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RESEARCH NOTE

BEHAVIORAL CONFIRMATION OF THE "SILENT PERIOD" DURING ADAPTATION TO BRIGHT LIGHTS

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The "silent period" is an interval of time following the onset of an intense background during which there is absolute refractoriness to incremental light stimuli. The phenomenon has been reported to occur at all levels of retinal processing in the skate (Dowling and Ripps, 1970, 1971, 1972; Green, Dowling, Siegel and Ripps, 1975), in the ERG of several other elasmobranchs (Hamasaki and Bridges, 1965), and in the retinal ganglion cells of the goldfish (Raynauld, 1969; Beauchamp and Daw, 1972). The possibility that the effect occurs only in isolated preparations of retinal tissue (which may be less responsive than the same tissue in an intact animal) can be eliminated on the basis of the results of Hamasaki and Bridges (1965) and Beauchamp and Daw (1972), who found it in intact paralyzed preparations. This note provides further confirmation of the existence of the silent period by showing that restrained but otherwise normal goldfish do not respond behaviorally to incremental light stimuli for several minutes following onset of an intense background.

We carried out two experiments, using two different behavioral techniques. In one, goldfish were conditioned to respond to increases in the intensity of a large spot of light. In the other, they responded reflexly, using optokinetic nystagmus (OKN), to movements of a striped drum.

Experiment 1. *Classical conditioning of respiratory rate*

The apparatus and procedures we used have been described in detail before (Powers and Easter, 1978a). Briefly, the unanesthetized fish was restrained in a box with its right eye near a diffusing screen. Visual stimuli were back-projected onto the screen, and the animal's respiration was monitored by means of a thermistor placed near its mouth (Northmore and Yager, 1975). After presentation of the visual stimulus had been followed by an electric shock to the tail for several trials, the fish's respiration rate typically slowed markedly as soon as the light appeared, and remained depressed until after the shock was delivered. When the rate slowed to half its usual value, we considered that the fish had responded to (and therefore had detected) the light. Catch trials, wherein no light was presented but all other conditions remained the same, were inserted in most sessions. Shock occurred on every trial, and trials were spaced at least 1 min apart.

The three subjects in this experiment had participated in earlier studies (Powers, 1978; Powers and Easter, 1978a,b), during which they had been conditioned to respond to increases in the intensity of a large spot of light near absolute threshold. For the present experiment the fish were conditioned to respond similarly at photopic levels of illumination.

The stimulus conditions and procedures during training were as follows. A background of 532 nm light (Optics Technology interference filter), about 130° in diameter and 5.7 log units above absolute threshold (Powers and Easter, 1978a), was on continually. Once every 1–2 min a circular wedge was electronically rotated to increase the intensity of the entire field by 0.5 log unit. After 5 sec the shock was delivered and the wedge was returned slowly by hand to its resting position, thus reinstating the original background intensity. The fish were given 10 trials per session until they responded to the increase in intensity on at least 8 trials. All three subjects met this criterion during the third session, and were tested for the presence of a silent period the next day.

Just before the test, we assessed each fish's general responsiveness. They were dark-adapted for 30 min to 2 hr, then exposed to a 532 nm background that was only 0.7 log unit above absolute threshold. After 20–25 min adaptation to the dim background, the conditioned response to 0.5 log unit increments of the background was measured. There were 5 trials and one catch trial in this pretest. Each fish responded on at least 4 of the 5 trials, and none responded during the catch trials (see Fig. 1). The results of this test, carried out on each fish immediately before it was tested with the intense background, showed that the subjects were capable of responding to the incremental stimulus.

Following the dark-adapted pretest, the intensity of the background was increased 5.0 log units by quickly removing neutral density filters from the beam. The background conditions at this time, and for the rest of the test, were identical to those during training. Increments of 0.5 log unit were presented in the same way as before, and we measured the per-

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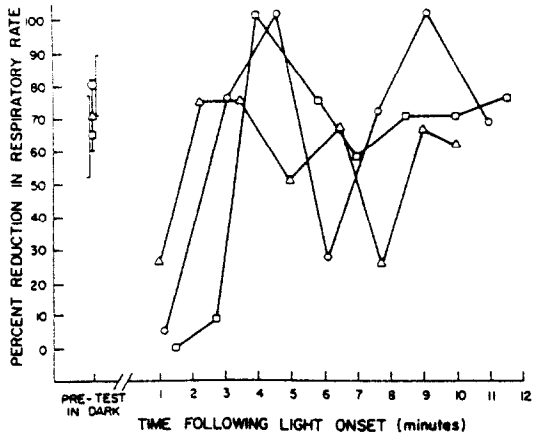

Fig. 1. Silent period during conditioned responding. The reduction in respiratory rate is expressed in terms of the difference, as a percentage, between pre-stimulus rate and rate during presentation of the conditioned stimulus, an 0.5 log unit increase in intensity of a 532 nm light. This value is shown for three different fish as a function of the time elapsed from onset of a 532 nm background light that was 5.7 log units above absolute threshold. The points on the left represent mean (± 1 S.E.M.) measurements on the same fish when the 0.5 log unit increment was on a background only 0.7 log units above threshold. All three fish responded poorly for 1–2 min following onset of the background.

cent reduction in breathing rate during each presentation. The results are shown in Fig. 1.

All three fish responded poorly during the first 1–2 min following sudden light adaptation. The reduction in their breathing rates during presentation of the incremental stimulus was only about 10–20%, compared to a reduction of more than 70% during presentation of the same increment while dark adapted (Fig. 1). After 3–4 min of adaptation to the intense background, however, the reductions in breathing rate were similar in magnitude to dark-adapted values.

These results alone would seem to confirm the existence of the silent period on a behavioral level. However, we were uneasy with them. We were concerned that the effect illustrated in Fig. 1 was due not to sensory factors, but to some nonsensory interfering factors such as "fear" of or "inattention" to the conditioned stimulus. Such factors could have interfered with the performance of a conditioned task, while having nothing to do with whether the stimulus was visible or not. Our uneasiness was increased by our observation that the interstimulus, baseline respiratory rates of all three animals were very irregular for about 5 min following onset of the intense background. In an attempt to avoid these complications, we carried out a second experiment using a reflex behavior, which we assumed would be relatively uninfluenced by such factors as fear.

Experiment 2. Optokinetic nystagmus

The apparatus and procedures we used have been described in detail before (Easter, 1971, 1972, 1975). Briefly, the unanesthetized fish was restrained in a sponge-lined holder and placed in a water-filled transparent plastic cylinder. The cylinder was held stationary inside a large vertically-striped drum, which could be rotated. The drum subtended about 100° vertically and 240° horizontally. The alternating black and white stripes were about 7° each, and their reflectances differed by 1.3 log unit. When the drum was rotating, its velocity was 15°/sec or 30°/sec. An opaque rigid stalk, which moved with the eye, was attached to the cornea of each eye by suction. A flying spot scanner sampled the orientation of each stalk in the horizontal plane, and these data appeared on a chart recorder.

The four subjects in this experiment were 10–13 cm in total body length. None of them had participated in any previous experiment. All were tested for and showed the presence of normal spontaneous eye movements (Easter, 1971) and OKN (Easter, 1972) before this experiment began.

Fish were dark adapted at least 1 hr, then placed in the restrainer under dim red illumination. They were allowed 35–45 min further dark adaptation in the apparatus, with the room in total darkness. Then the drum was set in motion and the (fluorescent) room lights or room lights plus two photoflood bulbs

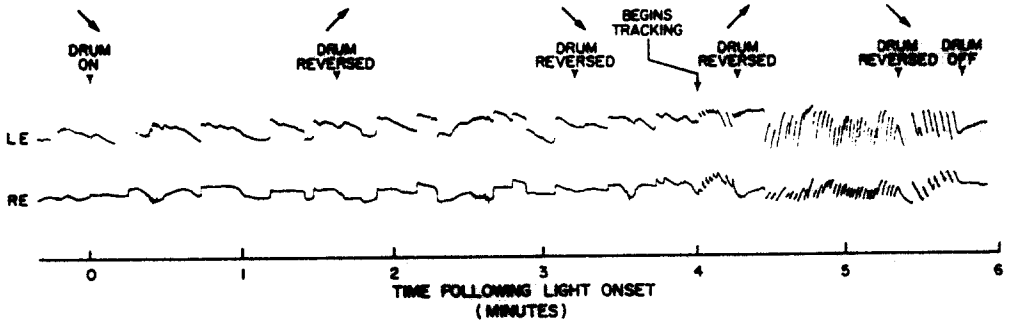

Fig. 2. Silent period for OKN. This is a record from one fish. Movements in the horizontal plane are shown for the left eye (top trace) and the right eye (bottom trace). A time scale has been drawn below the record, relative to the time the striped drum was illuminated with white light about 12.2 log units above threshold. Arrows above the trace indicate when the drum began to rotate, as well as when it was reversed. The arrows on top show the direction of the smooth pursuit component that should appear in the trace if the fish is performing OKN. Note that the fish did not begin tracking the drum until about 4 min had elapsed.

Table 1. Silent period for OKN

Fish no.	Dark adaptation (hr)	Background intensity (log)*	Latency to normal OKN (min)
11/1	1.25	10.7	1.92
23/1	5.67	12.2	1.88
23/2	6.67	12.2	4.05
23/3	7.58	12.2	2.93

* The value is shown relative to absolute threshold for 532 nm light in the goldfish (Powers and Easter, 1978a).

were simultaneously turned on. The illumination of the white stripes by the room lights was 1.0 log ft-L, and the room lights plus photofloods 2.5 log ft-L. A comparison of these measurements (SEI photometer) with similar measurements of the light used in the conditioning experiments indicates that the white stripes were 12.2 and 10.7 log units above absolute threshold, with and without photofloods, respectively.

Figure 2 shows a record from one fish during this experiment. The fish had been dark adapted for 6 hr 40 min, and was making normal spontaneous eye movements in the dark before onset of the background light. After onset of the intense background, the eye movements continued to appear spontaneous, even though the drum was rotating. The exact point where tracking began is difficult to define; the left eye tended to drift in the direction of the drum at about 3 min 45 sec, while the right eye showed no such tendency until later. It is clear, however, that only after the background had been on and the drum had been rotating for more than 4 min did normal OKN begin in both eyes. Table 1 summarizes the results from all four fish.

The results of both behavioral experiments are consistent with the existence of a period of reduced visual sensitivity during initial exposure to intense backgrounds. The duration of the insensitivity we found —1–4 min—is similar to the duration others have observed while recording from ganglion cell axons in the intact goldfish (Beauchamp and Daw, 1972) and while recording the *b*-wave of the ERG from skate eyecup (Green *et al.*, 1975), using backgrounds of similar intensity. Longer durations—up to 30 min—have been observed in preparations of isolated goldfish retina (Raynauld, 1969) and skate eyecup (Dowling and Ripps, 1970, 1972), using intensities in the same range as ours.

Although we did not attempt to determine thresholds during the silent period, those who have (Dowling and Ripps, 1971, 1972; Beauchamp and Daw, 1972; Green *et al.*, 1975) find that the system appears to be saturated; no increment they used was bright enough to elicit a response. However, there are two interesting differences between the conventional conception of saturation and the silent period phenomenon. First, the silent period can occur at relatively low intensities—in one instance at only 4 log units above threshold (Green *et al.*, 1975). Second, it is transient; in all cases reported in the literature, as well as our own, light-induced responses can eventually be elicited on the same intense background that previously had been saturating.

While the mechanism of the silent period remains a mystery, some possibilities can probably be eliminated. For example, it is unlikely that retinomotor movements are responsible, as suggested by Beauchamp and Daw (1972), because the time course of the movements of rods and cones relative to one another (cf. Ali, 1975) is much longer than the duration of the silent period we have observed. Likewise, the suggestion that the silent period is purely a rod-mediated response (Dowling and Ripps, 1970) seems unlikely because (1) it occurs in the behaving goldfish, which has a duplex retina with cones that are sensitive at both very low (Powers and Easter, 1978a) and high (Powers, 1978) intensities, and (2) it has been reported to occur in a goldfish retinal ganglion cell that had input only from cones (Beauchamp and Daw, 1972).

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