

Research Note

Arm Trajectory Formation in Monkeys*

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Summary. The formation of forearm trajectories of moderate velocities (0.3–1.3 rad/s) was studied in monkeys performing a simple visuomotor task. The experiments were designed to test the hypothesis that the transition from one position to another is subserved by a rapid shift to a final equilibrium of forces in agonist and antagonist muscles. This idea is attractive because it suggests the possibility that in simple movements the trajectory is determined by the inherent inertial and viscoelastic properties of the limb and muscles around a joint. The results indicate that these moderate speed movements are controlled by a gradual, and not a step-like, shift to the final equilibrium position.

Key words: Final position control

In this paper we describe a series of experiments directed at understanding the control signals generated by the central nervous system (CNS) during voluntary arm movements of a monkey. Recently, it has been proposed that movement and posture are subserved, to a first approximation, by a single mechanism. We owe this idea to Feldman who suggested that arm movements in man may result from a shift in the equilibrium point of the muscle-

load system (Feldman 1966a, b). Studies in intact and deafferented animals (Bizzi et al. 1976; Polit and Bizzi 1978) and humans (Kelso and Holt 1980; Sakitt 1980) are consistent with this idea. According to this view, the motor program specifies, through selection of a set of length-tension properties in agonist and antagonist muscles, an equilibrium point between the two sets of muscles that correctly position the joint in relation to a target (Fig. 1). This view may be illustrated by reference to a simple mechanical analogue in which the muscles are represented by a pair of springs acting across a hinge in the agonist-antagonist configuration. If the control signal were to specify a new length-tension relationship for the springs, movement would occur until a new equilibrium point was reached. In accordance with this hypothesis, movements are, at the simplest level, transitions in posture. This idea is attractive because it suggests that the CNS controls simple movements through a process specifying only the final position via a pattern of muscle activation. In keeping with this view, the details of a movement trajectory are determined by the inherent inertial and viscoelastic properties of the limb and muscles around a joint. It should be stressed that this explanation does not deal with the question of controlling how quickly the transition to the final equilibrium point is implemented.

In this paper we will present some results directed at understanding the time-course of the neural signals executing the transition from an initial to a final posture. It will be shown that, in monkeys, simple forearm movements are controlled by signals that induce a gradual shift of the equilibrium point. The movements which we have examined involve pointing with the forearm to a visible target. Their velocity profile displays one peak and the electromyographic (EMG) activity typically appears as a burst gradually blending with the tonic activity characteristic of the

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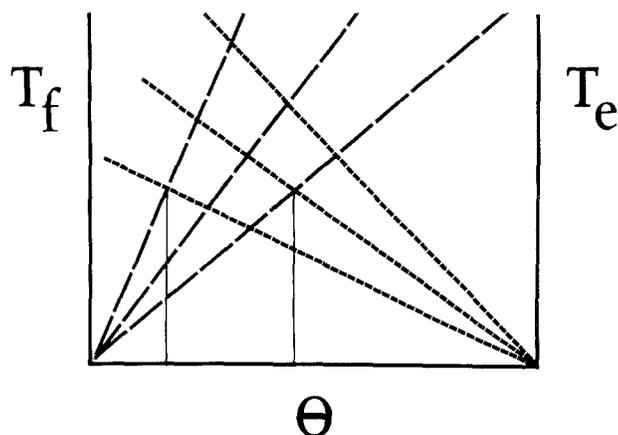


Fig. 1. Schematic representation of flexor (T_f) and extensor (T_e) length-tension curves. Θ represents joint angle

holding phase. These movements, which are also called "continuous" (Brooks 1979), are of moderate speed (0.3–1.3 rad/s) and should be distinguished from very fast ballistic (Desmedt and Godaux 1978; Freund and Büdingen 1978; Ghez and Vicario 1978a, b) movements which were not investigated in this study.

Three monkeys were used in our studies. During experimental sessions these animals were seated in a primate chair with the right arm strapped to a splint which allowed rotation of the forearm about the elbow in the horizontal plane. The pointing task required that the monkey position its forearm in front of a target light. Ten target lights were placed along a perimeter arc centered on the axis of rotation of the elbow. To obtain a reward, the monkey had to point to an electrically defined target zone (10 deg wide) centered on the target light. Arm movements were monitored by a precision potentiometer at the end of the pivot shaft. Muscle activity was recorded with Teflon-coated wires whose ends had been scraped and implanted percutaneously in the biceps and triceps muscles. During the experimental sessions, an opaque cover was placed over the arm to prevent the animal from seeing the moving arm.

The main experimental procedure involved the use of force and positional disturbances which were applied with a torque motor coupled to the shaft of the pivot arm on which the elbow rested. These positional disturbances normally induce stretches, which generate afferent information that is quickly relayed not only to the spinal cord, but also to the cortex and cerebellum where it may induce a change in on-going motor planning. To prevent the animal from detecting disturbances of forearm position, we surgically interrupted the sensory nerves conveying afferent activity from the arm, neck, and upper torso

by bilateral section of the dorsal roots from C1 to T3. Although this surgery is known to prevent sensory input from reaching the spinal cord, the sensory loss may be incomplete. In fact, a few afferent myelinated and many unmyelinated fibers running in the central roots have been described in some species (Coggeshall and Ito 1977; Kato and Tanji 1971). However, as discussed later, there was no evidence in the EMG activity of stretch related responses.

After deafferentation, the forearm visuomotor responses, which had been learned in the preoperative state, could be easily evoked by presenting the targets (Taub et al. 1975). The movements were very similar to those observed before deafferentation. The velocity profile continued to display one peak, and the EMG activity usually appeared as a moderate burst that gradually blended with the tonic activity characteristic of the holding phase (as in the preoperative recordings). However, occasionally, a slight overshoot in the arm trajectory appeared after the arm had reached the end position, suggesting an underdamped system (estimated damping ratio: 0.6). While it is entirely possible that deafferentation, like any other CNS lesion, might have induced modifications in motor programming, the fact that we obtained similar results in intact and deafferented animals suggest that the basic mechanism controlling these simple movements continued to be operative.

In the first set of experiments in deafferented animals, we adopted the following procedure: At random times, the position of the arm was suddenly displaced and maintained in a new location by the servo action of the torque motor, but no reward was delivered. Both because of the loss of sensory information and the presence of an opaque cover over its arm, the animals were unaware of any displacement. After completing this maneuver, a target light was turned on at the location corresponding to the new arm position. To our trained monkeys, the appearance of this target light represented a signal to start the neural process involved in pointing to the target. These processes became manifest to us through the appearance of EMG activity in the proper set of muscles, after the usual reaction-time delay (Fig. 2A). Simultaneous with the appearance of the evoked activity in the EMG, an electronic timer was started which turned off the servo action of the torque motor, thus releasing the arm, after a predetermined time had elapsed following the onset of the evoked activity in the EMG. We observed that the arm moved first toward the position from which it had originally been displaced, the starting position, then changed direction and returned to the position specified by the target light (Fig. 2A). While the to-and-fro movement took

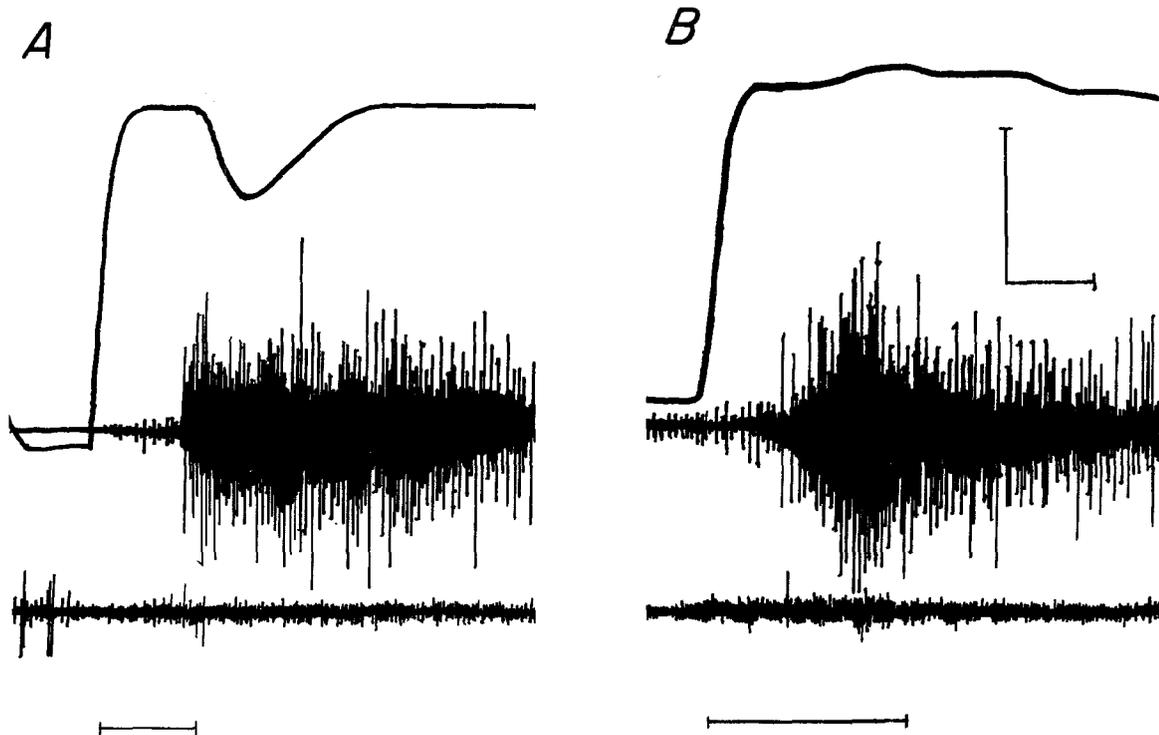


Fig. 2. A Forearm movements of a deafferented animal in the absence of visual feedback. Displacement of the forearm to a flexion position at which a target light was displayed. At the termination of the servo-motor action (indicated by horizontal bar), note the movement of the forearm toward extension and subsequent return to the position specified by the target. Flexor activity evoked by the target light is similar to that which was observed during undisturbed movements of same amplitude. Lower EMG corresponds to extensor muscles. In two animals 200 instances of this behavior were observed. **B** Same animal. Displacement of the forearm to a flexion position at which a target light was displayed. No movement of the forearm at the termination of servo-motor action. EMG activity from flexors is triggered by the appearance of the light and is similar to that observed during undisturbed movements. Lower EMG corresponds to extensor muscles. In two monkeys 220 instances like the one displayed here were observed. Time calibration, 500 ms. Vertical bar represents joint angle position, 20 deg

place, the agonist muscle developed an EMG pattern comparable to that observed during normal, undisturbed movements. Thus, in the presence of flexor muscle activity we observed movement toward extension. This cannot be explained if the muscles are regarded as pure force generators, but is readily explained if the length dependence of muscle force is taken into account. The amplitude of the movement toward the starting position varied depending upon the precise timing of the release of the arm by the servo. When the servo action was maintained after the appearance of the evoked EMG activity for a period corresponding to the normal movement duration, then no significant movement of the arm was observed after it had been released by the servo (Fig. 2B).

This experiment could not be performed in intact monkeys, since the animal must be unaware of the displaced position of its arm. However, we conducted a comparable experiment in intact monkeys by applying a brief pulse of torque at the beginning of the movement, with the aim of rapidly displacing the

limb to the position the animal was planning to achieve. Again, the limb tended to return to the starting position following the termination of the torque pulse, subsequently changing direction and moving to the position specified by the target light.

Taken together, these findings suggest the existence of a gradually changing control signal during movement of the forearm from one position to the next and are not consistent with a view postulating a step-like shift to a final equilibrium point. In addition, they illustrate the length dependence of muscle force, and as corollary, that muscles cannot be viewed as pure force generators.

In a second set of experiments, we obtained further confirmation of the view indicating a gradual change in the control signal establishing the final equilibrium point. Again, intact and deafferented animals were used and the following procedures adopted. Before the onset of visually triggered movement, the limb was clamped in its initial position and it was released at various times after the onset of evoked agonist EMG activity. The duration of the

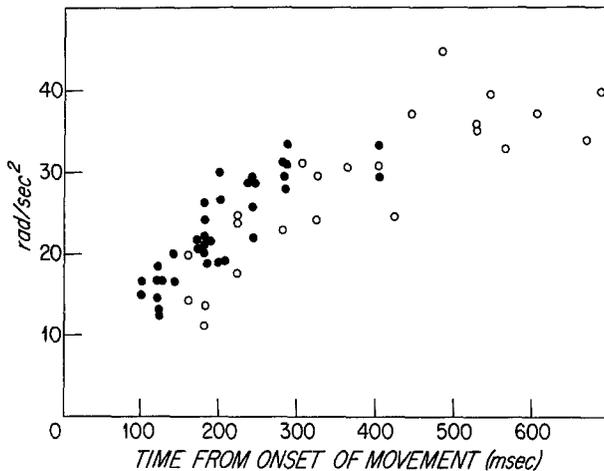


Fig. 3. The forearm of intact and deafferented animals was held in its initial position while the animal attempted to move toward a target light and released at various times. Plot of acceleration immediately following release vs. holding time. Abscissa: time in milliseconds (ms); ordinate: radians/s². Solid dots: intact animal; circles: deafferented animal

holding phase was varied randomly from 100 to 600 ms. Because of the deafferentation, there was neither an increase in EMG activity during the holding phase nor a pause in the agonist EMG activity after the sudden release. (In intact monkeys, both events were routinely observed.) We measured the acceleration of the limb immediately after the release and plotted it as a function of the holding time; i.e., the time elapsed since the beginning of the EMG activity in the agonists. The plot of the acceleration in intact and deafferented monkeys showed a gradual increase to about 400–600 ms following EMG onset (Fig. 3) and consequently, progressively faster movements after release. Moreover, isometric tension recorded in a separate set of experiments in which the arm was clamped for longer periods of time, reached a peak at about 488 ± 92 ms for movement amplitudes of 60 deg.

These findings are thus consistent with the hypothesis of a gradual shift in equilibrium point. As the equilibrium point moves further away from the position at which the limb was restrained, progressively larger torques are generated, resulting in progressively increasing values of acceleration following release and progressively faster movement trajectories. These findings are then not in accord with the hypothesis postulating that arm trajectory is controlled by a simple rapid shift to a final equilibrium position. According to this hypothesis, the trajectory of the released arm should have been simply delayed but its shape should not have been affected.

Physiologically, we do not know how the gradual shift in equilibrium point is programmed. Some of the factors responsible for the progressive increase in tension are the twitch contraction time of the muscle fibers (about 80 ms) (Collatos et al. 1977) and the recruitment order and the firing rate of arm muscles motoneurons (Desmedt and Godaux 1978; Freund and Büdingen 1978; Henneman 1965; Tanji and Kato 1973).

It should be stressed that the results described in this paper have been obtained by analysing forearm movements performed at moderate speeds. It is known that in very fast movements, the shift in equilibrium point is more abrupt (step-like) and may even transiently involve a shift to a position beyond the intended equilibrium point which would amount to a pulse step command of the type known to control eye movements and fast limb movements (Desmedt and Godaux 1978; Freund and Büdingen 1978; Ghez and Vicario 1978a, b; Robinson 1964). Although the movements we have studied occurred about a single joint, the gradual shift in equilibrium point may well be a general mechanism to generating trajectories in multi-joint movements as well. Because of the complex kinematics and dynamics of multi-joint movement, a step-like transition might generate forces difficult to control. The gradual transition between equilibrium positions, on the other hand, would facilitate coordination of multi-joint movement and reduce the problems of control.

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