Chapter 86
What about the So-Called Neck Reflexes in Humans?

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›stural factors in man induce changes in the tone of limb mus-es that resemble neck reflexes in animals. The study of these :ck influences seems to be a subject of considerable interest for veral reasons. First, modern concepts in this field are based on e application of data from animal experiments to man, although c legitimacy of such a transfer is dubious. Indeed, the bipedal thograde stance, liberating the forelimbs from their role as a ›stural support, considerably changes the conditions for and :havioral assignment of neck influences. It must also be ressed that the majority of experimental data were obtained in ıimal preparations with a significantly reduced central nervous /stem (CNS). Second, the data in humans are rather contradic-ıry. According to Magnus (1924/1988) there are no neck reflexes ı healthy persons, but it is possible to obtain such reactions in ıe human embryo and in patients with massive lesions of the ›rebrain. In contrast, a number of authors report that neck influ-nces do exist in normal persons, but only under the utmost ıuscular effort or under conditions of fatigue (Hellerbrandt et l., 1956; Fukuda, 1984). Other points of interest in the investiga-.on of neck influences in man are related to the fact that the tudy of these reflexes in animals has formed the basis for the .nderstanding of the cerebellar and brain stem mechanisms of ›ostural control. It may therefore be supposed that the analysis ›f neck reactions in humans will improve our knowledge of the ›asic mechanisms of postural control in man, especially with egard to the internal subconsious representation of the body body scheme).

The aim of the research reported here was to investigate to vhat degree the human neck influences represent "reflexes," in he traditional sense of this term, and to what extent they are letermined by the system of internal representation of the body.

Methodologic prerequisites

The greater portion of animal data on neck influences was obtained under conditions of increased levels of tonic muscle activity. As a rule the fragmentary data on man also represent cases of augmented muscle tone. It was shown also (Beritoff, 1915) that, in states of low decerebrate rigidity, neck and labyrinthine reflexes exist in latent forms and can be revealed by means of additional stimulation. Thus it seems reasonable to suppose that increase of background muscle tone is one of the main methodologic prerequisites for a systematic study of neck reactions in humans. In addition, neck influences are almost unrecognizable during voluntary movements controlled by central programs and corrected by various feedback loops. It is most likely that they can be seen if the muscular activation has an involuntary origin and no definite goal. This is another methodologic necessity.

Two well-known tonic phenomena are of interest from the point of view of these prerequisites. They are the so-called Kohnstamm phenomenon (which occurs after muscle contraction) (Kohnstamm, 1915), and the tonic vibration reflex (TVR) (Lance et al., 1966). The Kohnstamm phenomenon is an involuntary activation of a muscle lasting for a period of about 1 minute and induced by previous sustained voluntary effort. It was shown in our work (Gurfinkel et al., 1989a) that such postcontraction may appear not only after voluntary contraction of a muscle but also after its reflex activation by vibration. Besides the overt Kohnstamm phenomenon, we demonstrated the existence of concealed effects lasting for 15 to 20 minutes that can be revealed by additional activation. With regard to the TVR, it should be noted that the traditional TVR is not the only way to activate muscles with vibration. There are cases in which the tonic reflex contraction of a certain muscle is induced by stimulation with vibration (Gurkinkel and Latash, 1978) of another muscle (switched TVR).

We consider both the Kohnstamm phenomenon and the TVR to be methods that give rise to activation of special tonogenic structures of the CNS. It should be stressed that the effects revealed using these tonic phenomena do not cover all the diversity of neck influences in man (e.g., neck influences while standing). However, they do reflect some essential common features.

Methods

Previous experiments (Gurfinkel et al., 1989b) showed that both postcontraction and vibration-induced tonic activity are sensitive to changes of head position and to other postural factors. It was important to select a rather simple experimental procedure permitting us not only to see the signs of the reactions but also to evaluate them quantitatively. We chose the following paradigm. The subject was seated on an armchair high enough so that the feet did not touch the floor. An increased level of tonic activity of knee extensors was induced by one of two methods. In experiments using the Kohnstamm phenomenon, the subject executed an isometric contraction of both quadriceps muscles by pressing against a stop for a period of 40 to 60 seconds. Following a command the subject ceased the volitional effort and relaxed. An involuntary postcontraction then began in which the angle of the knee joint increased. In experiments using vibrational stimulation the tonic contraction of the knee extensors was induced by stimulation from vibrators placed at the Achilles tendons. Since there was no contact between the feet and the floor, the TVR did not occur in the soleus muscles; the quadriceps muscles were activated instead (switched activity). The effects of unilateral and bilateral vibrational stimulation had been compared in a previous series of control experiments. There were no significant differences between neck influences in these two cases if short vibration periods (10 to 15 seconds) were used.

Sixteen subjects participated in this study. In nine changes of muscular activity in response to head rotation were observed systematically. Generally the repetition of experiments in one subject resulted in the increase of his reactions from one test to another.

For quantitative evaluation of neck influences on the state of limb muscles we used an index of reaction asymmetry that was calculated as the ratio of the difference between the amplitudes of the changes in the knee joint angle in the left and in the right leg to the amplitude of the greater of the two reactions. The amplitude of reaction for each leg was determined after a specific period of time from the onset of vibration or from the command to relax when the Kohnstamm phenomenon was used. This time interval was selected individually for every subject in accordance with his characteristic rate of knee extension and represented the period of linear increase of the knee joint angle over time. The

'mmetry also could be evaluated as the difference in the laten-
s of the reactions, and from the slope of the electromyographic
ΛIG) activity in the quadriceps muscles.

:sults

e redistribution of the tonic activity of the upper and lower ıb muscles under the conditions of vibrational stimulation or : Kohnstamm phenomenon can be evoked by changing a num- r of postural factors. Among these are head rotation, tilt of the ad toward the right or the left shoulder, tilt of the head forward d backward, and rotations and tilts of the trunk. This paper is ıited to the description of the effects produced by static head tations around the vertical axis, which do not modify the ves- ıular signals.

fluence of static head rotation on tonic activity of knee ctensors

. our first set of experiments we studied the influence of static :ad rotation on the tonic activity of the quadriceps muscles ;ing both the Kohnstamm phenomenon and vibrational stimula- on; the data obtained were similar. In the basic experimental :ocedure, the subject sat in a comfortable, relaxed posture with s head directed forward. In the vibration stimulation protocol ıe onset of vibration led to the appearance on the electromyogram of quadriceps muscle activity producing an extension of the legs in the knee joints. After cessation of vibration the muscles typically relaxed rather abruptly (in 200 to 300 ms) and the legs returned to the initial position, making two to three swings of oscillation (Fig. 86–1). If the head was maintained in a neutral position the reactions of the legs were approximately equal (Fig. 86–1A). When the head was turned, the reaction on the side of the direction of the turn (chin side) was weakened and that on the side opposite the direction of the turn (occipital side) was strengthened. For example, head rotation to the left suppressed the extension of the left knee joint and increased the extension of the right one (Fig. 86–1B). In the most sensitive subjects the effect was so strong that flexion rather than extension was observed on the chin side.

An analogous asymmetry of reactions could be observed in experiments using the Kohnstamm phenomenon. The sign of the typical reaction is therefore opposite to that described by Magnus (1924/1988) for quadrupeds. However, the variability of neck influences among humans must be stressed. For example, in three of the subjects inverse reactions were sometimes observed (increase of the extension on the chin side). Trunk position had a definite role in these responses since forward inclination of the trunk could produce switching of the reaction to the inverse form.

The greater the angle of head rotation the stronger was the reaction asymmetry. However, gentle rotations of about 5° often did not produce any asymmetry. From these observations we concluded that a characteristic insensitive zone of leg muscle reactions to neck rotations does exist (Fig. 86–2). It should be mentioned that this zone was wider if the onset of vibration did

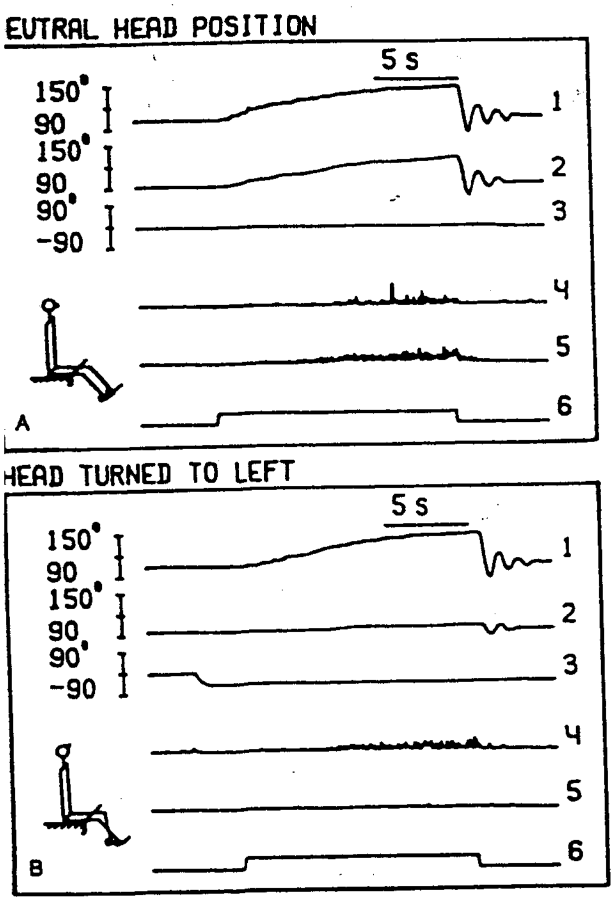


Fig. 86–1. Influence of head position on knee extension due to vibration. (A) Head in neutral position. (B) Head turned to the left. 1, knee angle of the right leg; 2, knee angle of the left leg; 3, angle of head rotation (− indicates rotation to the left); 4, electromyogram of the right quadriceps muscle; 5, electromyogram of the left quadriceps muscle; 6, vibration indicator (raised when vibration is being applied).

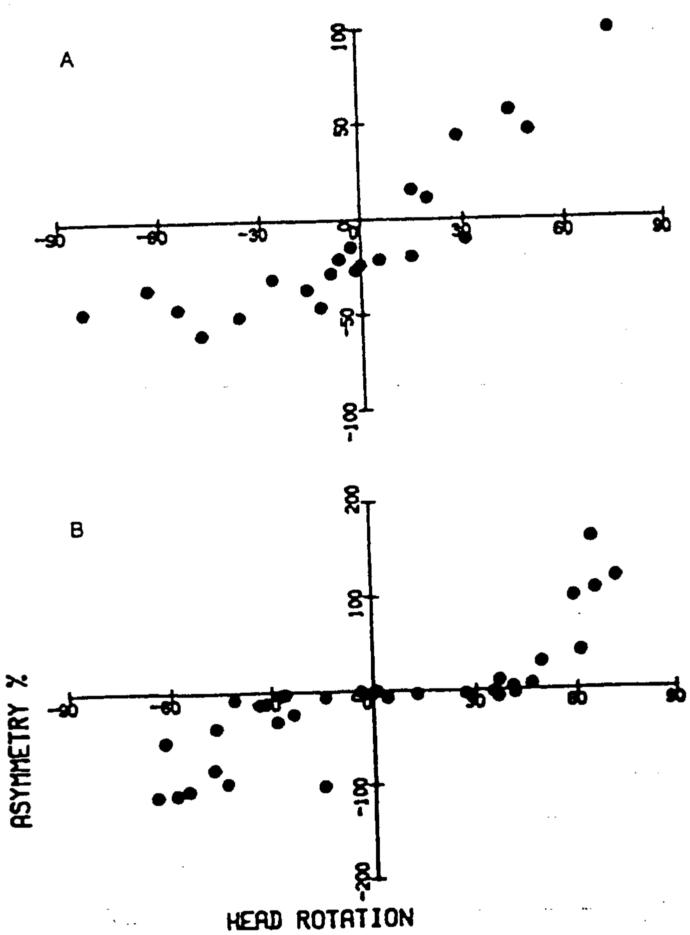


Fig. 86–2. Dependence of the asymmetry of the leg reaction upon the angle of head rotation. (A) Test executed immediately after the turn. (B) Asymmetry tested 10 seconds after the head was turned.

: immediately follow the head turn but instead was executed re than 10 seconds later; in that case the width of the insensi- : zone reached 20° to 25° (Fig. 86–2B). This fact led us to study :k influences under a condition of sustained rotation of the ıd.

›dification of leg muscle tonic activity during illusory ad "return" produced by sustained static rotation of ẹ head

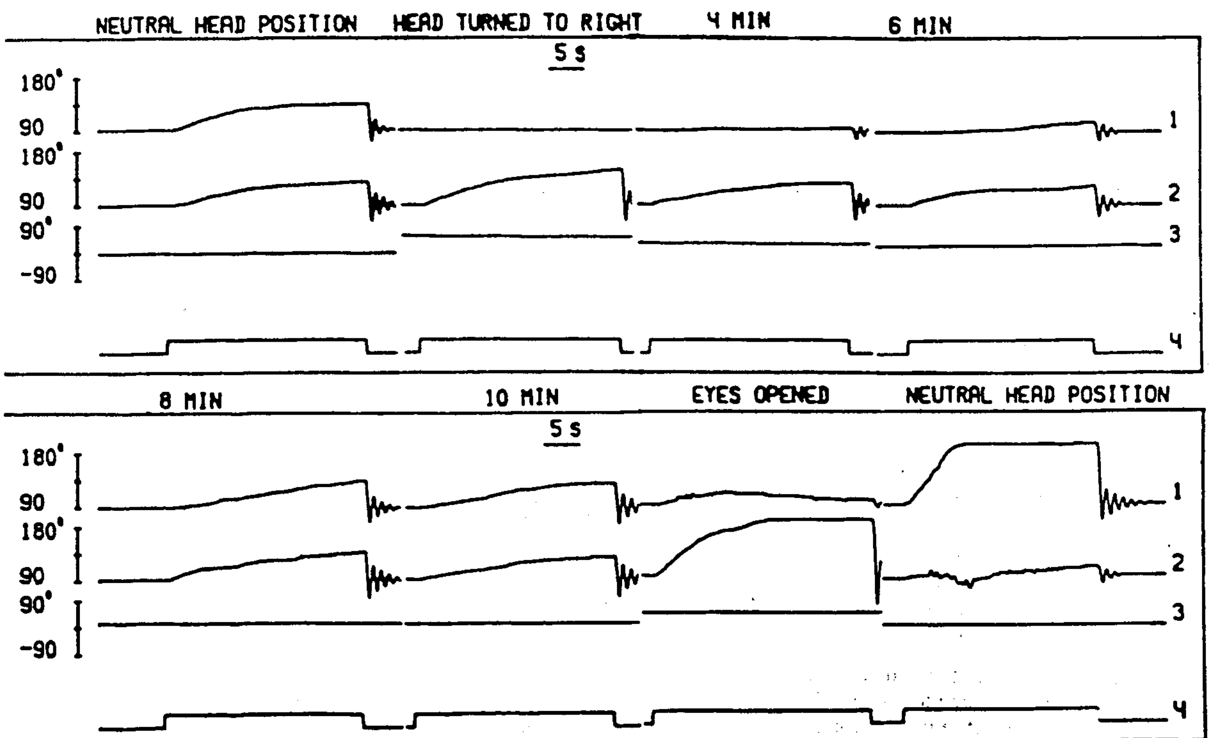
e examination of neck influences during sustained head rota- n was also of interest for us because preceding investigations :ried out in our laboratory (Gurfinkel et al., 1989c) had shown ıt both passive and active retention of the head in a rotated ıte, with the eyes closed, caused the perception of slow head ›vement toward the neutral position. The usual time required accomplish this subjective "return" was about 10 minutes, d passive retention was a slightly more effective condition for : phenomenon to take place.

Figure 86–3 presents a sequence of vibrational stimulation ıts of illusory head return. Responses were determined: (1) at 4, 6, 8, and 10 minutes after the beginning of a sustained ;htward turn of the head with the eyes closed; (2) following ›ening and then reclosing the eyes; and (3) following passive turn of the head to the neutral position. The subject indicated ; perception of head orientation by means of a joystick. While e subject's head was still in the neutral position (with the eyes ›sed), the legs responded symmetrically to bilateral vibration. ımediately after the head turn (1 minute) the reaction of the ;ht leg disappeared and the extension of the left knee joint creased. At four minutes the effect on the left leg diminished ıd a slight response of the right leg was recorded. The differ- ıce between the reactions of the legs decreased greatly at the ĸth minute as the subject began to indicate a "return" of the :ad to the neutral position. The asymmetry disappeared 8 to 10 inutes after the turn of the head in accordance with almost full usory return. When the eyes were opened and the perception of the real position of the head became available to the subject the asymmetry reappeared. If the eyes were closed again, the subjective return of the head to neutral position was much more rapid (3 minutes). Finally, the head was passively returned to the true neutral position by the experimenter while the subject kept the eyes closed. The subject perceived the new position of the head as small turn to the left. In agreement with this internal representation of head orientation the extension was suppressed in the left leg and sharply strengthened in the right.

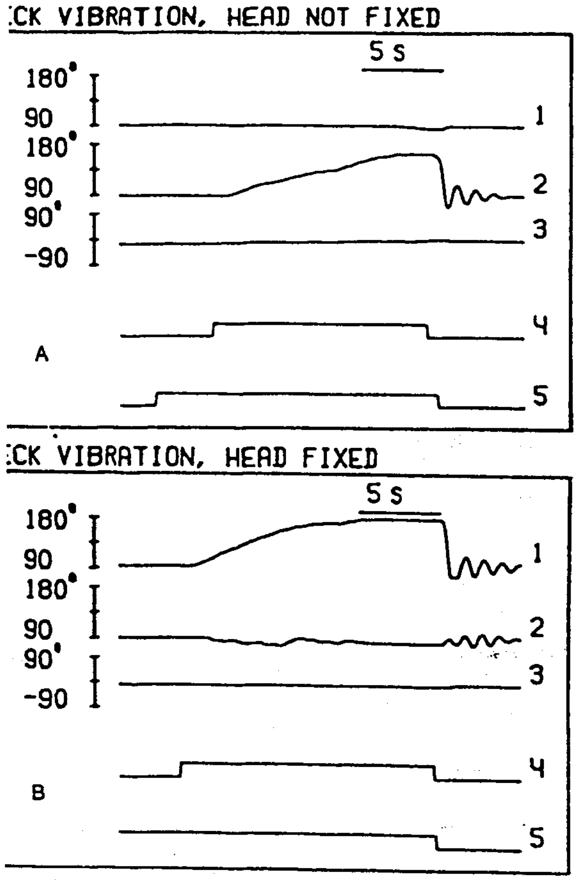
The effect observed cannot be explained by the adaptation of the neck receptors. In the first place, maintenance of the head in the turned position requires continuous activity of the neck muscles, and under such conditions neck receptor functioning does not change drastically. Also, the reaction that occurs when the eyes are opened confirms that the changes of the leg responses to vibration follow the perception of head position and are not based on an adaptation process. The "return phenomenon" has been known since the time of Helmholtz. We consider it a kind of "drift" in the system of internal representation to some usual "normal" position. That the redistribution of tonic activity of leg muscles revealed by vibrational stimulation tests is associated with changes in the system of internal representation of body parts is supported by the results of the following experiments.

Postural asymmetry induced by vibration of neck muscles

Experiments on postural asymmetry were performed using vibrational stimulation of neck muscles. The vibrator was located on the dorsum of the neck in such a way as to obtain a net head rotation without any additional tilt. In the experiment illustrated by Figure 86–4, the TVR appearing in the vibrated muscle produced a head rotation toward the right. After the beginning of the head turn, vibrational stimulation applied to the Achilles tendons produced extension of the left knee in accordance with the direction of the head rotation. The effect of vibration-induced head rotation did not differ from the effect of voluntary or passive turning (Fig. 86–4A).



ig. 86–3. Change of leg reactions to vibration during prolonged head fixation in the turned position (rotation to the right). 1, right knee angle; , left knee angle; 3, perceived position of the head; 4, vibration indicator. For explanation see text.



g. 86–4. Influence of vibration of neck muscles on knee extension oked by vibration of the Achilles tendons. (A) The head is not ed. The vibration evokes a slight head rotation to the right. (B) The ad and the trunk are fixed. Vibration evokes an illusion of head tation to the left. 1, right knee angle; 2, left knee angle; 3, head sition; 4, leg vibration indicator; 5, neck vibration indicator.

It is known that, under conditions of muscle vibration, pre-enting muscle shortening can produce an illusion of movement e direction of which corresponds to the elongation of the mus-e vibrated. The vibration of neck muscles when the head and unk are fixed also evokes the sensation of a head turn opposite the direction of vibration-induced rotation in the head-free ondition. During illusory head rotation the leg reactions also orrespond to the perception of head position. An example of bration-induced illusion of head rotation to the left is shown in igure 86–4B. The position of the vibrators was the same as in e previous experiment (Fig. 86–4A), but the head was isometri-lly fixed. The response asymmetry was even more pronounced uring the illusory rotation than during an actual turn. In particu-r, a small flexion of the left knee can be seen. These experi-ents show that vibrational stimulation of the same neck recep-rs can give rise to opposite influences on the tonic activity of g muscles depending on the interpretation of the receptors fired y the CNS.

ifluence of Hypnotically suggested head rotation on leg uscle tone

n an experiment conducted with the participation of a psycho-erapist, the perception of head rotation while true head posi-on did not change was obtained by means of a hypnotic sugges-on. Vibrational stimulation tests of leg muscles revealed ostural asymmetry identical to that seen during an actual head turn. It is interesting to note that the same asymmetry was seen when extension of the knees was hypnotically suggested (without giving information on degree of reaction on either side). These data show that the influence of perception of head rotation on the tonic activity of leg muscles can take place without activation of any kind of receptors, permitting us to conclude that internal representation of head position strongly affects reactions usually considered to be reflexes.

Neck influences in different types of foot-ground interaction

The last group of experiments was devoted to the study of the changes in neck influences with various types of foot-ground interaction. Figure 86–5 illustrates four types of this interaction: absence of support, fixed support platform, support platform with one degree of freedom, and support with two degrees of freedom. In these experiments the Achilles tendon of only one leg was vibrated. The EMG activity of the knee flexors and extensors of the soleus muscle of the stimulated leg was recorded. As seen in Figure 86–5A, a TVR of the soleus muscle is observed in the condition of fixed support; this TVR can be modulated by head rotation. The reaction also depends on head position if the supporting platform can rotate freely around the vertical axis (Fig. 86–5B): head rotation to the right is followed by activation of the right biceps femoris and external rotation of the foot. Head rotation to the left evokes the activation of the semitendinosus and semimembranosus muscles and internal rotation of the foot (not presented in Fig. 86–5). When the foot is suspended the vibration of the Achilles tendon reveals itself in knee extension, but activation of some other muscles in addition to the quadriceps can be also observed (Fig. 86–5C). In this case the effects of head rotation are the same as with the freely hanging leg (Fig. 86–5D).

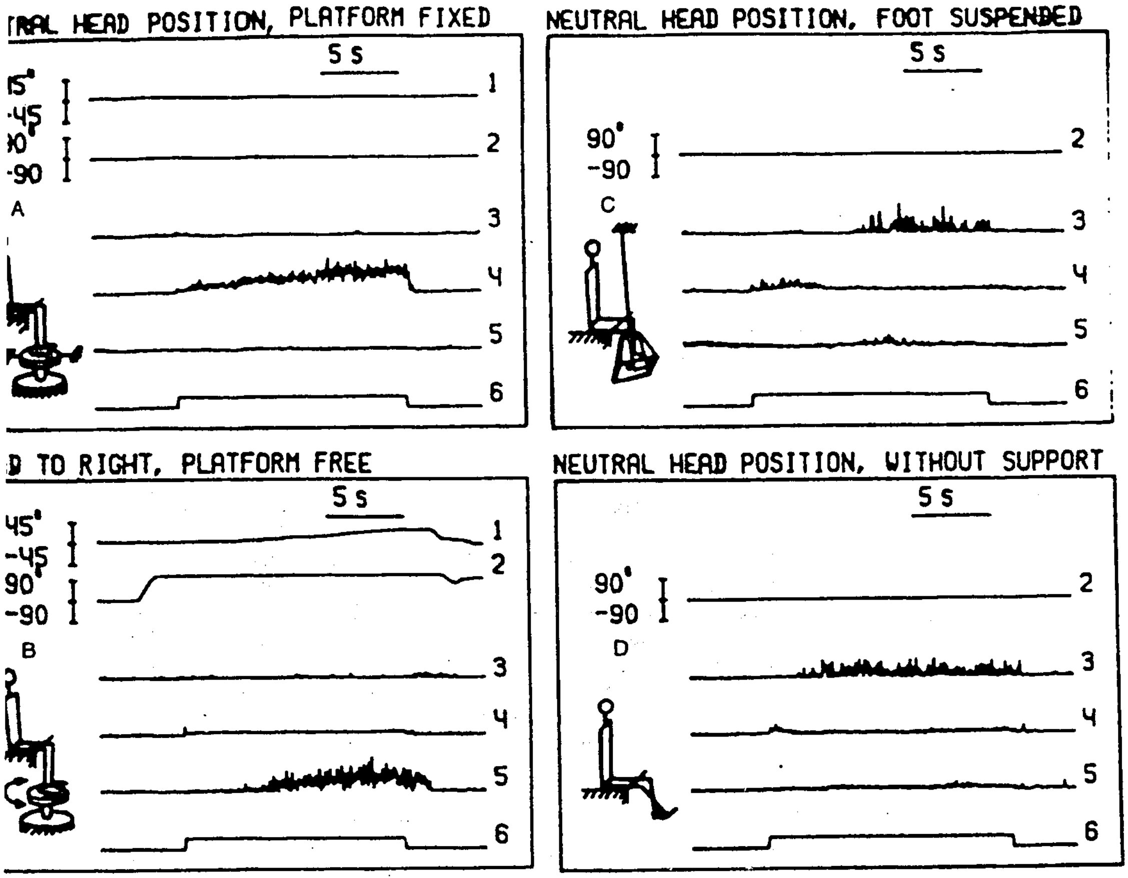
The modification of neck influences by support could be considered—as in the case of support influence on vestibulospinal reflexes (Kasper et al., 1986)—as a kind of competitive mode where the proprioceptive input gates the neck input. In our case the effects of foot-support interaction cannot be limited to modulation.

We also studied the effects of pressure applied to the foot that gave illusory information on foot-ground interaction. Local pressure was applied to the foot using a pneumatic cuff bandaged to the sole of the foot. Inflation of the cuff was perceived by a subject as pressure on the sole, despite the fact that pressures on the sole and the dorsum of the foot were equal. In this condition static pressure did not modify neck influences on leg muscles.

This complex picture testifies that neck influences cannot be reduced to stereotyped reflex automatisms. They are integrated in the intricate system of the context-dependent reactions of leg muscles. The behavioral value of these reactions is obvious, because they depend on the presence or absence of the support, on its stability, and so on.

Discussion

A healthy man possesses neck reflexes in a latent form that can be revealed in certain conditions. If such reflexes functioned irrespective of the physical situation, the freedom of movement would be greatly limited and the movements themselves machine like. It seems likely that the system of neck reflexes should be controlled by some structure(s) of the higher CNS level. Such relations between the higher and lower levels of the CNS are well known in, for example, presynaptic descending control and the brain stem regulation of spinal reflex gain. Unfortunately, this information details the "technology" of the expression of the descending influences and tells us little about the mechanism by which this control ensures purposive motor activity. Discussion



. 86–5. Neck influences on leg muscles for different characteris- ; of support. (A) Fixed support. (B) Support with one degree of :dom. (C) Support with two degrees of freedom (suspension). (D) :t free. The vibration is applied only to the Achilles tendon of the right leg. 1, angle of rotation of supporting platform around the vertical axis: 2, head position; 3, electromyogram of quadriceps muscle; 4, electromyogram of soleus muscle; 5, electromyogram of biceps femoris muscle; 6, vibration indicator.

the biologic meaning of descending control is usually in terms context-dependent reactions, most frequently interpreted as : dependence of the reaction on a number of external factors luencing the organism. Our experiments demonstrated this re- ionship quite clearly in the dependence of the reaction patterns the characteristics of foot support. However, context depen- nce does not cover all of the observed reactions.

Our experiments on subjective head return, the illusions in- iced by neck muscle vibration, and hypnotic suggestion show at the system of internal representation dominates in these ses. Little is known about this system; however, we may sup- se that the state of the internal representation of the body is t determined exclusively by the diverse afferent inputs. We ink that the internal model of the body (body scheme) performs essential role in this system. It is the existence of such a model at makes it possible for a discrepancy between perceived posi- on and actual position to be recognized. In our study, the de- endence of the pattern of neck influences not only on the pres- ice of foot contact with a support but also on the loading onditions and the number of degrees of freedom of the support- g platform shows that the context-dependent reactions are me- iated through some specific central organization. The concept of e body scheme, perhaps because of its neurologic origin, is ommonly expressed relation to various aspects of the perception of the body in external space. Our experiments seem to have revealed another functional aspect of the body scheme, that is, its connection with motor organization, including both voluntary movements and various postural reactions usually considered to be reflexes. The reason for body scheme involvement in motion control may be that motor coordination tasks in multijoint systems become extraordinarily complicated; their solution by means of a universal internal representation of the body is evidently more effective than construction of a bulky coordinative structure for each distinct reflex.

Conclusion

Head rotations induce changes in distribution of tonic activity of limb muscles in man that resemble neck reflexes in animals in many respects. Nevertheless, there is no reason to consider these influences in man as direct reflex responses to the activation of neck muscle receptors. More probably they are connected with head position in space independently of whether the information on this position originates from some external sensory input or from the intrinsic model of the body. These arguments can also be applied to animals in various conditions of natural behavior.