MOTOR FIELDS OF PRECENTRAL CELLS ELICITED BY OPERANT REINFORCEMENT OF UNIT ACTIVITY

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Motor responses in which a given motor cortex cell may play a functional role can be elicited by operantly reinforcing bursts of cell activity and observing the correlated behavioural responses. Under isometric conditions, operant bursts were often repeatedly correlated with EMG bursts in specific contralateral arm muscles. These EMG bursts broadly coincided with the operant unit bursts, but their onset and peak usually followed the onset and peak of the precentral unit burst. One may refer to the set of muscles co-activated with operant bursts of a motor cortex cell as the cell's "motor field". Under isometric conditions the motor field of a given cell generally remained stable over many bursts, not only with respect to the set of co-activated muscles, but also with respect to the relative intensity of their activation. Different units in the same cortical region could have quite different motor fields. Many of the unit-muscle correlations observed when the unit was reinforced were replicated during other reinforced response patterns.

To study relations between activity of motor cortex cells and movements, one may train the animal to make specific motor responses and study correlated cell activity (Evarts, 1968; Humphrey et al., 1970; Luschei et al., 1971; Porter et al., 1971); an alternative strategy is to reinforce cell activity and determine the

correlated motor responses (Fetz and Baker, 1973). The former approach offers advantages in that the reinforced movement may be standardized and quantified with respect to variables like position and force; however, its fruitfulness depends on the experimenter's accuracy in anticipating which responses would engage the cells of interest and his skill in isolating cells related to the pretrained responses. Usually only a proportion of the cells in a given area have been strongly related to a given movement. If the object is to determine for each cell the movements with which it may be optimally involved, a more direct approach would be to train the animal to activate that cell and determine the correlated movements.

To this end we operantly reinforced bursts of precentral cortex cells and observed correlated motor responses. Under conditions of relatively free limb movement operant bursts of different precentral cortex cells were observed to be correlated with different types of motor activity: bursts of some cells were associated with generalized and variable movements; other cells were repeatedly associated with simple movements of specific joints; some cells were driven in bursts with no observable movements. To better quantify the muscle activity associated with operant bursts of a cell, we recorded isometric activity of four representative arm muscles with permanently implanted electrodes (Fetz and Finocchio, 1971). With the arm held semiprone in a cast operant bursts of different precentral cells were reliably correlated with bursts of EMG activity in specific sets of muscles. The four units in Fig. 1 were located within 3 mm of each other in the precentral gyrus of one monkey. In each case, reinforcement was made contingent only on bursts of unit activity, and not on any muscle activity. Bursts of cell A were repeatedly associated with bursts of EMG activity in biceps and both wrist muscles; cell B was predominantly correlated with triceps and biceps; cell C with triceps and wrist muscles; and cell D fired in bursts without any correlated EMG activity. Thus the relative amount of EMG activity in each arm muscle was different for each cell. Although the unit and muscle bursts overlapped to a great extent, the beginning and peak of average unit activity preceded the beginning and peak EMG activity, respectively.

It proves convenient to call the set of muscles which are co-activated with operant bursts the "motor field" of the cell. Fig. 1 indicates that different cells in the same area of motor cortex had different motor fields. The fact that correlated muscle bursts were

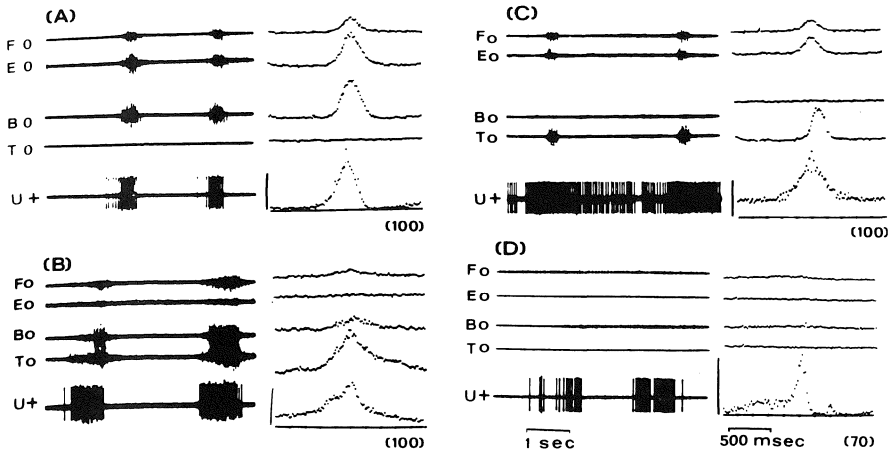

Fig. 1. Isometric muscle responses correlated with operant bursts of four precentral cortex cells in the same monkey. Sampled muscles include flexor carpi radialis (F), extensor carpi radialis (E), biceps (B) and triceps (T); U+ indicates that bursts of unit were reinforced. Sample of two successive responses is shown in 5 sec sweep at left; average at right was compiled over a number of responses in parentheses (vertical bar = 50 impulses/sec). Units B, C and D were identified as pyramidal tract cells.

usually temporally delayed with respect to operant unit bursts suggests that the motor field may represent an efferent analog of a sensory receptive field: it represents the loci of peripheral elements (muscles rather than receptors) whose activity is correlated with activity of the cell. However, insofar as it involves a behavioural response, the operational definition of motor field differs from that of a sensory receptive field. Whereas stimulating in a receptive field provides relatively secure evidence for a functional pathway from receptors to responding cells, the observation that certain muscles are consistently co-activated with a unit provides only suggestive evidence for a functional connection. A closer motor analog of a receptive field would be the set of muscles whose motoneurones a given motor cortex cell may synaptically affect. This set, which might be called the cell's "muscle field", could be determined experimentally by stimulating the cell in isolation and recording postsynaptic responses in

appropriate motoneurones. While this procedure is prohibitively complex, a practical approximation may be Asanuma's microstimulation technique which activates a local population of cortical cells (Asanuma and Rosen, 1972). The relation between the behaviourally determined motor field and the physiologically determined muscle field of a cell would be of considerable experimental interest.

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