

than intermittent stimulation. This suggests that the continuous stimulation used in our experiment did not significantly impair learning because it was less conducive to the development of competing ("superstitious") responses which might tend to interfere with the acquisition and performance of the "correct" response (9). (ii) In our study the stimulation was relevant to the testing situation in that it induced the animals to consume the food in the goal box. In the other studies the stimulation was not shown to have any such relevance. (iii) There is some evidence that highly motivated rats can overcome the disruptive effects of positively reinforcing brain stimulation (10), and that rats receiving lateral hypothalamic stimulation are more highly motivated to obtain food than are rats which have been deprived of food for up to 7 days (11). Although in the present experiment satiated animals received the minimum current intensity which would reliably induce eating, it is possible that, even at this threshold level, lateral hypothalamic stimulation produces a degree of hunger which is sufficiently high to overcome any deleterious effects of positively reinforcing brain stimulation on the learning of instrumental responses to obtain food.

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4. Positively reinforcing brain stimulation delivered to septal or hypothalamic loci at the onset of an auditory stimulus severely impairs the learning of a discriminative response to the stimulus [L. Stein and E. Hearst, *Amer. Psychol.* **13**, 408 (1958)]. Positively reinforcing lateral hypothalamic stimulation has been reported to disrupt performance on a food-rewarded, discrimination-reversal maze problem [M. E. Olds and J. Olds, *J. Comp. Physiol. Psychol.* **54**, 838 (1961)]. The disruptive effect is apparently not restricted to situations in which positive reinforcers are used to motivate learning; similar effects are reported in a study of shock-avoidance learning by R. M. Cooper and J. H. Bauer, *Can. J. Psychol.* **17**, 338 (1963).
5. Histological examination revealed that the electrode tips were located in the lateral hypothalamic "feeding area" as defined by Coons (2).
6. On rare occasions three of the animals left the goal area before 10 seconds elapsed. When this occurred, the animal was allowed to return to the choice point, where it was picked up and held for the remainder of the 10-second period.

7. The final 20 criterion trials were excluded in computing the learning scores reported here.
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18 June 1965

Temperature Independence of an Arbitrary Temporal Discrimination in the Goldfish

Abstract. Goldfish were taught to press a lever for food reinforcement and were placed on a 1-minute fixed-interval schedule. They developed the characteristic temporal discrimination (scalping) seen in rats and pigeons. There was no change in their relative response rate through the 1-minute interval when ambient temperature was decreased by 10°C. This 10°C temperature drop, which approximately halves the metabolic rate, approximately halved the absolute response rate. These results indicate that a temporal discrimination can be established in the goldfish, and suggest that discriminations of short intervals in fish are not dependent on a mechanism tied directly to metabolic rate.

A great deal is known about natural behavioral and physiological rhythms in the animal kingdom. These rhythms usually have a period of about 24 hours (circadian rhythms) and seem to reflect the operation of an endogenous clock, influenced by environmental factors. Much less is known about learned temporal discriminations involving short and arbitrary time intervals, although a few mammals and birds have been taught to perform particular responses at certain short intervals (1, 2). One purpose of the experiment described herein was to determine whether similar temporal discriminations can be established in a poikilotherm, the goldfish. Wolf and Baer (3) recently reported that such discriminations could be established in a single gourami fish maintained on fixed-interval schedules, but Gonzalez, Eskin, and Bitterman (4) failed to establish temporal discriminations in the African mouth breeder, *Tilapia macrocephala*.

Should a temporal discrimination be demonstrated in the goldfish, it could then be tested for temperature dependence to determine whether the "timing mechanism" is tied to metabolic rate. A number of circadian rhythms are not dependent on temperature (5). However, it has been suggested that variations in the diurnal environment may play some role in this independence (6). A discrimination involving arbitrary short intervals is almost certainly not correlated with significant environmental (diurnal) changes, and thus pro-

vides a possible means of analyzing a timing mechanism.

Three goldfish, *Carassius auratus*, were employed in the first part of this study. They were kept in small aquariums at a constant temperature of 30° ± 0.1°C and were trained to press a lever (7). Each time the lever was pressed, one white worm (*Enchytraeus albidus*) was released into the tank by an automatic dispenser (8). The fish were trained for 30 to 40 minutes each day in their home tanks. After a few days, they were required to press the lever three times in order to receive each worm, and then training on a temporal discrimination was begun. The same conditions prevailed for the rest of the experiment. The fish were trained on a 1-minute fixed-interval (FI-1) schedule. After the fish had received a worm for pressing the lever, a

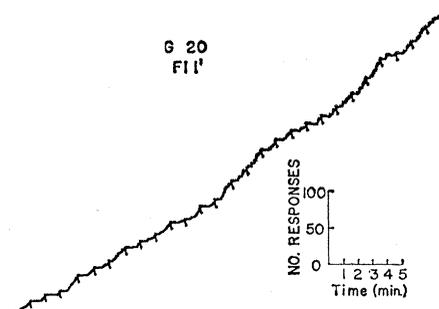


Fig. 1. Cumulative record of one session from a well-trained fish (G 20) on a 1-minute fixed-interval schedule (FI-1). Downward "blips" indicate delivery of reinforcement. Scale, lower right.

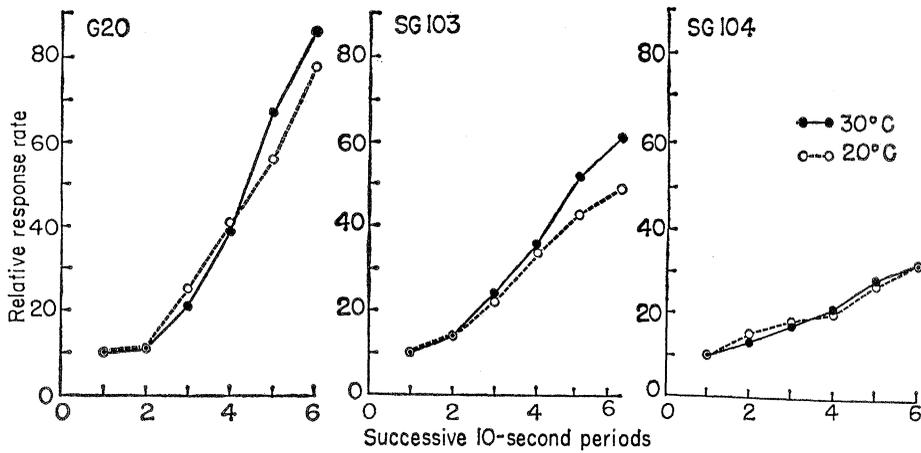


Fig. 2. Distribution of responses in 1-minute interval for each fish at 30°C and 20°C. The number of responses in the first 10-second period at each temperature was arbitrarily set at 10, and the other values were adjusted proportionately.

green light above the tank was operated for 5 seconds. During this time, the lever was inoperative. When the light went off, a 1-minute timer began operation. While the timer was operating, lever presses were recorded but not reinforced. At the end of 1 minute, the reinforcement was again available: the next time the fish pressed, it received one worm. The 1-minute timer started again when the light accompanying reinforcement went off.

Rats and pigeons show a characteristic performance after several sessions of training on this FI-1 schedule (1). They typically do not respond in the period immediately following reinforcement, and then show a positively accelerating response rate, terminated by reinforcement.

The three fish used in this experiment showed a similar pattern of response after they were exposed to this schedule for 30 to 60 sessions of approximately 30 minutes each. Figure 1 shows a good record for one session from a well-trained fish. In most of the 1-minute intervals, the fish responded slightly or not at all during the first part of the intervals, and then showed a positively accelerating rate. In order to analyze the temporal discrimination, each 1-minute interval was broken up into six consecutive 10-second periods, and response frequencies were tabulated for these periods. Well-trained fish responded 3 to 8 times as often in the 50th to 60th seconds (6th period) as they did during the first 10 seconds (1st period).

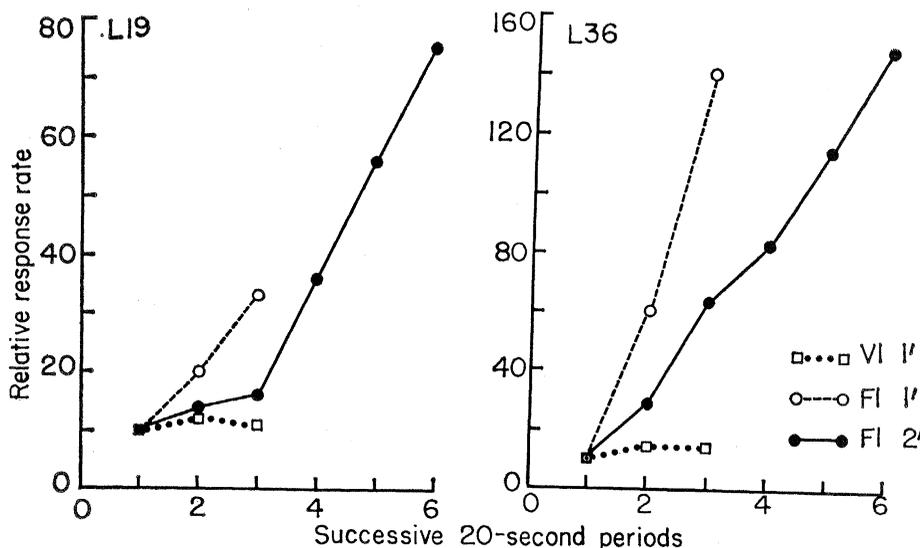


Fig. 3. Distribution of responses in 1- or 2-minute intervals for two fish on FI-1, VI-1, and FI-2 schedules at 25°C. Each curve represents data from four sessions. The curve for VI-1 represents the distribution of responses in the 1-minute intervals of the VI-1 schedule. The number of responses in the first 20-second period on each schedule was arbitrarily set at 10, and the other values were adjusted proportionately.

When the discrimination was stabilized, studies of temperature dependence were begun. Two days of performance at 30°C were followed by two at 20°C, and then two at 30°C. These temperature changes were effected within 3 hours following the end of the last session at either temperature. This 6-day experimental series was repeated 5 times for each of the three fish. Each 6-day series was separated from the next by at least 2 days of regular sessions at 30°C.

The three fish responded 1.86, 1.87, and 2.27 times as frequently at 30°C as they did at 20°C, so that their response rate approximately doubled along with their metabolic rate. Typically, a fish at 30°C pressed the lever about 250 times in 30 to 40 minutes. Curves showing the increase in relative response rate over the 1-minute interval at 20°C and 30°C are plotted in Fig. 2. The number of responses in the first 10-second period of each interval was arbitrarily set at 10, and the other response rates were adjusted relative to this. (For example, if the fish responded 5 times as often in the sixth 10-second period as in the first, a value of 50 would be plotted in Fig. 2 for the sixth period.) The curves for low and high temperatures match very closely for each fish. Though metabolic rate is cut approximately in half by the drop in temperature from 30° to 20°C (9), the increase in relative rate of response over the 1-minute interval remains constant. This is particularly clear in the curve for G 20, which is obviously nonlinear. At both 30°C and 20°C, fish G 20 shows a fairly constant and low rate of response through the first 20 seconds, followed by an abrupt increase in rate. If the temporal discrimination were dependent on temperature, or, in other words, if the fish's "clock" were slowed down by the temperature drop, one would predict that the onset of abrupt responding would come later and that the relative rate of increase in responding would be lower at the lower temperature. The invariance of relative response curves over a 10°C temperature range stands in contrast to these predicted differences, and suggests that this temporal discrimination is independent of temperature.

The analysis of this data depends on two assumptions: (i) the changes in relative response rate described here represent a true temporal discrimination, and (ii) the temperature invariance of relative response rate is not due

to rapid relearning of a "new" interval at the new temperature. To test these assumptions, a further experiment was performed on two other goldfish; the same basic situation was used as before and the temperature was kept at 25°C. The fish were trained on a 1-minute fixed-interval (FI-1) schedule (36 days), then a 2-minute fixed-interval (FI-2) schedule (36 days), and finally a 1-minute variable-interval (VI-1) schedule (21 days). In the variable-interval schedule, reinforcements within each session were separated by varying time intervals ranging from 3 minutes to a few seconds, averaging 1 minute. Performances during the last 4 days on each schedule were compared, with only the 1-minute intervals on the variable-interval schedule being used. The plot of relative response rate shown in Fig. 3 indicates that there is a slower acceleration in response rate under a longer (2-minute) fixed-interval schedule. Furthermore, on the VI-1 schedule, where reinforcements follow one another more or less randomly in time, there is no increase in relative response rate over the 1-minute interval. Response patterns on the initial days of FI-2 resembled those for the FI-1 schedule, suggesting that in the first experiment the fish could not rapidly relearn a discrimination based on a "new" interval.

This research shows that although absolute response rate is dependent on temperature, relative response rate is not. It appears then that the patterning of responses in a temporal discrimination is independent of temperature. The results suggest that the 1-minute temporal discrimination shown by these fish is not dependent on a mechanism directly tied to metabolic rate.

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Geniculate Unit Responses to Sine-Wave Photic Stimulation during Wakefulness and Sleep

Abstract. *The oscillation in firing rate of units of the lateral geniculate body in response to stimulation with sine-wave light was studied in unanesthetized cats with the brainstem sectioned immediately in front of the fifth nerve (pretrigeminal preparation). During wakefulness, as indicated by behavior and by electroencephalograms, the time course of the oscillation in firing rate followed very closely the change in intensity of sine-wave light. During synchronized sleep there was no such relationship.*

Hughes and Maffei (1, 2) studied the transfer properties of the cat's retinal ganglion cells in response to sine-wave light stimuli at different frequencies and found a very close relation between the time courses of stimulation and response. Even for quite low frequencies of light (as low as 0.01 cy/sec), the oscillation in firing rate shown by retinal ganglion cells was an almost perfect replica of the sine-wave photic stimulation.

In the experiments described here our aim was to investigate the response of single units of the lateral geniculate body (LGB) to stimulation with sine-wave light. We show that the behavior of these units is strikingly different during wakefulness and during synchronized sleep.

We used cats in which the brainstem was sectioned immediately rostral to the exit of the fifth nerve [midpontine pretrigeminal preparation (3)]. Pupils were dilated with atropine. Extracellular spikes were recorded by microelectrodes inserted in the dorsal nucleus of the LGB. The technique (2) can be summarized as follows. The light source was a Sylvania glow modulation tube 1130B, driven by a low-frequency oscillator (Hewlett-Packard). To average the rate of response and reduce random variations of cell firing, a Mnemotron computer of average transients (model 400B), including a modulator by-pass card, was used. The averaging time, the number of intervals per period, and the number of responses averaged were externally controlled and synchronized with the sine-wave generator. The EEG was continuously recorded through screws implanted in the skull.

Cats prepared in this way exhibit spontaneous periods of synchronized sleep and wakefulness, the EEG and

behavioral patterns of activity prevailing after midpontine transection (3). In good agreement with observations of free-moving cats (4) the spontaneous firing of LGB units is strikingly affected by sleep and wakefulness. During wakefulness the spontaneous activity is random; during sleep there are short-lasting, high-frequency bursts of activity (300 to 500) with long intervals of silence between (100 to 600 msec).

During periods of wakefulness (indicated by behavior and by the EEG's), the responses of the LGB units followed the light changes very closely (Fig. 1A) at the different frequencies of stimulation (from 0.1 to 1 cy/sec). The response was quite similar to that of retinal units (1, 2). The "on" cells were almost in phase with the stimulus, the "off" cells 180° out of phase (see Fig. 1, A and B), and the "on-off" cells showed a phase relation between the stimulus and response in the region between 0° and 180°. During synchronized sleep every relation between sine-wave stimulus and response was

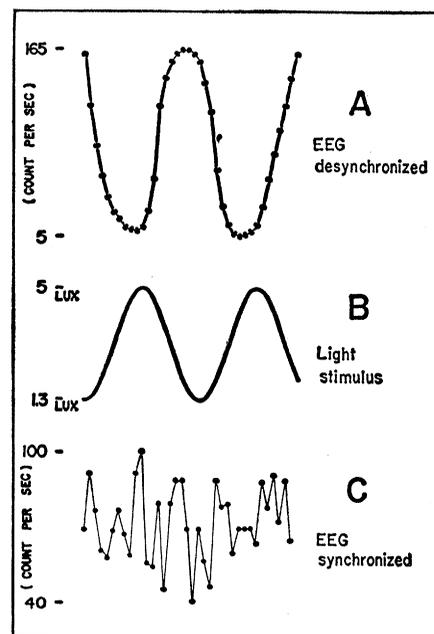


Fig. 1. Time course of firing rate of an "off" LGB unit in response to stimulation by low-frequency sine-wave oscillation of light intensity. Frequency of sine-wave oscillation, 0.1 cy/sec. The position of the dots (20 per cycle) gives the average frequency of firing: each measurement was made every 500 msec and 10 cycles were averaged by the Mnemotron computer. All numbers were converted to cycles per second by dividing the spike count by the duration of the interval. The time relation between stimulus (B) and response (A, C) are carefully preserved. The scales of abscissas and ordinates are linear. Synchronization of the EEG (in C) occurred spontaneously.