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Frequency of intermittent photic stimulation: Effect on photic afterdischarges, photic driving, and behavioral activity

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The effects of various frequencies of intermittent photic stimulation (1/7, 1/3.5, 1/1, 3/1, 6/1, 9/1, 15/1, 18/1, 24/1, and 60/1 sec) on photically evoked afterdischarges (PhADs), photic driving (PD), and behavioral activity (gridcrossings) were examined in rats. Results demonstrate that frequencies from 3/1 to 60/1 sec induced reliable increases in behavioral activity. Well elaborated PhADs were elicited only at frequencies of 1/7, 1/3.5, and 1/1 sec, but only when behavioral activity was at a minimum. While PhADs could be elicited during the frequencies of 3/1-, 6/1-, and 9/1-sec stimulation, the predominant pattern was one of PD. With frequencies of 15/1, 18/1 and 24/1, the cortical EEG pattern was primarily one of PD. These results suggest that PhAD suppression by fast intermittent stimulation, per se, occurs only at frequencies of 9/1 sec and higher, suppression at lower frequencies being a result of behavioral activation by intermittent stimulation.

Documentation has come from several laboratories that, as behavioral activation increases, the late components of the rat visually evoked potential decrease in amplitude and photically evoked afterdischarges (PhADs) become either suppressed or totally absent (Bigler & Fleming, 1976a, b; Bigler, Fleming & Shearer, 1976; Fleming & Bigler, 1974; Kimura, 1962; Pickenhain & Klingberg, 1965; Schwartzbaum, 1975). In a recent study, Yellin and Jerison purported to demonstrate that PhAD suppression could be attributed to interstimulus interval (ISI) effects, with shorter ISIs resulting in greater PhAD suppression. However, in our research we have found that PhADs could be elicited at ISI frequencies which Yellin and Jerison reported to completely suppress PhAD activity. In the present series of experiments, we sought to clarify these conflicting results by assessing and controlling for the effects of ISI frequencies on PhAD activity, induction of photic driving (PD), and on behavioral activity.

METHOD

Nine adult Holtzman albino rats were prepared with indwelling visual cortical electrodes positioned over the primary visual cortex, according to procedures previously described by Fleming and Bigler (1974). A detailed description of the apparatus has also been described by Fleming and Bigler (1974). Briefly, it consisted of a Plexiglas grid-floor chamber with a slip-ring connector located in the ceiling. All four sides and a sliding surface located beneath the grid were painted flat white. A Grass Model PS22 photostimulator was centrally placed in the overlying clear Plexiglas. By this means, each light flash met the unrestrained animal in all positions of location at nearly the same intensity (5 fc). Movement activity was measured by four intersecting photocell beams. Interruption of a beam resulted in an increment of a BRS/LVE counter and a pen deflection on the EEG record. Thus, the subject was allowed to freely ambulate at all times, while brain EEG responses and movement activity were simultaneously monitored. The apparatus was enclosed in a darkened electrically shielded room. All conditions were carried out in unanesthetized animals with mydriatic pupils (5% atropine sulfate). Brain responses were amplified with Grass 5P5 preamplifiers and Model 5 polygraph driver amplifiers (band-width, .3-60 Hz), and ink written records were obtained.

The experiment proper was carried out in the following manner. Each subject was placed in the Plexiglas chamber, connected to the slip ring, and allowed to dark adapt and acclimate to the experimental apparatus for 15 min. Following the elapse of 15 min, a 1-min period of movement activity was monitored and scored. Following this control period, iterative photic stimulation was initiated at a randomly selected frequency: 1/7, 1/3.5, 1/1, 3/1, 6/1, 9/1, 15/1, 18/1, 24/1, and 60/1 sec (10-μsec light pulse). Iterative stimulation was maintained for 1 min, during which time activity was also monitored and scored. As a post-iterative stimulation control, the 1 min following iterative stimulation was also monitored and scored for activity. Five minutes were then allowed to elapse before iterative stimulation was resumed at a different randomly selected frequency. The entire procedure yielded three measures of activity and one measure of visual cortical EEG responding for each frequency tested. The entire procedure took approximately 65 min to complete. During iterative stimulation, the cortical EEG was examined and scored for the occurrence of PhAD bursting, and/or PD activity

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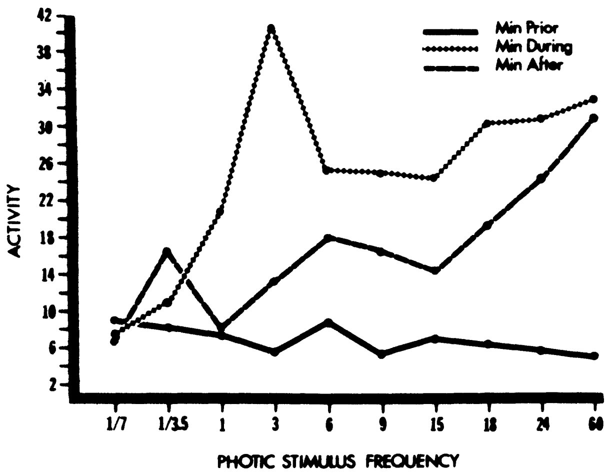

Figure 1. The effects of different frequency rates of photic stimulation on behavioral activity counts.

concomitant with the presence or absence of grid-crossing activity.

RESULTS AND DISCUSSION

The behavioral results are summarized in Figure 1. Changes in iterative frequency stimulation produced corresponding and systematic changes in activity ($F = 9.36$, $df = 29/232$, $p < .001$). Mean pair comparisons (Newman-Keuls tests) revealed that the increased activity during 3/1 stimulation could be significantly differentiated from all other periods of changes in activity. Increased activity during periods of 6/1, 9/1, 15/1, 18/1, 24/1 and 60/1 sec also could be reliably differentiated from preiterative stimulation activity scores and from activity scores recorded during 1/7- and 1/3.5-sec stimulation.

Well elaborated PhADs were only elicited at frequencies of 1/7, 1/3.5, and 1/1 sec, and only when behavioral activation was at a minimum. Photic driving predominated during 3/1-, 6/1-, and 9/1-sec stimulation, but some PhAD activity, particularly at 3/1-sec stimulation, could be elicited and sustained but, again, only when behavioral activation was at a minimum. With frequencies of 15/1, 18/1 and 24/1 sec, the cortical EEG pattern was mainly one of photic driving. Stimulation of 60/1 sec produced flicker fusion, which did not alter cortical EEG except at onset.

These results suggest that suppression of PhADs during ISI frequencies ranging from 1/7 sec to 6/1 sec is dependent mainly upon a by-product of behavioral activation which indirectly suppresses PhAD bursting (see Bigler & Fleming, 1967a, b; Bigler et al., 1976; Fleming & Bigler, 1974). If the novelty and/or aversive qualities of fast-frequency intermittent stimulation can be controlled for (i.e., through habituation training), well elaborated PhADs can be recorded at these frequencies. At even faster ISI frequencies (9/1 to 24/1 sec), photic driving predominates, and it is only at these levels that PhADs are likely blocked as a true result of ISI frequency.

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