OPERANT CONDITIONING OF ISOLATED ACTIVITY IN SPECIFIC MUSCLES AND PRECENTRAL CELLS

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In investigating the possible role of precentral motor cortex cells in generating voluntary movements, previous experimenters have trained monkeys to perform specific motor responses by making operant reinforcement contingent on the net mechanical parameters of the movements — *i.e.*, the position and force trajectories of the responding limb. These experiments have shown that many precentral cells alter their activity before a sudden movement[2,9,10], and that such activity may be more strongly correlated with the force exerted than the position of the limb[3,4,7]. These results imply that motor cortex cells may be causally involved in initiating muscle activity. However, since the chosen motor patterns involved coordinated activity of many muscles[4,11], such experiments were not designed to resolve the question of which specific muscle(s) a given precentral cell may facilitate. In order to determine the degree to which activity of a precentral cell may be correlated with activity of specific limb muscles, we trained a monkey to isometrically contract any of 4 arm muscles in isolation[6].

During recording sessions the monkey sat in a primate chair with his head restrained and his left arm placed semiprone in a moulded cast. In order to render muscle activity isometric the cast could be immobilized, fixing the elbow position at 90° and the wrist and fingers at 180°; under isometric conditions muscle force is proportional to integrated EMG activity[1,8]. Pairs of stainless steel EMG electrodes implanted in the belly of a flexor and extensor of elbow (biceps and triceps) and wrist (flexor carpi radialis and extensor carpi radialis) led subcutaneously to a connector cemented on the skull. In arm area of contralateral precentral cortex we recorded activity of single precentral cells, most of which could be characterized with respect to pyramidal tract (PT) projection.

Under isometric conditions specific patterns of cell and muscle activity were detected and reinforced with an electronic 'activity integrator' (Fig. 1), which delivered a fruit juice reward whenever a weighted sum of activities in muscles and cell exceeded a criterion level. The input voltages to the activity integrator consisted of the rectified EMG activity of each muscle and voltage pulses triggered from the cell's action potentials. Each input voltage (v_i) was multiplied by a weighting factor (a_i) whose algebraic sign and magnitude were controlled through a polarity switch and

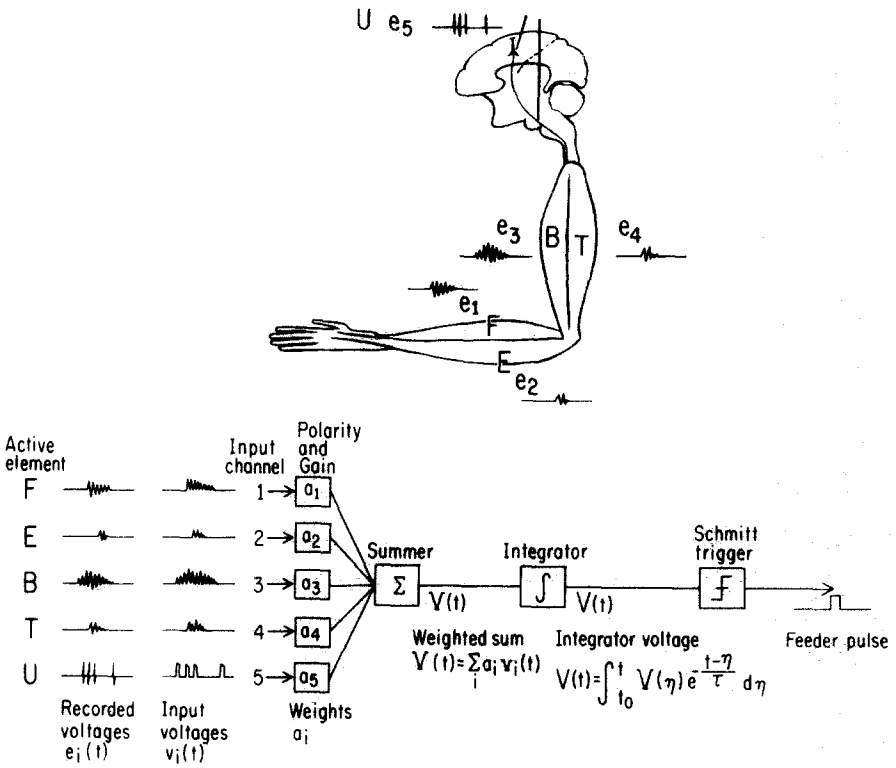

Fig. 1. Top, Schematic diagram of monkey showing relative location of arm muscles and cortical cell, whose activities were operantly conditioned, and pyramidal tract stimulating electrode. F, flexor carpi radialis; E, extensor carpi radialis; B, biceps; T, triceps; U, cortical unit. Bottom, Schematic diagram of 'activity integrator' used to monitor and reinforce specific patterns of activity in these elements under isometric conditions. The input voltages (v_i) were derived from the recorded potentials (e_i) by rectifying the EMG activity of each muscle and by triggering voltage pulses from the cell's action potentials. The weighted sum of the input voltages determined which pattern of activity in these elements was reinforced (see text). The integrator voltage was the temporal integral of the weighted sum; when this reached a criterion level set by the Schmitt trigger, the feeder discharged and a relay (not shown) briefly reset the integrator voltage to zero.

gain control for each channel. A summing network derived the weighted sum ($V(t) = \sum_i a_i v_i$) of the input voltages, which was then temporally integrated in a parallel RC circuit with a passive decay constant of 100 msec. When this 'integrator voltage' reached a preset criterion voltage level the feeder discharged and the integrator voltage was briefly reset to zero.

For example, when the desired response pattern consisted of isolated activity of a specific muscle, the weighting factor on that muscle channel was made positive so that activity of the chosen muscle drove the integrator voltage toward the criterion level and would be reinforced. The weights for the remaining 3 muscles were made negative so that activity of any of these muscles drove the voltage away from the criterion level and prevented reinforcement. If the unit activity was not part of the

reinforcement contingency, its weight was made zero. At the beginning of a reinforcement period the monkey typically emitted bursts of EMG activity in several muscles every few seconds and the gain controls were set to reinforce about half of these responses. After several minutes the monkey typically modified his response pattern so as to produce more activity in the chosen muscle and less in the other muscles. By decreasing the gain on the channel of the chosen muscle we could require greater activity of this muscle for reinforcement, and by increasing the (negative) gain on the other muscle channels we required greater suppression of these muscles for reinforcement. Thus we continually reinforced better approximations to the desired pattern, until finally responses typically consisted of repeated bursts of EMG activity in the chosen muscle with negligible coactivation of the other 3 muscles. During reinforcement periods the monkey also had continuous visual feedback in the form of an illuminated meter whose needle deflection was proportional to the integrator voltage, and which therefore signalled the degree to which the monkey's response pattern met criteria for reinforcement. After about 6 weeks of training the monkey had learned to reliably contract each of the 4 arm muscles in relative isolation, under appropriate stimulus control.

In order to obtain more reliable measures of temporal correlations between cortical unit and muscle activity we recorded and averaged 50–150 examples of each response pattern. These response averages, computed over the two-second intervals straddling the feeder discharges, showed the average activity of each muscle and the unit for each reinforced response pattern. At least 50 examples of each response pattern were averaged for the correlations discussed below.

During the 6–10 h that a precentral unit was reliably isolated, we recorded its activity under as many of the following conditions as possible.

(A) We determined the unit's response to passive joint movements and cutaneous stimulation, while rewarding the monkey for sitting quietly. Most precentral cells were found to respond clearly and repeatably to passive movements of one or more joints of the contralateral arm in the absence of any recorded EMG activity[5].

(B) With the arm held semiprone in the cast, and the cast released to pivot at the elbow, we reinforced active flexions and extensions of the elbow. Most cells altered their activity during some phase of these movements, usually changing their activity before the first recorded EMG activity.

(C) With the cast immobilized we reinforced isometric contraction of each of the 4 muscles in isolation; this produced bursts of EMG activity predominantly or exclusively in the reinforced muscle. So far 9 precentral cells (6 PT) have been observed in relation to isometric contraction of each of the 4 arm muscles; of these, 3 units changed their activity in relation to contraction of only one or 2 of the 4 muscles; 4 cells fired in some relation to each of the 4 muscles (2 of these exhibited the same pattern in relation to all 4 muscles); the remaining two cells showed no correlated activity with any of the 4 muscles. Under isometric conditions the pattern of cell activity associated with activity of two antagonistic muscles of one joint were more often the same (6 cases) or not comparable (5) than reciprocal (3). Unit–muscle correlations seen in the isometric case were usually, but not always, consistent with

those seen during active elbow movements; two cells became active before isometric contraction of both biceps and triceps, but were reciprocally related to active flexions and extensions of the elbow, becoming active before one and inactive before the other.

(D) With the monkey's arm still held in the cast, we reinforced bursts of activity in the cortical cell, with no contingency on muscle activity. Under such conditions the monkey typically produced correlated bursts of EMG activity in several arm muscles, including those muscles whose isolated contraction (condition C) involved activation of that unit. The two cells which did not fire in relation to any of the 4 arm muscles were also activated on this schedule, but their activity was not accompanied by any recorded EMG activity.

(E) In 6 cases in which cell activity had been previously correlated with specific muscles (under condition D and condition C and/or B), we reinforced bursts of cortical cell activity with simultaneous suppression of all muscle activity. In each case the monkey readily learned to fire the cell in bursts with negligible correlated EMG activity. The reverse dissociation (muscle activity and unit suppression) was attempted only twice; in the one documented case, the response pattern shifted in the reinforced direction, but unit activity was never completely suppressed[6].

These observations would lead us to conclude that the temporal correlations one sees between activity of precentral cells and some other component of the motor response — such as muscle activity, force or position — may depend as strongly on the specific response pattern which is reinforced as on any underlying physiological connection. Under such circumstances the appropriate experimental strategy would seem to be to look at the activity of each cell in relation to a repertoire of response patterns, to determine which correlations are most stable. One can directly test the stability of any consistently observed correlation by making operant reinforcement contingent on its dissociation.

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