Mechanical properties of muscles

Implications for motor control

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Recent experiments suggest a simple relationship between posture and movement. Posture appears to result from the CNS setting the activity levels of agonist and antagonist muscles around the joint, resulting in an equilibrium force, the ratios of which are different for different positions. Control of movement is accomplished by changing the set of opposing length/tension curves. However, the experimental evidence also indicates that during movement there is active control of the trajectory, in addition to control of final position. A simple strategy of choosing a new posture via the length/tension curves and letting a limb move until equilibrium is established is not the control algorithm used by the vertebrate motor system.

What control strategies have been adopted by the CNS to execute simple visually evoked movements? In order to answer this question, we believe it is necessary to look first at the mechanical properties of the musculo-skeletal apparatus, and only then begin to ask questions about the rules of the neural controller. Such an approach is based on the assumption that the features displayed by the neural controller have been developed by the need not only to control, but also to take advantage of the mechanical properties of the musculo-skeletal apparatus. A case for this approach was made years ago by Feldman[9,10], who investigated the spring-like properties of the human arm. Muscles do indeed behave like tunable springs in the sense that the force generated by them is a function of length and level of neural activation[20]. In addition, muscles are arranged about the joints in an agonist-antagonist configuration. If we attribute spring-like properties to muscles, then a limb's posture is maintained when the forces exerted by the agonist and antagonist muscle groups are equal and opposite. This implies that when a force is applied, the limb is displaced by an amount proportional to both the external force, and the stiffness of the muscles. When the external force is removed, the limb should return to the original position. This prediction is nothing else than a restatement of Hooke's Law, but in a biological context. Evidence supporting the idea that muscles *in vivo* have indeed spring-like properties is briefly discussed in the first part of this report. In the second part, the implication of these findings for trajectory control is discussed.

I. Control of head and arm posture

In one series of experiments, monkeys are trained to make co-ordinated, horizontal eye–head movements in order to fixate visual targets. In the intact animal, the unexpected application of a constant torque to the head during the movements is followed by an increase in electromyographic (EMG) activity of the neck muscles, presumably the result of an increase in muscle-spindle and tendon-organ activity (visual stimuli are turned off during these disturbances). In spite of these changes in the flow of proprioceptive activity, the head still reaches the target position after the constant force is removed (Fig. 1). This finding suggests that the program for final position is maintained during force application and is not readjusted by proprioceptive signals acting at segmental or suprasegmental levels[3]. It should be stressed that in these experiments force disturbances were totally unexpected and that the monkeys had not been trained to move their head to a certain position, but chose to program a head movement together with an eye movement in order to perform a visual discrimination task[3].

In a second set of experiments[5] the effects of sudden, unexpected increases in inertia applied during centrally initiated head movements were studied. Under these conditions, due to the kinetic energy acquired when the load is applied to the decelerating head, the head initially overshoots before finally returning to the target position (see Fig. 2). These changes in head trajectory produce corresponding modifications in the lengths and tensions of the neck muscles. The agonists are first sub-
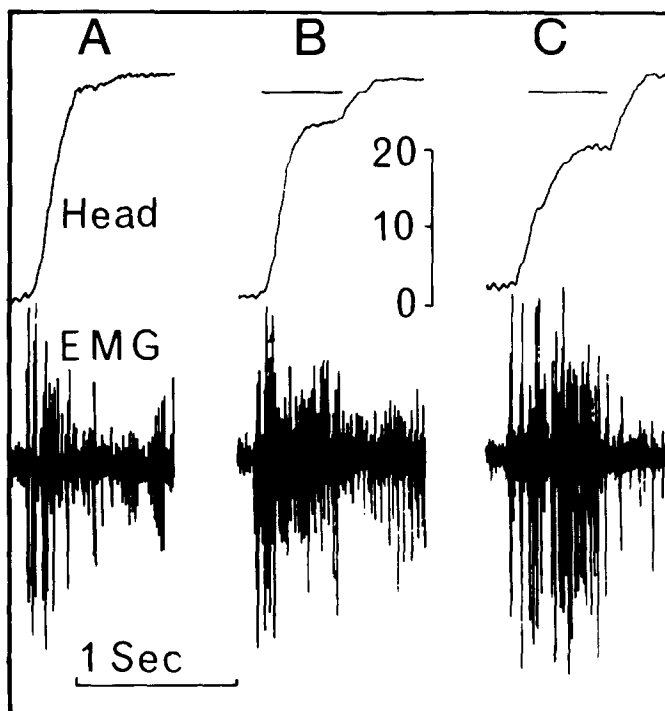

Fig. 1. *Typical visually triggered head movements in chronically vestibulectomized monkey to appearance of target at 40° but performed in total darkness. (A) Shows an unloaded movement. In (B) a constant force load (315 g cm⁻¹) was applied at the start of the movement resulting in an undershoot of final position relative to A, despite increase in EMG activity. In (C) a constant force load (726 g cm⁻¹) was applied. Note head returns to same final position after removal of the load. Vertical calibration in degrees; time marker is 1 s; EMG recorded from left splenius capitis. [From Bizzi, Polit and Morasso (1976) J. Neurophysiol. 39, 435–444.]*

jected to increased tension because the presence of the additional inertial load reduces their rate of shortening, and then during the overshoot phase, their rate of shortening is facilitated. This sequence of loading and unloading should provoke the classical muscle-spindle response mediated by group Ia and group II afferent fibers, which, in turn, would affect the agonist EMG activity. Fig. 2B shows that initially there was a greater increase in motor unit discharge during muscle stretch than would have occurred if no load had been applied, and then a sudden decrease in activity at the beginning of the overshoot phase. Therefore, we can assume that the unexpected inertial load induces a series of waxing and waning proprioceptive signals from muscle spindles, tendons and joints, yet even in the complete absence of other sensory cues (visual and vestibular), the intended head position is still eventually reached. Like the observations on the effect of constant-torque loads, these findings suggest that the central program establishing final head position is not dependent on a read-out of proprioceptive afferents generated during the movement, but instead, is preprogrammed.

To test this hypothesis further the attainment of final head position in monkeys deprived of neck proprioceptive feedback was investigated[3]. To ensure 'open loop' conditions, the animals were vestibulectomized 2–3 months before deafferentation (vestibulectomized monkeys are known to recover eye–head co-ordination[8]). After deafferentation, the animals could still respond accurately to the visual targets. A constant torque was applied to the head during centrally initiated movements. Just as with intact animals, when the load was applied unexpectedly at the beginning of a visually triggered movement, the position attained by the head fell short of the target position. Whereas, after removal of the constant torque, the head attained a position which was not significantly different from the one reached in the 'no-load' case.

Thus, the behavior of the head motor system with respect to head position is qualitatively the same before and after deafferentation. These findings can be explained by postulating that, by selecting a set of length-tension properties for agonist and antagonist muscles the motor program specifies an equilibrium point between these two sets of muscles that correctly positions the head in relation to the target. If this hypothesis is correct, it is not surprising that the head overshoot during the inertial loading is corrected with a return movement to the intended position. By the same token, because the head position is the result of muscle-length and force parameters, an undershoot is observed when a constant
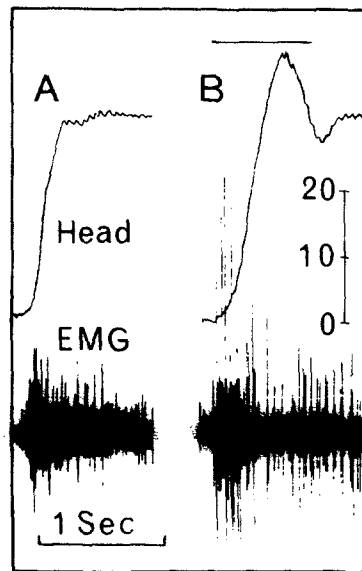

Fig. 2. *Typical head responses of a chronically vestibulectomized monkey to sudden appearance of target at 40°.* **(A)** *Shows an unloaded movement, whereas in* **(B)**, *a load of approximately six times the inertia of the head was applied at the start of the movement, as indicated by the force record. Both movements were performed in total darkness, the light having been turned off by the increase in EMG (splenius capitis). Peak force exerted by the monkey is approximately 750 g cm⁻¹; head calibration is in degrees; time marker is 1 s.* [From Bizzi, Polit and Morasso (1976) *J. Neurophysiol.* 39, 435–444.]

opposing torque is applied (Fig. 1). The same hypothesis explains why the head reaches the target position when a constant torque is removed.

Thus, the final head position in both intact and deafferented monkeys appears to be an equilibrium point dependent on the firing rate of the alpha motoneurons innervating agonists and antagonists, the length-tension properties of the muscles involved in maintaining the posture, the passive elastic properties of the musculoskeletal apparatus, and the external load. In the intact animal, however, in parallel with this basic process, the proprioceptive system participates in the attainment of final position by increasing muscle stiffness when a load disturbance is applied. In fact, any stimulation of the proprioceptive apparatus, by virtue of its reflex connections, will modify the firing rate and the recruitment of alpha motoneurons and will, therefore, force the selection of a new length-tension curve[2,14,16].

A complementary set of experiments on pointing movements of the forearm in adult rhesus monkeys[10] have extended the findings described above. During experimental sessions, the monkey sat in a primate chair

with its forearm fastened to an apparatus permitting flexion and extension about the elbow in the horizontal plane. Several small targets were spaced at 10° intervals along an arc which was centered on the axis of rotation of the elbow. The monkey had been trained to point to whichever light was on and to hold the arm for about 1 s in an electrically defined target zone 12–15° wide, centered on the target light, in order to obtain a reward, water. A torque motor in series with the shaft of the arm apparatus was used to apply positional disturbances to the arm. On random pointing trials, the initial position of the forearm was displaced. In most cases, the torque was applied immediately after the appearance of the target light and was stopped just before the activation of the motor units in the agonist muscle. Hence, when the motor command specifying a given forearm movement reached the agonist and antagonist muscles, the positional disturbance had altered their length, and the proprioceptive stimulation resulting from this disturbance had altered their state of activation. In spite of these changes, the target position was always attained; this was true whether the torque motor had displaced the forearm further away from, closer to, or even beyond the intended final position. There were no significant differences among the final positions achieved in these three conditions.

Naturally, the attainment of the target position in this experiment can be explained by assuming that afferent proprioceptive information modifies the original motor command. However, the results of the work on final head position suggest an alternative hypothesis: that by selecting a new set of length-tension curves the motor program underlying arm movement specifies an equilibrium point between agonists and antagonists that correctly positions the arm in relation to the target. To investigate this hypothesis, Polit and Bizzi[19] retested the monkeys' pointing performance after they had undergone a bilateral C1–T3 dorsal rhizotomy[6]. The animals were again required to produce pointing movements in an open loop mode, since no proprioceptive activity could reach the spinal cord, and there was no visual feedback of the arm position. Under these conditions, the animals could still produce pointing responses very soon after surgery (within 2 days in one case). The forearm was again displaced in randomly selected trials immediately after the appearance of the target light and released before the activation of motor units in the agonist muscles. For each target position, no significant differences were found between the average final position of movement with undisturbed and disturbed initial positions. These
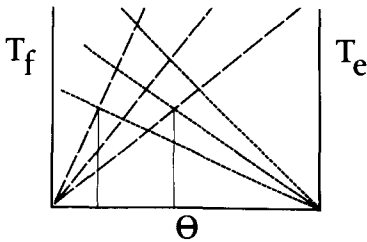
Fig. 3. *Schematic representation of flexor (Tf) and extensor (Te) length-tension curves. θ represents joint angle.* [From Bizzi, Accornero, Chapple and Hogan (1982) *Exp. Brain Res.* 46, 139–143.]

observations suggest that, as in the case of head position control, the final forearm position is directly programmed through alpha motoneuronal activity, which selects the appropriate length–tension relationship for each of the muscles involved in the movement.

It is tempting to speculate that the representation of posture as an equilibrium point between agonist and antagonist length–tension curves (see schematic representation of length–tension curves in Fig. 3) also has implications for movement[6,9,10]. If through a change in alpha motoneuronal activity the CNS was to specify abruptly new length–tension relationships for the muscles, movement would occur until a new equilibrium point was reached. Clearly, the suggestion that the CNS may control simple movements by specifying only final position is attractive because, in this way, a single process would subserve both posture and movement – the 'final position control' hypothesis[17,22]. The details of the trajectory would be determined only by the inertial and visco-elastic properties of the limbs and muscles. However, recent experimental findings reviewed in the next section, indicate that the CNS actively controls the trajectory in addition to the final position.

II. Trajectory formation

The goal of this series of experiments was to determine whether the 'final position control' hypothesis is sufficient to account for all of the characteristics of elbow movements such as initial acceleration, shape of the velocity profile, deceleration, overshoots, etc. To accomplish this goal, the time course of the neural signals executing the transition from initial to a final position was investigated[1]. Basically, there are two possibilities. In the first, which we have called the 'final position control' hypothesis the transition to the final alpha motoneuron levels is essentially step-like. Note that an abrupt change in alpha motoneuronal activity does not imply a rapid movement, since the speed of the movement produced will be a function of

the inertia, viscosity and stiffness of the musculature, and of the dynamics of cross-bridge formation in the muscles. In this manner, the CNS may control speed and final position via a single process. The second possibility is that there is active central control of the trajectory, in addition to control of the final position.

In this series of experiments, monkeys performing a pointing task similar to the one described in Section I were studied. Again, force and positional disturbances were applied to the forearm with a torque motor coupled to the shaft of the pivot arm on which the elbow rested. In some experiments, the animal was prevented from detecting disturbances of forearm position by surgically interrupting sensory roots conveying afferent activity from the arm, neck and upper torso (C1–T3). After deafferentation, the forearm pointing responses learned before the operation could be easily evoked by presentation of the targets[1]. The movements were similar to those observed before deafferentation. While it is entirely possible that deafferentation, like any other CNS lesion, may induce modifications in motor programming, the similarity of the findings in intact and deafferented animals suggests that both used the same mode of control.

Two experimental paradigms were used to determine whether the motor controller adopted the simple strategy of final position control. In the first set of experiments both intact and deafferented animals were used and the following procedures adopted. In randomly selected trials evoked by the presentation of a target, the arm was clamped in its initial position before the onset of visually triggered movements, and was released at various times after the onset of evoked agonist EMG activity (no visual

feedback was allowed). The duration of the holding period was varied randomly from 100 to 600 ms. The acceleration of the arm immediately after its release was plotted as a function of the holding period (i.e. the time elapsed since the onset of EMG activity in the agonists). In both intact and deafferented monkeys, the initial acceleration increased gradually with the duration of the holding period, for holding periods up to 400–600 ms, and the movements were, therefore, progressively faster after the release of the arm (Fig. 4).

This experiment suggests that these simple forearm movements do not result from rapid shifts in the equilibrium point. According to the final position control hypothesis, we would expect the steady state equilibrium position to be achieved after a delay due to the dynamics of muscle activation. To estimate this dynamic effect, we made a 'worst-case' assumption that all of the motor units recruited have twitch contraction time corresponding to the slowest observed value of 80 ms (Refs 4 and 5). A simple summation of these twitches (corresponding to the summation of motor-unit tensions in the tendon) yields a net muscle force which rises to within a few percent of final value within 150 ms. Our experimental results indicate instead that for a movement of at least 600 ms duration, the mechanical expression of the alpha motoneuronal activity does not reach steady state until at least 400 ms have elapsed following the onset of action potentials in the muscle (Fig. 4). These findings are consistent with the notion of a centrally generated control signal specifying a gradual shift in the equilibrium point. As the equilibrium point moves further away from the position at which the limb was restrained, progressively larger torque are
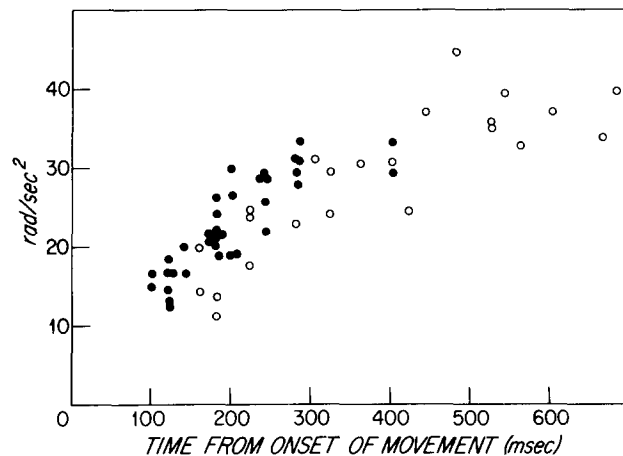

Fig. 4. *The forearm of intact and deafferented animals was held in its initial position while the animal attempted to move toward a target light and released at various times. Plot of acceleration immediately following release v. holding time. Abscissa: time in milliseconds (ms); ordinate: radians/s². Solid dots: intact animal; circles: deafferented animal.* [From Bizzi, et al. (1982) *Exp. Brain Res.* 46, 139–143.]

generated, resulting in progressively increasing values of acceleration after release and progressively faster movement trajectories.

In a second set of experiments, performed in deafferented monkeys, we provide further evidence against final position control. The arm was suddenly displaced and maintained at what would be the location of the next target by the servo action of the torque motor. The animals could not have expected a reward, as no new target was illuminated. In fact, because of the absence of any proprioceptive or visual information regarding arm position, the animals were unaware of the displacement. Now, with the arm still constrained in the new position by the servo-motor, the target light corresponding to the new arm position was illuminated. To the trained monkey, its appearance was a signal to start the neural process involved in pointing to the target. We detected the onset of this process through the appearance of EMG activity in the appropriate set of muscles, after the usual reaction time. After a predetermined time had elapsed following the onset of the EMG activity, the torque motor was turned off, releasing the arm. At this point, the arm was in exactly the correct position for receiving a reward. It is therefore remarkable that the forearm did not remain stationary after release. Instead, the arm first moved toward the position from which it had originally been displaced, and then changed direction and returned to the position specified by the target light. This finding cannot be explained if muscles are regarded merely as force generators, but is readily explained if the length-dependence of muscle force is taken into account. It should be pointed out that, if alpha motoneuronal activity evoked by the target light had rapidly achieved levels appropriate for the new final position, then no return movement should have taken place (see Fig. 3). The fact that a return movement did occur indicates that the control signal shifted gradually toward the final position. This conclusion is consistent with the observation that the amplitude of the movement toward the starting position decreased as the period of servo restraint of the arm was prolonged. Finally, when the servo action was maintained after the appearance of the evoked EMG activity for a period corresponding to the normal movement duration, the arm showed no significant movement after its release.

These findings suggest the existence of a gradually changing control signal during movement of the forearm from one equilibrium position to another and are not consistent with the hypothesis of a step-like shift to a final equilibrium point. Thus, in the transition from the initial position to the final position, the alpha motoneuronal activity is defining a series of equilibrium positions, which constitute a trajectory whose end-point is the desired final position.

It should be emphasized that the slowly changing control signal has been obtained by analysing forearm movements performed at moderate speeds. However, the character of the control signal may vary depending upon the goal. For example, in very fast movements, the shift in equilibrium point must be more abrupt. In the latter case, the control signal may even transiently code a shift to a position beyond the intended equilibrium point. This would amount to a pulse-step command of the type known to control eye movements and fast limb movements[7,11,13,21].

Concluding remarks

The experiments described here were designed to determine whether the motor controller adopted the simple final position control strategy in order to generate the trajectory of highly practiced, stereotyped, but not ballistic, forearm movements. The results were found to be inconsistent with this hypothesis and indicated, instead, that the transition from the initial to the final position is implemented by a gradual change in the control signal establishing both a trajectory and a final equilibrium condition.

It may be useful at this point to consider the potential advantages of such a control strategy. Clearly, one advantage for the gradual shift to equilibrium is to allow the animal to specify the amount of initial acceleration and terminal deceleration in the course of a movement. Beyond this, distinguishing between these two strategies of control has important implications for physiological research. In the case of final position control, one would not search for a neural process that generates different trajectories because they are not explicitly programmed, but result from setting the intrinsic mechanical properties of muscles at some final equilibrium value. In contrast, experimental results described here imply the existence of a gradually changing control signal and raise the question of the physiological mechanisms by which the intended movement is mapped into ensemble alpha motoneuronal activity which constitute what we have called a changing control signal. A precise solution to the problem of mapping a desired trajectory into the torques applied at the joints (the calculation of the necessary torques is called the inverse dynamic problem) has been found for the domain of man-made, computer-controlled multi-linked manipulators[16,18]. Clearly, animals must be doing something equivalent to the inverse dynamic computation, but the rules for executing this transformation are unknown.

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