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16. Abstract This article presents some viewpoints on the vertical human posture, explaining what an extremely complex physiological study this entails, and the relation between postural adaptation during voluntary movements and the guarantee of stable locomotor movements. Various complex sensory systems are discussed.					
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SIGNIFICANCE OF VESTIBULAR AND PROPRIOCEPTIVE AFFERENTATION IN THE REGULATION OF HUMAN POSTURE

V. S. Gurfinkel'*

The vertical human pose is an interesting, and at the same time, /1**
an extremely complex object of physiological study. Posture is not
only the maintenance of a certain position of the links in relation
to each other and the entire body in space, but also fine mechanisms
of postural adaptation during voluntary movements, and the guarantee
of stable locomotor movements. The realization of posture is linked
to the presence of a certain frame of reference that is common for an
evaluation of the mutual position of the body links and the body ori-
entation in relation to the extrapersonal space. Therefore a link
exists between the mechanisms of postural regulation and the mechanisms
of spatial orientation. The postural mechanisms are also important
because according to a number of indicators they occupy a seemingly
intermediate position between the motor automatisms of the locomotion
type and the voluntary movements. Therefore a knowledge of the
mechanisms for postural regulation can be viewed as a prerequisite
for an understanding of the mechanisms for voluntary movements.

In different animal species, depending on their body structure,
structure of the organs of movement, habitat, nature of motor activity
and many other factors, the forms of postural activity significantly
differ: from the prolonged maintenance of the mollusk valve in the
closed position, to the human positions in gymnastics, figure skating
and ballet that are surprising in their complexity and beauty. It

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should be stressed that in vertebrates the entire diversity of postural activity is guaranteed by the exceptionally high activity of the nerve-muscle apparatus. Postural activity is especially complicated and enriched in the erect, two-legged animals and in man.

From the biomechanical viewpoint the body of a standing man can be viewed as a multiple-link hinged-rod system whose links are inverse pendulums resting on each other. Stabilization of such a system in the vertical position is possible only with the active participation of the musculature. Despite the fact that in numerous clinical observations (affection of the posterior labyrinthine trunks, different structures of the trunk and cerebellum) and experimental studies a considerable number of facts have been accumulated that refer to muscle tone and tone innervation of the skeletal muscles, only the works of Ch. Sherrington initiated a systematic investigation of the physiological mechanisms for regulation the postural activity of muscles. For a number of years, Sherrington attempted to substantiate the mechanisms for "standing" based on the reflex to stretching. In discussing the reflex aspects of the proprioceptive system in an article dedicated to Haglin Jackson (1906) Sherrington wrote: "... reflex tone is an expression of the nerve discharges linked to maintenance of body position." He distinguished the posture of the entire animal and its component "postures of individual parts of the body, segmental postures." The proprioceptors of the extremities to a strong measure are responsible for the reflex posture and the compensatory reflexes of the extremities, while the labyrinthine proprioceptors are responsible mainly for the reflex posture and the compensatory reflexes of the head. Sherrington united the muscular-tendinous, articular and vestibular receptors into a unified system of proprioception. /2

The research of R. Magnus and his followers made a detailed investigation of diverse reflexes that develop due to the stimulation of the retina, kinesthetic and vestibular receptors and that are directed towards maintaining body position and restoring the disrupted position. In characterizing this system of reflexes Magnus wrote: "...we

hardly know of any other example of mutual activity of such a large number of different reflexes to implement a unified goal." This unified goal naturally is stabilization of the body position in space. /3 If we are concerned with a rigid, unchangeable body, then it would be fairly simple to solve the problem of its position in space and stability. The position can be assigned by three coordinates of the center of mass, and the stability by the distance from the projection of the center of mass to the boundary of the support contour. The question of a multiple-link system such as the body of animals and man is much more complicated. The position of the center of mass does not unequivocally determine the position of the body links and the entire body in space, while the stability depends to a small degree on the mechanical conditions. It is mainly determined by the condition of the nervous system. What is the postural regulation directed towards in the first place? Which of the body links is the frame of reference for the mutual position of the links and the entire body in space linked to? How can the interaction of kinesthetic and vestibular afferent systems in regulating the position of the multiple-link systems present itself? Our report will search for answers to these questions.

We will restrict our examination to the orthograde human posture. It has already been stressed that it is a fairly difficult task to preserve the orthograde posture from biomechanical viewpoints since the center of mass is located high above the support, while the area of the latter is small. A large number of systems that form the multiple-bond system of regulation are involved in postural regulation. It is not always easy to define the link that is the main object of regulation. Starting with Flurans (1824) an idea was formed in the literature that the mechanisms of postural regulation are directed in the first place towards stabilization of the correct position of the head in space. Based on the experimental data of Magnus et al. it was convincingly demonstrated that, on the one hand, the main effects on the distribution of stress in the musculature of the extremities

start from the head position, and that, on the other hand, the system of labyrinthine, neck as well as the regulating reflexes from the body /4 to the head is directed towards bringing the head into a normal position. A number of refinements can be found in the works of T. Roberts. However they do not change this main conclusion. It is apparently correct in relation to those objects on which studies have been made. At the same time it also covers man. As additional arguments one can indicate that the correct and stable position of the head is important for the normal functioning of the organs of vision and hearing, for the implementation of acoustic and haptic analysis of the environment. There is also a known attempt to substantiate the presence in man of an "... anatomical-physiological center of the cranium, head and central nervous system."

At the same time we know that in the orthograde posture many vestibular effects and neck tone reflexes are expressed in a very weakened form, since they have little influence on the lower extremities in animals.

Based on anthropometric data it was established that in healthy people the axis of the head is deviated from the longitudinal body axis. This deviation from the vertical is $2.6^{\circ} \pm 0.6$. The incline of the head towards the right shoulder dominates. With age this asymmetry rises. The accuracy of reproducing the angle of incline of the head is $2.8 \pm 1.4^{\circ}$. With a lateral incline of the head and its stay in an inclined position for 5 seconds, the angle of nonreturn is usually from 1 to 3 degrees. After turning of the head and maintenance in this position for 10 sec. the angle of nonreturn is about 6° . In other words, the position of the head is not symmetrical, while the accuracy of its voluntary establishment is very low. We note that it is lower than the accuracy of stabilization of the angular position of the leg joints.

Are not the leg joints the main link whose stabilization guarantees the stability for the entire body?

Is it impossible to see in the orthograde body position a certain analogy to the sports figure the "pyramid" in group acrobatics? It seems that if the lower acrobat is stable then the entire "pyramid" will be stable. /5

We will examine how the body position is stabilized during comfortable standing by comparing the movements in the talocrural joint with the electromyograms of the gastrocnemius group of muscles. It is apparent that fairly often the incline of the body forwards is accompanied by activation of the muscles, while leaning backwards is accompanied by a reduction in the level of the electromyograms. However, the observed changes in the activity of the gastrocnemius muscles can be governed by their stretching or movement of the body forwards. In order to determine what the reactions of equilibrium are linked to it is necessary to create conditions in which the movements of the legs and movements of the body will stably differ. This can be attained by using, for example, a rocking platform. The subject is set on a platform in such a way that the axes of the talocrural joints coincide with the rotation axis of the platform.

With changes in the rocking rate of the platform one can observe definite phase shifts between the movements of the legs and the upper part of the body. The phase shift between the movements in the talocrural joint and the movements of the upper part of the body is fairly stable already starting with the first movement of the platform. The amplitude of platform movement is $\pm 2^\circ$. With rocking rate of the platform 0.5 oscill./sec. distinct flashes of the EMG corresponding to the forward incline of the body appear on the electromyogram of the soleus muscle. Such activation is detected not only on the surface EMG, but also at the point of contact for individual motor units of the soleus muscle. We focus attention on the fact that in a number of cases during rocking of the platform spontaneous oscillations of the body are superposed on its forced oscillations. In these cases the activation of the gastrocnemius muscles occurs after the forward leaning of the

body. If the subject closes his eyes while standing on the platform /6
(this moment is marked by an arrow) then the amplitude of oscillations
of the body rises, the frequency is reduced, and the flash of electrical
activity of the gastrocnemius muscle correlates with the movements of
the body forwards. We note that in all these cases the flash of the
EMG occurred on the phase of shortening of the gastrocnemius muscle.

The dependence of the electrical activity of the gastrocnemius
group of muscles on the position of the body is systematically traced
with the use of different frequencies of platform rocking. If a histo-
gram is constructed for the beginning and end of the flash of elec-
trical activity of the gastrocnemius group of muscles in relation to
the position of the upper part of the body (solid line) and the talo-
crural angle (dotted line) with movement rates of the platform 0.5,
0.8 and 1.6 oscill./sec., then it is apparent that the appearance of
electrical activity correlates with the incline of the body forwards and
does not depend on the change in the length of these muscles.

Thus one can come to the conclusion that the electrical activity
of the muscles develops when the body is tilted. This activity is
directed towards its stabilization. The correctness of this con-
clusion follows from another modification of the experiment during
which the body was fixed with the help of a broad belt and braces. In
this case the body was stabilized by using external forces. In this
case during movement of the platform with rate of 0.5 oscill./sec.
there are no modulations in the activity of the gastrocnemius muscles.
With an increase in the rate of platform oscillations to 0.8 and 1.6
oscill./sec., the activity of the gastrocnemius muscles rises into their
stretching phase.

Yet another modification of the experiment was the fixing of the
head position in space with the help of a belt and braces. In this
case, as in the original experiments, the stabilization reactions
developed in response to the tilting of the body.

The presented experimental data, as it seems to us, support the idea that the main object of regulation in the orthograde posture is the position of the body. The upper part of the human body is the most massive and comprises (together with the arms and the head) about 63% of its weight. It is clear that the essence of the problem of maintaining the vertical posture consists of guaranteeing the stability of precisely the upper part of the body. /7

A concept exists in the literature that in order to match the position of the body links and the spatial orientation man uses a frame of reference. Here he can use signals of different modalities: visual, vestibular, and proprioceptive. Under normal conditions all of these signals are congruent. They give man coincident information about the position of his body in space. And here the previous question again arises: what body links are the frames of reference linked to?

It is customary to believe that the vestibular apparatus supplies man with information about the gravity vertical, while vision is adapted for perception of the horizontal. Since both systems are arranged in the head, then the frame of reference for spatial orientation is linked to the head. It is also stressed in the literature that in animals with movable head, in order to obtain ideas about the body position, the visual and vestibular information must be supplemented with information about the condition of the neck section of the spine. For the erect body position of man the situation is complicated to an even greater degree. For this case the visual and vestibular information must be supplemented not only by information about the condition of the neck section of the spine, but also the lumbar region (the most movable sections of the spine) and feet. Therefore there are not sufficient grounds to link the frame of reference for the human body position with the head coordinates.

We have already noted that the position of the head is asymmetrical, while the accuracy of its voluntary establishment is low. As follows from the book of Professor V. Wilson, the position of the semicircular canals in man significantly deviates from the orthogonal. Apparently /8

these and other deviations from the ideal position are not very significant due to the functioning of the mechanisms for constancy of perception.

With a change in the external conditions man can switch from one frame of reference to another, for example, in darkness, from visual to proprioceptive. We will examine yet another example, standing and walking of man on a test stand with side board. In this case the common center of gravity of the body is not located above the support contour. The signals from the visual and vestibular systems do not correspond to the normal. At the same time the mechanisms for coordination of posture and walking, and the spatial orientation remain constant. The orientation line in this case is the direction of the resulting support reactions that affect man through the support surface of the feet.

The cited data taken together permit us to advance the hypothesis that the proprioceptive vertical is linked to the most massive part of the body, its framework. Thus we see that when man stands the object of regulation is the frame, while the activity of the musculature of the legs is directed not towards stabilization of their natural position, but the position of the frame.

Now we will pass to the last question raised in the title of this report: how can one present the mechanism for interaction of the vestibular and kinesthetic afferentation in regulation of the human posture? A large number of facts have been accumulated in the literature on this question. These facts were obtained in experiments and are mainly directed towards clarification of which of the afferent systems is more important in the processes of regulating equilibrium.

Such an analytical approach in which a study is made of the effects of disengaging one or another of the afferent systems has its advantages and disadvantages. We would like once again to draw attention to the generally known position that states that none of the afferent systems which participate in regulating body position functions in

isolation. If one examines the situations that are natural for daily life, then it is evident, for example, that the effect on the vestibular apparatus of the animal of angular and linear accelerations is mainly governed by active movements of the animal itself, and consequently, by a simultaneous stream of vestibular, visual and kinesthetic signals. Therefore the reactions to the "active" and "passive" vestibular stimulation differ. It seems to us that for an understanding of the role of different afferent systems in postural regulation and spatial perception, their interaction in these processes, and the possibilities of adaptation with a change in conditions one should start from the fact that under natural conditions these systems function as a unified sensory complex.

We will present the simplest example that illustrates the role of the sensory complexes in the mechanisms of postural regulation. It has been known from the time of the classic work of Goldshider that the threshold for perception of movement in the talocrural joint of man surpasses one degree. At the same time, during comfortable standing, the movements linked with equilibrium in this joint comprise fractions of a degree. It is necessary to note that these small angular shifts in the talocrural joint are measured during comfortable standing while Goldshider's data were obtained during passive movement of the unloaded foot. At the same time, under natural conditions of standing the movements in the talocrural joint are accompanied by changes in the length of the muscles, redistribution of pressure to the support surface of the foot, and shifts in the frame and head. As shown by the studies conducted in our laboratory, the threshold of movement perception in the talocrural joint in the sitting position with constant angular velocity of foot movement $0.2^\circ/\text{sec}$. equals $0.35-0.54^\circ$. In the standing position it is reduced to $0.04-0.13^\circ$, i.e., 5-10 times. Study of the effect of different factors, axial load, muscle stress, stress and load, indicated that the isolated action of these factors does not result in significant reductions in the threshold of perception, and only during the functioning of the entire

sensory complex accompanying the orthograde posture does it lead to a significant reduction in the threshold.

Another example is somewhat more complicated. In daily life the movements in the talocrural joint are a consequence of the shift in the crus and the higher links of the body in relation to the fixed foot. Here a change occurs in the angle in the joint, a change in the length of different muscles, and consequently, their stress, redistribution of the pressure to the support surface of the foot, and shifts in the frame and head. The reactions in equilibrium that develop here are directed towards stabilization of the body position. By unloading one can induce a tilting of the body forwards. This will be accompanied by such a stabilizing reaction. One can, however, modify the conditions of the experiment and cause movement of the feet in relation to the fixed frame. In this case there will also be movement in the talocrural joint, changes in the length of muscles and redistribution of pressure to the support surface of the foot, but the reaction will be changed.

The presented example indicates that a complicated sensory complex participates in regulating the vertical human posture. The coordinated activity of this complex is the basis for regulation. Selective intensification of a certain component can with certain intensity result in the disruption of the complex's functioning. This is indicated by postural illusions that can be caused by vibration.