Reports

Generalized Neocortical Responses and Corticospinal Neuron Activity

Abstract. Long-latency responses evoked by ipsilateral sciatic nerve and hippocampal-fornix stimulation in barbiturized cats are associated with activation of corticospinal neurons. Differences in latency and configuration of generalized responses and patterns of relayed corticospinal neuron discharges indicate that a variety of extrathalamic projections are involved in activation of Betz cells.

The existence of extrathalamic centripetal pathways to neocortex was originally inferred from data on the mode of propagation and distribution of long-latency generalized "secondary discharges" to peripheral nerve or brainstem stimulation in barbiturized animals (*1*, *2*). Despite the fact that these evoked responses may be of extraordinary magnitude in sensorimotor cortex, it has been suggested that they are not associated with discharges of pyramidal neurons that give rise to the corticospinal tract (*3*).

The present study, part of a series of investigations on the regulation of corticospinal neuron activity by nonspecific projection systems (*4*), was undertaken to define the relationship between corticospinal neuron activity and two varieties of long-latency generalized neocortical responses: secondary discharges and the responses described by Morison, Dempsey, and Morison that follow stimulation of "the corpus callosum or the immediately subjoined fibers of the fornix system" (*2*). The present study establishes that the latter responses are attributable to stimulation of the hippocampal-fornix system.

Experiments were performed on adult cats maintained at various depths of anesthesia by repeated injections of small amounts of thiopental sodium. The animals were prepared for recording of long-latency responses evoked in motor cortex by stimulation of the ipsilateral sciatic nerve and direct stimulation of the exposed ventricular surface of the dorsal hippocampus, fimbria, or fornix. Corticospinal neuron activity was recorded with 100-μ Teflon coated wires inserted into the medullary pyramidal tract or by means of extracellularly located saline-filled micropipettes in the motor cortex. Betz cells were identified by high-frequency (250 per second) stimulation of the medullary pyramidal tract.

The results summarized in Fig. 1 indicate that long-latency (35 to 80 msec) responses in anterior sigmoid gyrus (motor cortex) evoked by ipsilateral sciatic stimulation under moderately deep thiopental anesthesia were associated with temporally dispersed relayed corticospinal tract discharges (Fig. 1, *A–B*), as well as low-frequency discharges of Betz cells (Fig. 1, *D–F*). Betz cell discharges were usually superimposed on various components of evoked subsurface focal long-latency responses that were predominantly negative in configuration.

Subsurface focal responses were complexly related to secondary discharges recorded from the surface of the motor cortex, as were discharges of single Betz cells. Discharge frequencies of the latter elements ordinarily did not exceed 10 per second. Although the number of discharges in a particular response sequence was rarely greater than three or four, frequently a unit might fire once during the subsurface focal response or not at all.

Like the secondary discharge evoked by stimulation of the sciatic nerve, very long-latency responses elicited by direct stimulation of the exposed hippocampus, fimbria, or fornix were also associated with relayed discharges in the corticospinal tract (Fig. 1*C*). As pointed out by Morison, Dempsey, and Morison (*2*), such generalized neocortical discharges were similar but not identical in wave form and cortical distribution to evoked secondary discharges. Hippocampal-evoked generalized discharges were best obtained at deeper levels of barbiturate narcosis than those required for eliciting maximal secondary discharges. Under optimum conditions for demonstrating both varieties of long-latency generalized responses, associated relayed corticospinal tract volleys might be of equal magnitude despite the fact that hippocampal-evoked tract discharges were twice the latency of those elicited by ipsilateral sciatic nerve stimulation (Fig. 1, *B–C*).

Corticospinal neuron discharges were related to early components of sciatic-evoked secondary discharges in pericruciate cortex when the latter were of maximum amplitude and predominantly positive-negative in configuration.

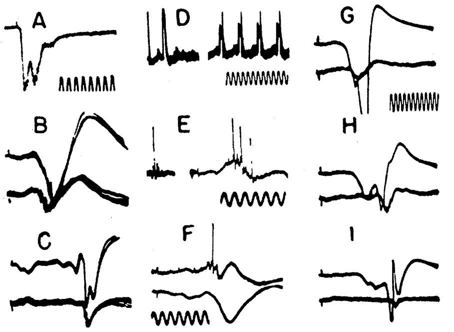

Fig. 1. (Three different experiments illustrated in *A–D, D–F*, and *G–I*.) *A*, Corticospinal tract discharges recorded in the medullary pyramidal tract following weak motor cortex stimulation; time calibration, 1000 cy/sec. *B* (upper channel), Secondary discharges recorded monopolarly from surface of motor cortex following ipsilateral sciatic nerve stimulation (0.5 per second). B (lower channel), Associated corticospinal tract discharges recorded as in *A*. *C* (upper channel), Surface responses to fimbrial stimulation recorded as in *B*. *C* (lower channel), Associated corticospinal tract volleys. Calibrations for *B* and *C* as in *A* but 100 cy/sec. *D*, Betz cell in motor cortex activated by 25 per second (left) and 250 per second (right) stimulation of medullary pyramidal tract. Calibration, 1000 cy/sec. *E*, Same unit as in *D*; (left), antidromic stimulation; (right), ipsilateral sciatic nerve stimulation. Calibration, 100 cy/sec. *F*, Betz cell discharge and surface-evoked secondary discharge to ipsilateral sciatic stimulation. Calibration, 100 cy/sec. *G–I*, Secondary discharges in motor cortex (upper channel) and relayed pyramidal tract volleys to ipsilateral sciatic nerve stimulation. Explanation in text. Calibration, 100 cy/sec.

During the relatively brief period in which it was possible to maintain a steady level of moderately deep thiopental anesthesia, secondary discharges evoked by 0.5 per second ipsilateral sciatic nerve stimulation were unaltered in latency and configuration (Fig. 1*B*). At deeper levels of narcosis the *first* of a train of 0.5 per second stimuli evoked a maximal secondary discharge and relayed tract activity associated with the surface-positivity of the motor cortex response (Fig. 1*G*). Successive stimuli elicited secondary discharges of longer latency and complexity which were associated with marked increases in the latency of relayed tract responses (Fig. 1*H*). Under these conditions, corticospinal tract volleys, though considerably reduced in magnitude, were associated with a prominent very long-latency (150 msec) triphasic component of the cortical surface secondary discharge which evolved during repetitive (0.5 per second) stimulation (Fig. 1*I*). At this stage, secondary discharges were completely different in wave form from those recorded initially (Fig. 1*G*).

The finding that long-latency, generalized responses initiated by peripheral stimulation reflect activity in synaptic organizations linked to corticospinal neurons indicates that diffusely projecting *extrathalamic* pathways play an important role in the regulation of the corticospinal system. That a multiplicity of extrathalamic pathways may be involved in this regulation is evident from the variability of secondary discharges and associated relayed corticospinal tract discharges observed at different levels of barbiturate narcosis. In view of this, it is likely that such pathways may mediate effects on corticospinal neurons that have been reported to follow stimulation of diffuse peripheral fields under different experimental conditions (*5*).

Evidence is also presented here that diffusely projecting centripetal pathways activated by hippocampal efferents are capable of initiating corticospinal neuron discharges. This would appear to extend the range of action of archicortical efferent projection systems in the modulation of neocortical activity to a degree which has been previously unsuspected (*6*).

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References and Notes

1. A. Forbes and B. R. Morison, *J. Neurophysiol.* **2**, 112 (1939).
2. E. W. Dempsey, R. S. Morison, B. R. Morison, *Am. J. Physiol.* **131**, 713 (1941).
3. H. D. Patton and V. E. Amassian, *Handbook of Physiology, Neurophysiology* (American Physiological Soc., Washington, 1960), vol. 2, p. 8 → K. Iwama and C. Yamamoto, *Electroencephalog. and Clin. Neurophysiol.* **13**, 2 (1961).

→ D. P. Purpura and E. M. Housepian, *Electroencephalog. and Clin. Neurophysiol.* **13**, 365 (1961).

5. V. B. Brooks, P. Rudomin, C. L. Slayman, *J. Neurophysiol.* **24**, 302 (1961); H. D. Patton, *Federation Proc.* **19**, 287 (1960).
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Behavior Studies by Capacitance Sensing

Abstract. The movements of small burrowing animals submerged in sand are monitored through capacitance changes which detune radio-frequency oscillators. A new dimension of reptilian activity studies is possible by using this technique. Some early observations of several reptile species maintained in darkness in isothermal sand are given. Patterns of behavior during active phases, depth and rate of diving, and duration of quiescent periods are being revealed in detail for the first time.

The capacitance-sensing technique provides a potentially valuable tool for the ethologist and ecologist. Although the method is highly versatile, it apparently has not been used heretofore to study animal movements. One application of this technique is illustrated; extensions to other uses will suggest themselves readily.

Our initial studies have dealt with burrowing reptiles of the genera *Chionactis, Chilomeniscus, Anniella*, and *Leptotyphlops*. A wide variety of other lizards and snakes burrow with great facility in loose sand or soil. In desert regions, such burrowing animals often spend a large part of each day buried beneath the surface. It has been suspected that their subsurface stay is not always a simple quiescent period, but may involve movements related to temperature stratifications (*1*), food searching (*2*), or selection of moisture levels (*2*). The data relating to these suppositions are fragmentary and have resulted from observations of (i) humped-up surface soil or sand displaced by the shallowly buried animal (*3*), (ii) animals submerged in glass-walled chambers and occasionally revealing themselves by pressing against the panes (*1, 2*), or (iii) the actual depths of buried animals uncovered by excavation (*4*). These methods give only a very incomplete picture of subsurface activity. A continuous monitoring method, allowing the investigator to detect the position of an animal constantly, is needed.

Capacitance sensing seemed most likely to fulfill this requirement. The method depends upon the production and detection of changes in capacitance of a regenerative radio-frequency oscillator. In the present application, the capacitance changes are brought about by the approach or contact of reptiles with a buried sensing element coupled with the oscillator condensers. Since the dielectric constant of sand is quite low (about 4), while that of animals is relatively high, the capacitance changes generated in this way are sufficient to make the method practicable.

Capacitance sensing has a number of advantages over other possible techniques: it is exceedingly sensitive (being able to detect large animals at distances over 15 inches); the sensing elements can be structured in any way desired; the geometry of the enclosure and environment is more or less immaterial; the experimental animals are undoubtedly insensitive to minute electrostatic fields oscillating at radio frequencies.

The enclosure illustrated in Fig. 1*A* was adopted after numerous trials. Its internal dimensions are 2½ × 18 × 46 inches. The ¼-inch Plexiglas side panels are held in position by ¼ × ¼-inch sand-tight grooves from which they are removable from above by sliding. External supporting structures are of wood.

The sensing and ground elements consist of linear grids of 24-gauge tinned copper wire strung back and forth with a horizontal spacing of ¼ inch. We have no reason to believe that the grids hamper free passage. Ten grids are spaced 4 inches apart, beginning 1 inch above the base. The grid-wire ends are fastened to binding posts on one side. These posts also serve as jacks to receive the oscillator lead-cables and grounds. The first, fourth, seventh, and tenth grids are used as sensors; the others are isolating grounds which reduce field coupling. The ground shield of each coaxial lead-cable is connected to both adjacent ground grids (except for the top and bottom shields).

For runs with an uncompacted fill, sand is poured into the chamber to the