Differential effects of reinforced and non-reinforced stimuli upon electrocortical recruiting responses¹

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Abstract

Cats trained in a classical differential conditioning situation exhibited the same pattern of EEG desynchronization during both the reinforced (CS) and non-reinforced (DS) stimuli, although they responded only to the former. In contrast, thalamically induced electrocortical recruiting responses, evoked prior to stimulus onset, were differentially affected; recruiting was attenuated by the CS but not by the DS. The results demonstrate the sensitivity of recruiting responses in the absence of gross EEG changes, and suggest that reticulothalamic interactions may comprise part of the neural substrate of attention.

Problem

The search for electroencephalographic (EEG) correlates of behavior is characteristic of many attempts to understand the neural bases of learning, perception, and attention. Alterations in electrocortical activity during the presentation of stimuli have been noted in a variety of situations. For example, investigators have reported that, during classical conditioning, the presentation of a non-reinforced stimulus results in the appearance of high-amplitude cortical slow waves which are typical of drowsiness or sleep (Gluck & Rowland, 1959; Kogan, 1960). This phenomenon has been observed during habituation, extinction, and differentiation, when stimulus presentation does not elicit a response.

In a recent study of classical differential conditioning, Weinberger et al (in preparation) failed to find cortical slow waves consistently during presentation of the non-reinforced stimulus. The EEG was often of low-voltage, fast activity (i. e., desynchronized) during both the conditioned (CS) and differential (DS) stimuli, although the behavioral effects of these stimuli were quite different. That is, Ss maintained orientation to the foodcup throughout the CS and often licked it during the last second of the CS-US interval. However, they turned away from the cup and often lay down during the presentation of the DS. The present report concerns a subsequent attempt to find a measure of electrocortical activity which was more sensitive to differential stimulus effects than was the spontaneous EEG. The method employed consisted of evoking electrocortical potentials by stimulation of recruiting sites in the thalamus and observing alterations in these evoked waveforms during the CS and DS.

Method

The Ss were two of the four adult cats used in the foregoing experiment. They were chosen for further study because, in addition to extra-dural screw elec-

trodes, they also carried bipolar stimulating electrodes (0.010" stainless steel, Epoxylite insulated wires, bared at their tips) in intralaminar regions of the thalamus. These placements were later histologically verified as being in n. centralis lateralis. Repetitive, low-frequency stimulation in this area produces electrocortical recruiting responses (Dempsey & Morison, 1942). The stimuli used in the present study were monophasic, square wave pulses at a frequency of 8 per sec., 0.5 msec. in duration, 2 to 5 v, produced by a Grass S-4 stimulator through SIU-4 isolation units. Stimulus current was monitored by measuring the voltage drop across a known resistance which was in series with the stimulating cathodal electrode. Stimulus current did not vary with changes in the amplitude of recruiting responses.

The reinforced, i. e., conditioned stimulus, consisted of dim light flashes at the rate of 2 per sec. from a row of six lamps mounted above the foodcup; the differential, i. e., non-reinforced stimulus was constant illumination of the stimulus lamps. The unconditioned stimulus was 4 cc of milk, delivered at CS termination. The CS or DS to US interval was 10 sec. Fifteen trials were given during a daily session, five DS trials being interspersed among 10 CS trials; inter-trial intervals averaged 2 min. The cats were maintained at 75-80% ad lib weight throughout the experiment. Both of the Ss had undergone this classical differential conditioning procedure for the preceding three months, and were overtrained, i. e., they no longer responded to the DS.

Results

The effects of stimulus presentation upon ongoing electrocortical recruiting responses were identical for both cats. Representative EEGs of one cat are presented in Fig. 1. The upper record depicts changes in recruiting during presentation of the CS. At stimulus onset, S oriented to the cup, as usual. Coincident with this, recruiting responses were blocked, that is, greatly attenuated in amplitude, and remained attenuated throughout the CS. In contrast, except for an initial brief orientation at the onset of the non-reinforced differential stimulus, the cat remained inactive behaviorally and appeared inattentive. In the lower record, it can be seen that there is a brief reduction in recruiting, coincident with S's orientation at DS onset. Orientation was not maintained, and recruiting returned to normal amplitude within 1 sec., and remained so throughout the remainder of the DS. Behavioral orientation, whether spontaneous or stimulus induced, was invariably accompanied by blocking of recruiting. However, gross movements were not necessary for this effect, as blocking of these potentials

persisted during the balance of the CS, when S was not moving. Blocking of recruiting was most effective when stimulus voltages were barely supra-threshold. At such voltages, stimulation caused no movement and response latencies to the CS were unchanged. During control trials without recruiting stimulation, the EEG was desynchronized during both the CS and DS.

Extinction of the blocking of recruiting effect by the CS could also be demonstrated. Figure 2 illustrates the effects of non-reinforcement of the conditioned stimulus. No milk was delivered on trials 16 through 20. On trial 16, the CS diminished recruiting, as usual, but during succeeding CS presentations, recruiting became more prominent and was virtually of normal amplitude during trial 20. Reinforcement was then reinstituted, and by trial 23, and CS once again caused an attenuation of recruiting responses.

Discussion

The present findings indicate that thalamically induced cortical recruiting responses are more sensitive to the differential effects of reinforced and nonreinforced stimuli than is the spontaneous electroencephalogram. Blocking of recruiting appears to be highly correlated with attention, in agreement with the findings of Evarts & Magoun (1957). Stimulation of the brain stem reticular formation is known to block recruiting (Moruzzi & Magoun, 1949), and it has been well established that reticular stimulation is capable of producing arousal in sleeping animals, and attention in waking animals (Lindsley, 1960). It seems plausible that, in the present study, recruiting blockade was due to CS induced reticular activation. According to this interpretation, the amplitude of electrocortical recruiting may be utilized

Fig. 1. The effects of CS and DS presentation on recruiting responses elicited by stimulation of the right n. centralislat. eralis, 8/sec., 0.5 msec., 4.5 v. The onset of both stimuli causes initial orientation (OR!) with concomitant blocking of recruiting. The blocking continues throughout the CS, but is brief and transient during the DS. Slow waves in the top record, extreme right, are due to licking artifact following presentation of the US (milk). Abbreviations: R, right; L, left; F, frontal; O, occipital; SS, suprasylvian.

Fig. 2. The effects of discontinuation of reinforcement (extinction) following the CS. Recruiting responses, blocked as usual during CS presentation on trial 16, become progressively less attenuated during trials 17-20, following non-reinforcement on trials 16-20. Reinforcement was reinstituted following trial 20, and recruiting was once again blocked starting at trial 23. Recordings from right to left suprasylvian gyri. Calibration, 1 sec., 50 μ v.

as an index of the level of arousal in the absence of gross changes in the EEG. Thus, an aroused animal, exhibiting a typical desynchronized EEG, would show no further EEG changes when presented with an arousing stimulus (e. g., a conditioned stimulus), but would additionally exhibit an attenuation of recruiting responses. Electrophysiological analysis of interactions between recruiting potentials and the reticular formation should permit more definitive specification of the neural bases of attention than is presently available.

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Notes

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