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Mechanisms Underlying Achievement of Final Head Position

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IN RECENT YEARS, several investigations have been directed toward understanding the mechanisms whereby the central nervous system initiates movement (8, 14, 31). In contrast, the study of how movements are terminated has been relatively neglected. In this paper we have considered the latter question by studying whether the termination of movement and the subsequent maintenance of posture depend on a readout of proprioceptive afferent input generated during the movement itself or are, instead, centrally programmed. To answer these questions, we examined those head movements which are part of the monkey's coordinated eye-head response to the unexpected appearance of a stimulus in the animal's visual field (5). During these head movements, the neck proprioceptive apparatus provides a wealth of afferent signals from which tension, velocity of contraction, muscle length, and joint position could be extracted. We investigated whether this information provides a signal necessary for the accurate termination of visually triggered movements.

Years ago, Merton (21), in the context of a hypothesis that viewed gamma rather than alpha motoneuron activity as the first event in the initiation of voluntary movement, postulated that termination of centrally initiated movement was accomplished by a cessation of muscle spindle afferent activity. A somewhat different view, proposed by Stark (29), postulates that the control of final position is due to the activity of the gamma spindle system that provides "clamping and damping" of the centrally initiated movements. Another current hypothesis assumes that the pattern of supraspinal commands which initiates movement might be terminated when the afferent input, which is derived from various receptors stimulated by the muscle contraction, indicates that the intended position has been achieved (17). This hypothesis assumes that there is a "comparator" in the central nervous system receiving inputs from both the motor commands and from the afferent feedback. The output of this hypothetical comparator might provide a signal leading to a cessation of the ongoing motor pattern (10, 17).

In contrast with these views that have stressed the crucial role and the importance of the peripheral apparatus for the determination of final position, experimental evidence derived from chronically deafferented animals (30) and man (19) indicates that centrally initiated movements can be executed accurately even in the absence of sensory feedback. According to these findings, the process whereby a movement comes to a stop is determined centrally. It should be emphasized, however, that these conclusions, which are based exclusively on observing the motor behavior of deafferented animals, may not be applicable to intact animals because it is possible that extensive postoperative training might have produced an adaptive rearrangement of motor preprogramming.

Given these widely divergent opinions concerning the mechanism of movement termination and subsequent posture, we chose to reinvestigate these questions in both intact and deafferented monkeys by means of two different experimental approaches. First, using vestibulectomized, but otherwise intact monkeys, we applied load disturbances unexpectedly at the beginning and throughout centrally initiated head movements with the aim of provoking a proprioceptive response in all types of neck receptors. Our intent here was to stimulate these receptors during head movements, generate an unexpected afferent input, and observe the outcome of this stimulation on the head final position. In a second set of experiments, we adopted a complementary strategy; i.e., rather than stimulating the proprioceptive system, we interrupted the flow of afferent input by cutting cervical and upper thoracic dorsal roots. Our

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goal here was to observe how the absence of proprioceptive feedback would affect the achievement of final head position in both loaded and unloaded conditions.

METHODS

Procedure to elicit visually triggered eye-head movements

Three adult chronically vestibulectomized monkeys (*Macaca mulatta*) were trained to make a visual discrimination between a horizontal and a vertical bar (3 min in width). The animals were reinforced with drops of water if they pressed a lever only when the vertical bar appeared.

A PDP-11 computer was programmed to provide automatic presentation of the target light which elicited the coordinated eye-head movements. The lights were placed in a horizontal perimeter arc 60 cm from the animal and were spaced at intervals of 10° of visual angle along the arc, ranging from 40° left of the midsagittal plane to 40° to the right of it. To generate sets of movements with uniform starting positions, the first part of the sequence (blank light) appeared directly in front of the animal at the center of the perimeter arc, with the result of attracting the animal's gaze to it. The blank light at the center was then turned off while the sequence containing the horizontal-vertical lines or the vertical line alone appeared at some other position in the arc. In this way it was possible to collect sets of rather stereotyped eye-head movements starting from the center of the arc and directed to targets at 30° and 40° on either side. Although the animals could make the discrimination by turning only their eyes, they consistently chose to make the coordinated eye-head movement toward the target light.

Recording of head movements

Screws were permanently implanted in the skull to be used as connectors to the head holder (11). A lightweight apparatus (moment of inertia $J = 670\ g \cdot cm^2$), which restricted head movements to the horizontal plane, was attached to the head screws and used to monitor these movements by means of a low-torque potentiometer connected to the shaft of the head holder. The shaft of the head holder could be suddenly and unexpectedly loaded with an additional mass, thereby increasing the animal's head inertia (Fig. 1*A*). (Head inertia varied with the size of the animal between 7,000 and 10,000 $g \cdot cm^2$.) In experiments reported here we have used loads that increase head inertia by a factor of 4 or 7. The same head holder, appropriately coupled with a constant-torque load (315 $g \cdot cm$), could also be used to apply constant-torque disturbances during the head movement (Fig. 1*B*). (Peak head torque produced by the animal for a 30° movement is approximately 1,000 $g \cdot cm$.)

Surgical interventions

Because our aim was to study the effect of neck proprioceptors during head movements, we eliminated other sources of afferent input such as vestibular, visual, and the afferences from the periosteum surrounding the screws in the skull. We also performed a bilateral labyrinthectomy 3 mo prior to the actual experimental sessions (33). This operation was performed under Nembutal anesthesia by drilling through the mastoid, exposing and opening the canals, and filling them with dental cement. The effectiveness of the labyrinthectomy was tested by repeatedly rotating the animals in the dark and observing the lack of nystagmus. Eye movements were recorded with silver-silver chloride electrodes placed in the outer canthus of each eye. Chronically vestibulectomized monkeys recover their ability to perform very effective visually triggered eye-head movements (9). Removal of periosteum with local anesthesia during each experimental session was used to eliminate cues from stress on the skull during application of loads. Occasionally, during the experimental sessions we prevented the visual feedback by turning off the triggering light just prior to the initiation of the head movement (leaving the room in complete darkness). All of the head movements which have been considered for computation in this study were performed in complete darkness.

Cervical rhizotomy (C_1-T_3) was accomplished under a dissecting microscope in order to spare small vessels intermingled with dorsal rootlets. The dorsal roots were reached by first separating the neck muscles from the spinous processes and then removing the laminae with the help of a ronguer. The dura was opened in the midline along the entire length of the laminectomy. After dorsal roots section, the dura was sutured so that it was watertight. The wound was closed in layers.

Recovery of head movement

The monkeys hardly moved their heads during the first postoperative week. After 8-10 days they progressively recovered eye-head coordination and by 15-20 days, fully developed head movements were observed. No testing or train-

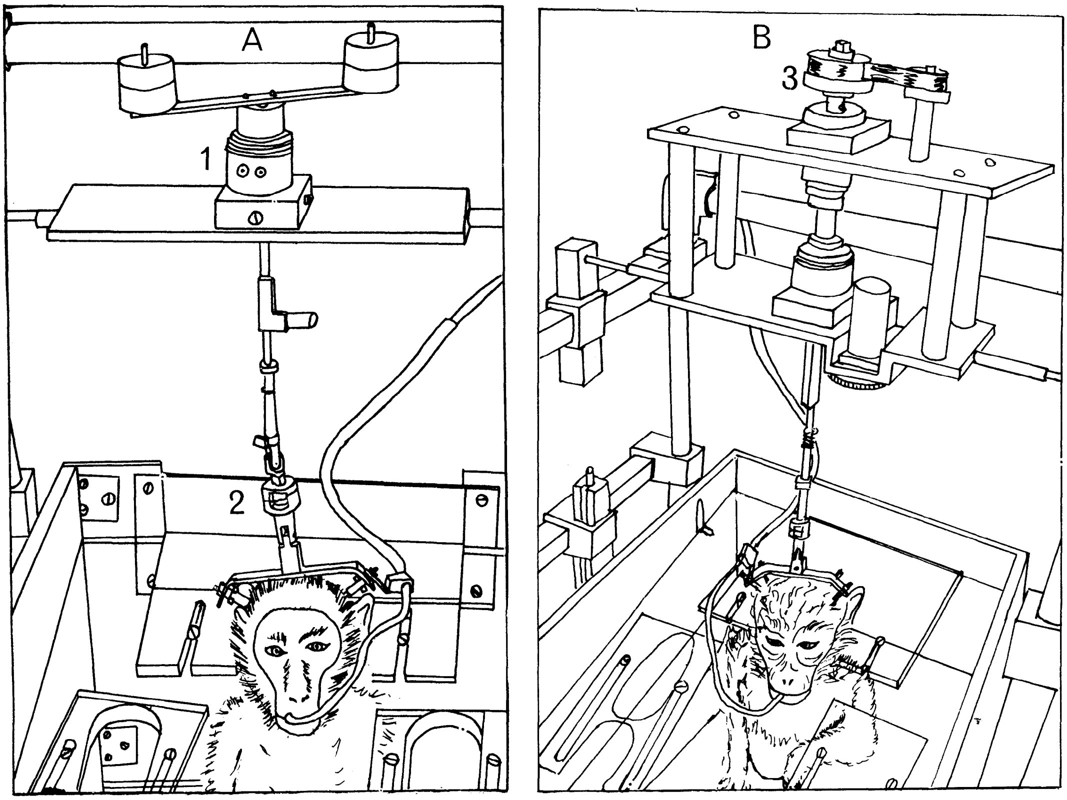

FIG. 1. Schematic representation of the equipment used to monitor horizontal head movements. In both *A* and *B* the load is coupled to the shaft by means of a clutch, 1, which is engaged by a triggering circuit which monitors the EMG signal. In *A*, weights at the top of the drawing and the length of the arms determine the inertial load. In *B*, several different constant-load springs, 3, can be used in order to vary force load. 2, Strain gauge glued over the shaft.

ing was done during this period of time. Regular experimental sessions were resumed after the 3rd wk.

Completeness of dorsal roots section

Functionally, the completeness of dorsal roots section was indicated by the absence of any short-latency response in the EMG following a sudden head displacement in complete darkness. In addition, unexpected application of loads during centrally initiated head movements were not followed by an increase in EMG activity. Since the literature reports the presence of sensory afferents in the ventral roots (6) and because of the impossibility of sampling all motor units in all the neck muscles for short-latency stretch responses, clearly this test is not an entirely conclusive indicator of deafferentation. Anatomically, the dorsal roots section was found to be complete by examining stained serial spinal cord sections. Muscle electrical activity (EMG) was recorded by way of wires (100 μm) which were chronically implanted in right and left splenii capitis.

Data analysis

Data (head position, velocity, force) were sampled by computer on-line every 10 ms per channel and converted to physical units (deg, deg/s, g·cm). Data were recorded simultaneously on an FM tape recorder and on a paper recorder (Honeywell Visicorder). Recordings of the movements were shifted along the time axis to a common origin point as determined by a constant-velocity threshold. The movements could then be averaged and the standard deviation at each point in time computed. The position of the head approximately 100 ms after it came to rest was used as a measure of final position. A two-tailed *t* test was used to test the hypothesis that the loaded and unloaded averaged final positions were the same.

RESULTS

Load disturbances during head movements in chronically vestibulectomized monkeys with intact proprioception

In the experiments described here, we applied load disturbances during centrally initiated movements with the aim of provoking a proprioceptive response in all types of neck receptors and observing the outcome of this stimulation on the head final position. To this end we used two types of loads: first, a constant-torque load whose effect extended beyond the dynamic phase of the movement and second, an inertial load which stimulated the proprioceptive apparatus only during the dynamic phase. There is evidence that the proprioceptive afferent input resulting from sudden application of these loads has not only a segmental influence, but is also quickly transmitted to a number of structures including the motor and sensory cortex (7, 12, 13, 27, 32, 34) and the cerebellum (4). Although there is little doubt that this evoked afferent input has a role in keeping the head trajectory within a preestablished course, it is not clear whether these unexpected proprioceptive signals can affect structures responsible for setting final head position. Accordingly, in our first set of experiments, we applied unexpectedly, and with exclusion of visual and vestibular cues, constant-torque disturbances at the beginning and throughout centrally initiated movement which produced a constant degree of head undershoot (Fig. 2). During the application of the constant load, there was an increase in muscle spindle discharge as evidenced by a higher EMG activity (Fig. 2), more tendon organ activity, and a modification of postural information from joint receptors. However, in spite of this change in the flow of proprioceptive input from muscles, tendons, and joints, there was a lack of quick and effective position resetting (Fig. 2). Following the removal of the constant torque (animal still in complete darkness) the head reached the "intended" final position (Table 1 and Fig. 2). The fact that the head position attained after removal of constant-torque load was equal to that reached in the unloaded condition suggests that the program for final position was maintained during load application and that this program was not readjusted by proprioceptive signals acting at segmental and suprasegmental levels.

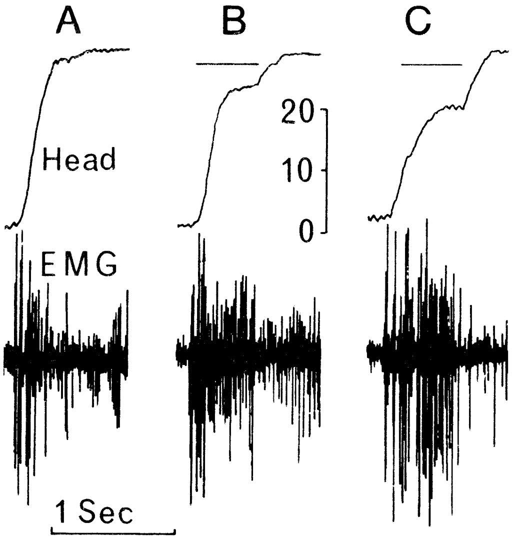

FIG. 2. Typical visually triggered head movements in chronically vestibulectomized monkey to appearance of target at 40° but performed in total darkness. *A* shows an unloaded movement. In *B*, a constant-force load (315 g·cm) was applied at the start of the movement resulting in an undershoot of final position relative to *A*, despite increase in EMG activity. In *C*, a constant-force load (726 g·cm) 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.

These observations lead naturally to the question: How is final head position determined? It can be assumed that final position is an equilibrium point resulting from the interactions of a number of factors: *1*) the centrally patterned commands to alpha and gamma motoneurons, *2*) the length-tension curves of agonist and antagonist muscles, *3*) the passive elastic forces, and *4*) other external loads. Accepting this assumption, any change in external load, such as a constant-torque load, is bound to change the equilibrium point; i.e., the head position. This hypothesis is in keeping with the observation shown in Fig. 2*B* and *C* and it indicates that the central, preprogrammed pattern of neural activity calling for a given final position is not reset by the unexpected proprioceptive feedback arising from the loaded muscles and tendons.

We believe that we were helped in reaching this conclusion by the nature of our preparation: our monkeys were not 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 the discrimination task. Because we rarely observed any evidence of reprogramming after the initiation of a trial, we were in a favorable condition to observe the effect of an unexpected proprioceptive feedback while a program calling for a given final position was maintained by the animal (5). We do not know, of course, whether requiring the animal to achieve a given final

TABLE 1. *Final head position attained during unloaded and constant-torque-loaded movements in three monkeys with intact proprioceptors*

	Monkey 1		Monkey 2		Monkey 3	
	Unloaded	After load	Unloaded	After load	Unloaded	After load
Day 1	24.1 ± 2.3 (18)	25.0 ± 2.5 (15)	27.0 ± 3.2 (15)	27.8 ± 3.2 (20)	29.1 ± 2.7 (22)	29.2 ± 2.1 (22)
	t = 1.06		t = 0.716		t = 0.124	
Day 2	29.8 ± 2.8 (16)	30.8 ± 2.9 (28)	23.3 ± 4.0 (16)	24.8 ± 4.4 (8)	30.8 ± 3.4 (10)	31.8 ± 3.0 (13)
	t = 1.24		t = 0.833		t = 0.729	

Values are means ±SD. Numbers in parentheses = N. The after-load condition indicates the head position achieved following removal of load as measured within 100 ms after reaching steady state. This position was found not to be significantly different from the unloaded condition using a two-tailed t test at the 0.05 level of significance.

head position would have led to different results.

The constant-torque load provided a disturbance during the dynamic phase of the movement and continued to have an effect after the head stopped, as evidenced by the undershoot. In a second set of experiments we examined the effect of stimulating proprioceptors only during the dynamic phase. To this end we used as a stimulus a load which modified the trajectory but did not represent a steady-state disturbance. This was done by using an inertial load.

As a result of the sudden and unexpected increase in inertia during a centrally initiated head movement, the following changes in head trajectory, relative to unloaded movement, were observed: first, a slowing down of the head, followed by a relative increase in velocity (due to the kinetic energy acquired by the load being transmitted to the decelerating head), culminating in an overshoot; finally, the head returned to the intended position in spite of the absence of any visible target (Fig. 3 and Table 2).

The changes in head trajectory brought about by the sudden and unexpected increase in head inertia induced corresponding modifications in the length and tension of neck muscles. The agonist muscles were, in fact, first subjected to increased tension because the application of the load slowed down the process of muscle shortening, then the shortening of the same muscles was facilitated during the overshoot phase of the head movement induced by the kinetic energy of the load. Such loading and unloading did, of course, provoke the classical muscle spindle response presumably mediated by group Ia and group II afferent fibers which, in turn, affected the agonist EMG activity. Figure 3*B* shows that there was first a greater increase in motor unit discharge during muscle stretch than would have occurred if no load were applied (Fig. 3*A*), followed by a sudden decrease in activity at the beginning of the overshoot phase. Traditionally, these changes in the electromyogram have been attributed to the activity of muscle spindle afferents, but clearly this is an oversimplification because tendon organs and, possibly, joint receptors may also contribute to the EMG pattern (20). It should be mentioned that antagonist muscles underwent the same series of changes in length and tension, but in a complementary fashion.

Therefore, during a head movement, an unexpected inertial load induced a series of wax-

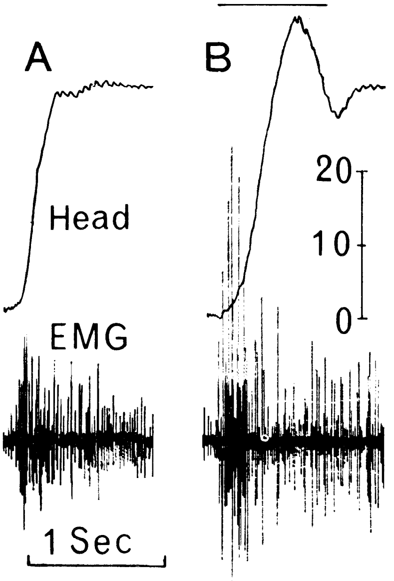

FIG. 3. Typical head responses of a chronically vestibulectomized monkey to sudden appearance of target at 40°. *A* shows an unloaded movement, whereas in *B* a load of approximately 6 times the inertia of the head was applied at the start of the movement, as indicated by the force record. Both movements 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; head calibration is in degrees; time marker is 1 s.

TABLE 2. *Final head position achieved during unloaded and inertially loaded movements in three monkeys*

Unloaded	N	Inertial Load	N	
		Monkey 1		
33.565 ± 2.215	10	33.915 ± 2.611	7	0.298
25.476 ± 2.840	7	26.346 ± 2.084	13	0.785
30.857 ± 1.896	7	30.960 ± 2.641	10	0.088
28.565 ± 4.560	9	27.685 ± 4.483	9	0.413
26.750 ± 1.977	9	25.447 ± 2.152	9	1.338
		Monkey 2		
27.265 ± 0.804	23	27.325 ± 0.968	12	0.196
		Monkey 3		
0.062 ± 2.744	16	−0.286 ± 2.283	21	0.421

Values are means ± SD. In monkey *1* and *2*, the head responses are elicited by the sudden appearance of target at 40° (head starting from the primary position). In monkey *3*, head starting position was approximately at 30° and target at center. Day-to-day variations indicated only for monkey *1*.

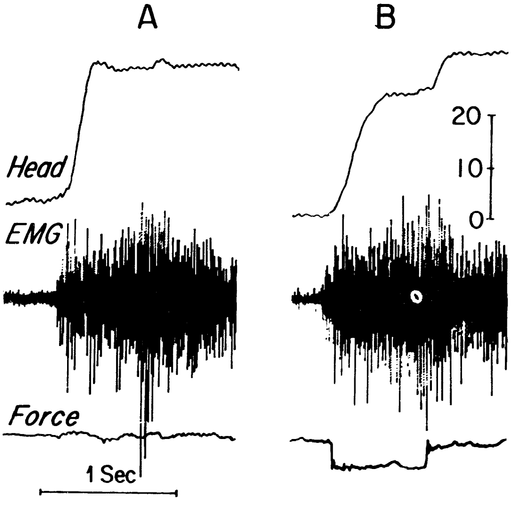

FIG. 4. Typical movements of a chronically vestibulectomized monkey with sectioned dorsal roots (C_1–T_3) made open loop (in total darkness). In *B*, constant-force load (315 g·cm) was applied at the start of movement, resulting in an undershoot while the load was on. Similarity of EMG pattern in *A* and *B* shows lack of a stretch reflex. Peak force in *B* approximately 315 g·cm. Vertical calibration in degrees.

ing and waning proprioceptive signals from muscle spindles, tendons, and joints, but the intended head position was eventually reached even in the complete absence of other sensory cues (visual and vestibular).

This observation, together with those on the effect of constant-torque loads, suggests that the central program establishing final head position is not dependent on a readout of proprioceptive afferents generated during the movement but, instead, is preprogrammed. It should be pointed out that this conclusion does not speak to the question of whether or not the proprioceptive apparatus is an effective aid in reaching final position.

Load disturbances during head movement in deafferented monkeys

To provide a further test of the hypothesis that final head position is preprogrammed, we investigated how our chronically vestibulectomized monkeys reached final head position without visual feedback when they were deprived, in addition, of neck proprioceptive feedback. The goal here was to observe how monkeys moving their heads in an "open-loop" mode were able to deal with the application of constant torque applied during centrally initiated movements.

Figure 4 shows that following the unexpected application of a constant-torque load at the beginning of a visually triggered movement, the posture attained by the head was short of intended final position. It should be emphasized that the target elicited the movement, but there was no target light to guide the orienting head movement and that these animals were chronically vestibulectomized. After the removal of the constant torque, the head attained a position that was found to be equal to the one reached by the head in the no-load case (Table 3). When the disturbance was an inertial load, we did not expect and did not find any change in final head position. The head trajectory, however, was greatly disturbed by this type of load in the deafferented animal. Because of the

TABLE 3. *Final head position attained during unloaded and constant-torque-loaded movements in three monkeys after deafferentation*

	Unloaded	After Load
Monkey 1	25.3 ± 2.9 (7)	24.9 ± 2.5 (7)
	t = 0.33	
Monkey 2	36.4 ± 2.1 (7)	37.1 ± 1.9 (8)
	t = 0.68	
Monkey 3	27.6 ± 1.6 (9)	27.8 ± 1.5 (7)
	t = 0.30	

Values are means ± SD. Numbers in parentheses = N. The after-load condition indicates the head position achieved following removal of load as measured within 100 ms after reaching steady state. This position was found not to be significantly different from the unloaded condition using a two-tailed *t* test at the 0.05 level of significance.

open-loop condition, the head overshoot shown in Fig. 5 must have been corrected by an increase in antagonist tension generated not by an increase in alpha motor outflow to antagonist muscles, but by the intrinsic length-tension properties of the muscle tissue. The effectiveness of this mechanism is, of course, dependent on the central programming of alpha activity to both agonists and antagonists which determines the stiffness of these muscles (18).

These results indicate that the head motor system behaved qualitatively in the same way before and after deafferentation with respect to head posture. We should hasten to say, however, that there are differences between an animal with intact proprioceptive apparatus and the same animal after dorsal rhizotomy, particularly in the dynamic characteristics of head movements. For instance, there is a clear difference in the way head movements terminate: before rhizotomy, final head position is reached with a smooth deceleration, whereas afterward, the transition from movement to posture is much more abrupt (compare Figs. 2*A* and 3*A* with Figs. 4*A* and 5*A*). The postoperative pattern of neck muscle EMG activity was considerably different from that recorded preoperatively. After dorsal root section, the agonist muscles achieved head turning by way of a sharp increase in activity which started before the movement, continued unmodified throughout, and persisted while the head remained in the intended final position (see Figs. 4*A* and 5*A*). In addition, cocontraction of agonists and antagonists occurred. Preoperatively, the most common pattern displayed by the agonists consisted of a burst of EMG activity followed by a steady but lower degree of activity (Figs. 2*A* and 3*A*). In addition, the final head position in deafferented animals is not as steadily maintained as before rhizotomy (compare again Figs. 2 and 3 with Figs. 4 and 5), and the degree of head overshoot for the same inertial load is much smaller before deafferentation due to the presence of the stretch reflex (Fig. 5). Thus, there is little doubt that the proprioceptive apparatus has a role in keeping the head trajectory within a preestablished course, particularly when external disturbances are unexpectedly applied.

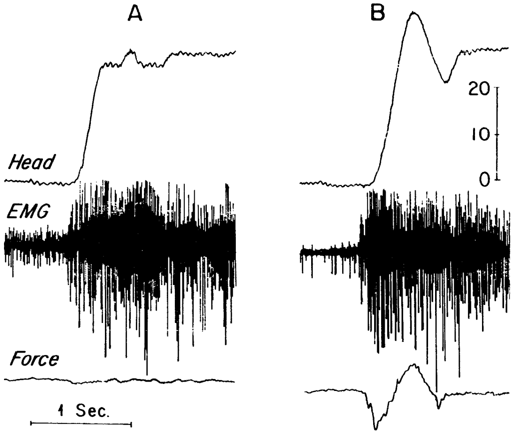

FIG. 5. Head movements of chronically vestibulectomized monkey with dorsal roots C_1–T_3 sectioned. In both cases the eliciting stimulus was turned off just before the start of the movements so that the performance was accomplished open loop. *A* shows an unloaded movement. In *B*, a load of approximately 4 times the inertia of the head was applied at the start of the movement. Note lack of evidence of a stretch reflex (compare with Fig. 3*B*) in EMG. Peak force exerted by the monkey in *B* is approximately 375 g·cm. Vertical calibration is in degrees. EMG recorded from splenius capitis. Compare overshoot in *B* with that in Fig. 3*B*, but note that there the load is 50% larger.

DISCUSSION

The studies described in this paper are directed toward understanding the mechanisms whereby the central nervous system terminates movement and maintains a newly acquired position.

Before discussing our findings, some of the factors underlying acquisition and maintenance of final head position should be mentioned; among these are the length-tension properties of both agonist and antagonist neck muscles, the passive elastic forces that tend to oppose any deviation from the primary position and, above all, the frequency of alpha motoneuronal discharge. The firing rate of the alpha motoneurons will select a particular length-tension curve (18, 28) for both agonist and antagonist muscles and, in absence of other forces, the final resting length will be determined by the interactions of the two curves; i.e., when tensions on the two sets of muscles are equal and opposite (2, 15, 16).

This view explains a number of our results. For instance, it is not surprising that the head overshoot during inertial loading is corrected with a return movement to the intended position because, even with no change in motor outflow, the change in muscle length due to the inertial load will generate an increase in antagonist tension and, hence, a return head movement (Fig. 5*B*). By the same token, because head position is the result of muscle-length and load-length parameters, an undershoot is observed when a constant opposing torque is applied (Figs. 2*B* and 4*B*). Finally, the same hypothesis explains why head movements reach their intended final position when the constant torque is removed.

Thus, it seems that final head position in both intact and deafferented preparations should be viewed as an equilibrium point dependent on the firing rate of the alpha motoneurons to agonists and antagonists, the length-tension properties of the muscles involved in maintaining the posture, and the passive, elastic properties. In the intact animal, however, in parallel with this basic process, the proprioceptive apparatus, especially the gamma muscle-spindle loop and tendon organs, participates in the process of reaching final position by increasing muscle stiffness when a load disturbance is applied (18, 22, 28). 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, therefore, force the selection of a new length-tension curve with a different slope. It is certain that in this way more tension is transiently produced by the muscle (compare differences between Figs. 3 and 5); however, the effectiveness of the proprioceptive apparatus in generating, reflexively, muscle tension will be dealt with quantitatively elsewhere (unpublished observations).

It should be pointed out that there are two processes occurring while the head is moving toward its intended final position. First, there is the centrally preprogrammed alpha motoneuron activity and second, there is the segmental and suprasegmental activity caused by the expected or unexpected inflow of proprioceptive signals resulting from the load. Given that the correct achievement of final head position depends on the precise amount of alpha activity to both the agonist and antagonist muscles, it follows that centrally programmed activity must not be reset by expected or unexpected proprioceptive input. Given that the proprioceptive afferent input resulting from sudden application of a load is quickly transmitted to a number of structures including the motor and sensory cortex (7, 12, 13, 27, 32, 34), the cerebellum (4), and the brain stem (1, 3, 23-25), it is at present difficult to suggest where the structures responsible for presetting final position, which are not directly impinged on or reset by sensory proprioceptive disturbances, might be located. In addition, we do not know whether the positional commands are delivered at the beginning of the movement or toward its completion, and whether there is a private line for preprogrammed final position which acts in parallel with the lines which are responsible for the dynamic changes.

In conclusion, our studies of the mechanism underlying the termination of visually triggered head movement have indicated *1*) that the final head position is an equilibrium point dependent in part on centrally programmed patterns of neural activity, and *2*) that these patterns are not reset by the afferent proprioceptive impulses generated during the intended movement. These conclusions are based on the observation of head movement and final head position of intact monkeys; the findings in deafferented animals simply provide further, although qualified, support of our interpretation. In fact, the motor behavior of deafferented animals may not only be the result of proprioceptive deprivation, but also of adaptive motor rearrangement.

It should also be stressed that our conclusions apply only to the particular strategy of movement we have investigated; there is no doubt that other modes of movement, for instance, exploratory movements, might be terminated following an evaluation of afferent feedback.

Finally, although our evidence shows that proprioceptive signals originating from the moving neck fail to reset the central patterns responsible for final position, these signals are certainly important in conjunction with other sensory input for establishing the programs for movement and posture (26).

SUMMARY

The studies reported here are directed toward understanding some of the mechanisms whereby the central nervous system terminates a given phase in a motor sequence and maintains a newly acquired position.

In particular, we investigated the extent to which the termination of a centrally initiated head movement in monkeys and the subsequent maintenance of posture depend on a readout of proprioceptive afferent input generated during the movement itself or are instead centrally programmed. We approached this question in two ways: first, using vestibulectomized, but otherwise intact monkeys, we applied load disturbances unexpectedly at the beginning and throughout centrally initiated head movements with the aim of provoking a proprioceptive response in all types of neck receptors and to observe the outcome of this stimulation on the head final position. In a second set of experiments, we interrupted the flow of afferent input by cutting cervical and upper thoracic dorsal roots and observed how the absence of proprioceptive feedback affects the achievement of final head position. The results indicated that the central pattern of neural impulses establishing final head position is preprogrammed and it

is not reset by the afferent proprioceptive impulses generated during the intended movement. In addition, our findings are consistent with the view that final head position is an equilibrium point dependent on a number of factors, such as the firing rate and the recruitment of the alpha motoneurons, the length-tension properties of the muscles involved in posture, and passive elastic properties of external loads.

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