probability of a response rises throughout the R-S interval. This measure of avoidance behavior is the frequency of responses in a given interresponse interval divided by the frequency of opportunities to respond in that interresponse interval. While the form of conditional probability functions of rats in a lever-response task is generally increasing, this gradient is often complicated by short-latency bursts of responses (*e.g.*, Sidman, 1958). To obtain uncontaminated temporal performance, the subjects in the present experiment were trained on an unsignalled avoidance shuttlebox baseline. Regular increasing condi-

tional probability functions uncontaminated by short-latency bursts have typically been reported for rats in a shuttlebox (Johnson and Church, 1965; Riess and Farrar, 1972).

The conditional probability measure from a single R-S interval is insufficient evidence to demonstrate timing behavior. For example, increasing conditional-probability functions can be generated from a latency that is assumed to involve a series of subresponses, each of which occurs at random intervals of time (Gibbon, 1972). Thus, a regular change in the response rate as a function of time since the previous response does not necessarily imply that an animal is placing its responses in accordance with the temporal properties of the schedule of shock presentation. The best evidence for timing is a regular change in the latency or conditional probability distribution as a function of changes in the R-S interval. Gibbon (1971) provided asymptotic latency distributions from three rats in an unsignalled lever-box avoidance situation that supported the view that each avoidance response represents a time estimate, and that changes in the R-S interval simply serve to transform the time scale. In that experiment, conditional probability of response distributions shifted as a function of change in R-S intervals, and the subjects appeared to be timing the interval from the last response in units proportional to the response-shock interval (scalar timing).

The present experiment serves to describe the temporal gradient of avoidance respond-

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ing, and provides a further test of the assumption that scalar timing is the basic latency mechanism underlying unsignalled avoidance behavior.

METHOD

Subjects

Three male albino Norway rats (Charles River CD), that arrived from the breeding laboratory at 42 days of age, were individually housed and given free access to food and water. They were 10 weeks old at the start of the present experiment.

Apparatus

Four shuttleboxes constructed from 0.64 cm (0.025 in.) aluminum (each 39.4 cm long, 13.9 cm wide, and 20.3 cm high) were enclosed in ventilated, sound-attenuated boxes. Each shuttlebox had a grid floor of 26 (0.32 cm diameter) stainless steel bars, and was divided into two equal compartments by a partition with a 7.6-cm square opening at floor level to permit the subjects to shuttle between the two compartments.

The shock circuit consisted of an autotransformer, a power transformer, and a 150,000-ohms resistor in series with the subject. The shock was delivered to the input of a Grason-Stadler grid scrambler (Model E1064GSP), the output of which was connected to the bars and the walls of the shuttlebox.

To register responses, a photocell and light source were inset on opposite walls in each compartment of the shuttlebox 3.5 cm above the floor and 7.6 cm from the partition. The location of the subject in the shuttlebox was continually monitored, and a response was completed when the subject broke the photocell circuit in the opposite shuttlebox compartment. Implementation of the procedure and collection of the data were controlled by a time-shared PDP-12 computer.

Procedure

The rats were given 30 sessions of unsignalled avoidance training with an S-S interval of 5 sec and an R-S interval of 20 sec. Shock duration was 1 sec and the intensity was 180 V. The first response following a shock changed the shock schedule from the S-S interval to the R-S interval and was counted as an escape response. Responses made while the R-S interval

was in effect were counted as avoidance responses. Only the data from the last 50 min of each 60-min session were included in the analysis to eliminate warmup effects (Riess and Farrar, 1972). After these sessions, the animals were continued on unsignalled avoidance training with the same S-S interval and shock parameters but with different R-S intervals. For two subjects, the schedule was switched to an R-S interval of 40 sec; for the third, the schedule was switched to a R-S interval of 10 sec for 10 sessions. Then, eight additional sessions were provided with the R-S intervals reversed for the three subjects; thus, two subjects experienced the various R-S intervals with a 20-40-10 sequence and the third was given a sequence of 20-10-40. The data reported were obtained from the last five recorded sessions at each R-S interval.

RESULTS

The conditional probability of a response per second is shown in Figure 1 for each of the subjects, and for the mean. This dependent measure is equivalent to a response rate measure. For example, a conditional probability of 0.5 responses per second is equivalent to a rate of 30 responses per minute. Under all conditions, the conditional probability of a response increased as a function of time since last response, but the function rose more abruptly, and to a higher level, when the response-shock interval was short than when it was longer.

Although the conditional probability functions for the three R-S intervals were substantially different, the animals in each case presumably were timing the interval and making a response when a criterion time had been reached. Presumably, the mechanism underlying this temporal behavior was the same regardless of the particular R-S interval used; therefore, there must be an underlying similarity in all the distributions. To identify this similarity, it was necessary to find the sense in which the response distributions for different R-S intervals were identical.

The same data shown in Figure 1 are replotted in Figure 2 to reveal the underlying similarity of the response distributions under R-S intervals of 10, 20, and 40 sec. The vertical axis represents the momentary response rate relative to the maximum response rate of the

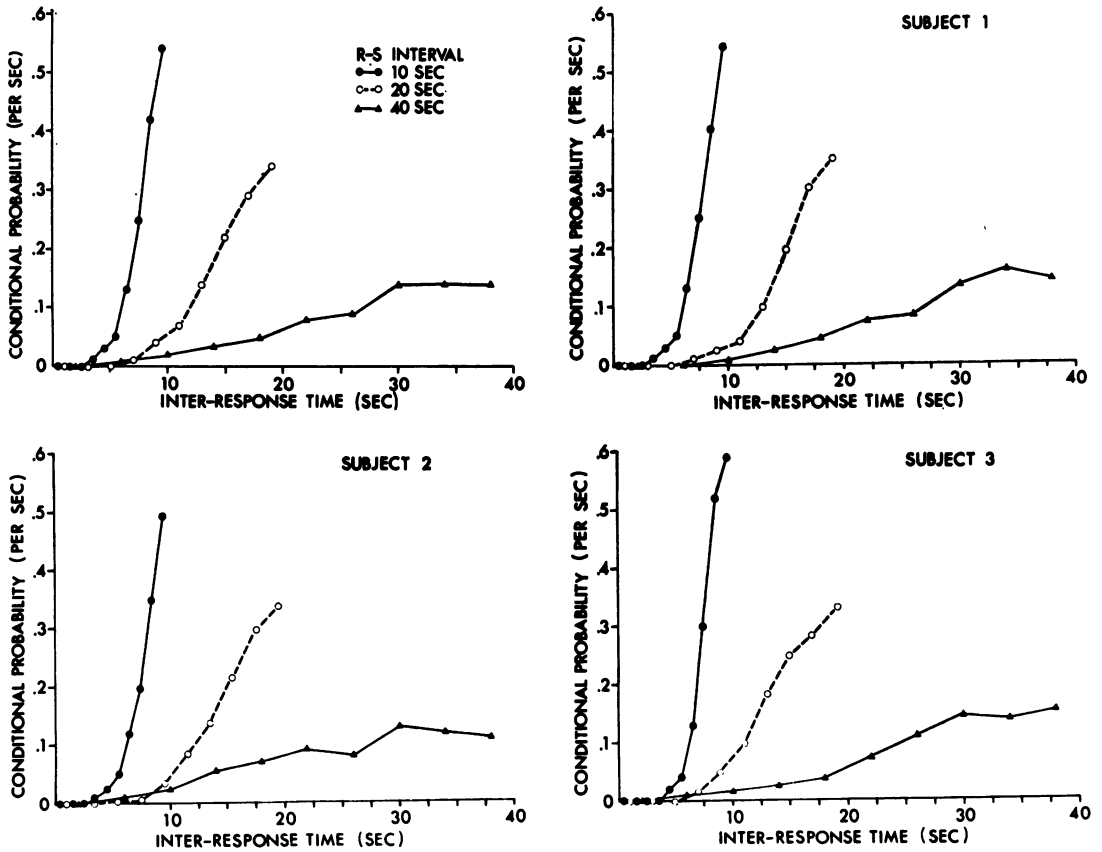


Fig. 1. Conditional probability of a response (per second) given an opportunity for response as a function of time since last response. Data are presented for each of the three subjects, and for the mean of the three subjects under response-shock intervals of 10, 20, and 40 sec.

subject. Each point was obtained by dividing the conditional probability for a given inter-response time by the maximum conditional probability for that R-S interval. The horizontal axis is the proportion of the interval from completion of the response to shock. The time from initiation of a shuttle response until its completion is assumed to require about 5 sec, and fewer than 2% of all responses were made within 5 sec of the previous response. Therefore, the proportion of the interval elapsed was calculated starting with 5 sec and, consequently, the number of points varies for the different R-S intervals. The fact that the individual data points lie close to a straight line from the origin with a slope of one suggests that the rats in all conditions were timing the interval from the completion of a response in units that were proportional to the response-shock interval.

Table 1 shows the mean and standard deviation of the number of avoidance responses per minute, and the mean and standard deviation of the number of escape responses per minute, for each of the subjects during the last five sessions under each of the conditions. The rate of avoidance responses was inversely related to the R-S interval ($F = 296$, $df = 2$, 36 , $p < 0.001$), as was the rate of escape responses ($F = 88.2$, $df = 2$, 36 , $p < 0.001$). The proportion of responses that were escape responses was also inversely related to the R-S interval ($F = 79.7$, $df = 2$, 36 , $p < 0.001$).

DISCUSSION

The basic empirical results of variations in the R-S interval in unsignalled avoidance responding are qualitatively similar in the shuttlebox and the lever box. As the R-S interval is increased, rats in the unsignalled lever-box

Table 1
Mean Number of Responses per Minute
(Standard Deviation of Response Rates in Parentheses)

Subject	Avoidance R-S Interval (Seconds)			Escape R-S Interval (Seconds)		
	10	20	40	10	20	40
S1	6.12 (0.48)	3.50 (0.23)	2.27 (0.44)	1.12 (0.20)	0.18 (0.01)	0.04 (0.01)
S2	6.40 (0.29)	4.01 (0.38)	2.33 (0.12)	0.76 (0.21)	0.14 (0.04)	0.08 (0.02)
S3	5.83 (0.90)	3.78 (0.23)	2.24 (0.36)	1.39 (0.63)	0.17 (0.06)	0.05 (0.03)

situation (a) decrease the rate of avoidance responses, and (b) receive fewer shocks, which is equivalent to a decrease in the rate of escape responses (Clark and Hull, 1966; Sidman, 1953; Verhave, 1959). Similar results were obtained in the present experiment. In addition, there were decreases in the proportion of escape responses with increases in the R-S interval. As the R-S interval is increased, the conditional probability of response function of rats in the unsignalled lever box may show a more gradual rise (Sidman, 1966). A similar function was obtained in the present experiment.

The regular change in the response distribution as a function of changes in the R-S interval provides strong evidence for timing behavior by rats in the present experiment. Typically, an animal crossed from one compartment to

the other, turned around to face the opening between the compartments, and then waited a period of time before making another shuttle response. The simplest description of the temporal gradient of the avoidance observed in the present experiment suggests that the timing began with response completion, and that it occurred in units proportional to the R-S interval. Under all of the R-S interval conditions of the present experiment, the relative response rate was always approximately equal to the proportion of the R-S interval. The data therefore support the notion that rats in unsignalled avoidance are estimating time, and that the units of the estimate are proportional parts of the response-shock interval.

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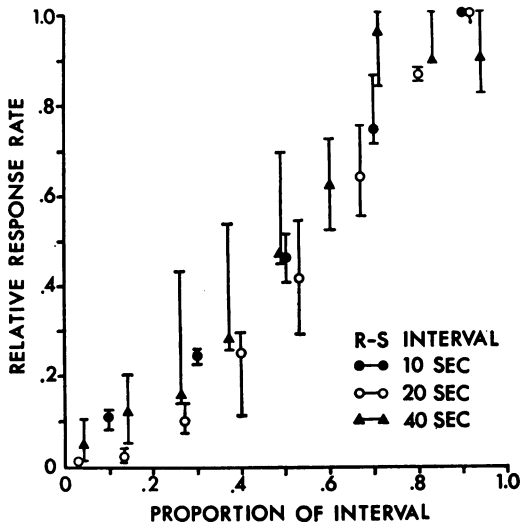


Fig. 2. Response rate relative to maximum response rate of subject as a function of the proportion of the interval from response completion to shock. The points indicate the median and the lines indicate the range of the three subjects.

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