Postural changes accompanying voluntary movements. Normal and pathological aspects

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Summary. Voluntary movements are the source of a perturbation of posture and equilibrium. They are accompanied by postural adjustments which show three main characteristics: they are "anticipatory" with respect to movement and minimize the perturbation of posture and equilibrium due to the movement; they are "adaptable" to the conditions in which the movement is executed, they are influenced by the instructions given to the subject concerning the task to be performed. The central organization of the postural adjustments associated with movement is still largely unknown. The possibility is examined that a "repertoire" of postural adjustments exists; the possible sites of the repertoire are discussed as well as the level at which the parallel or "sequential" control of posture and movement might be organized.

Key words: Posture — Equilibrium — Movement — Coordination — Anticipation

Movement and posture are two different and often conflicting aspects of motor control. Movement tends to displace a body segment with respect to another or the whole body with respect to the ground. This is achieved by taking the support either of other body segments or of a surface located in the immediate surroundings of the body. By contrast, posture or attitude is characterized by the position of the body segments at a given time; maintained posture is an active process regulated by a large variety of sensory and central inputs, which tend to prevent any change of position. Taking account of the fact that movement and posture control systems may come into play at the same time, it is apparent that both controls should be coordinated in order to result in an integrated action.

Before examining the mechanisms of this coordination, a brief survey of the postural and equilibrium mechanisms will be given.

Posture is built up by the sum of several basic mechanisms. First, the muscles' tone gives the muscles a rigidity that helps to maintain the joints in a defined position. An additional tone, the postural tone is added to this basic tonus, mainly in the extensor muscles, which exert a force against gravity. Its caricatural aspect, decerebrate rigidity, which was observed by Sherrington (1906), is distributed among the antigravity muscles. Postural fixation is a local mechanism that maintains the position of one or several joints against an internal force, such as the weight of other body segments or against an external force, as for example, a load supported by one of the segments of the fixated joint (Martin 1967). Fixation is obtained by co-contraction of the antagonistic muscles around the joints. Examples of postural fixation are the shoulder fixation that provides the support of the arm, the neck fixation for the support of the head by the trunk, and the limb fixation (positive supporting reaction) that is used for the support of the body weight.

Equilibrium maintenance is a notion distinct from that of posture. From a theoretical point of view, a wide variety of positions can be taken by the various body segments, which would result in many postures. However, each posture has to obey the laws of equilibrium. This means that under static conditions while standing, the center of gravity (CG) should project inside the area delimited by the surface of the feet on the ground. Different types of reflex action intervene when a displacement of the center of gravity is observed, in order to provoke corrective postural changes under the action of labyrinthine, visual, and somesthetic receptors (Dichgans et al. 1972; Leschiende et al. 1977; Nasher 1977).

A coordination between movement and posture is observed with the voluntary movements of one or several body segments. Movement is accompanied by an adjustment of posture which can be explained by the conjunction of different factors. 1. An adjustment of posture is necessary under static conditions in order to maintain equilibrium. Contrary to rigid objects, the body can undergo changes in the position of given segments with respect to others, resulting in a change of the CG position. The shift of the CG position is a source of a disequilibrium which must be compensated by the change in position of other segments. This occurs with slow movements performed in near static conditions. Babinski (1899) observed that dorsiflexion of neck and trunk was accompanied by a simultaneous flexion of the knees, resulting in the maintenance of the CG projection on the ground at the same place (Fig. 1). The coordination was lost in cerebellar patients and asynergia was observed. Coordinations of this type were described by Gurinke and Elner (1973) with respiratory movements. Inspiratory displacements of the thorax were accompanied by simultaneous opposite displacements of the hips. Martin (1967) illustrated another example of adjustment of posture, that is the displacement of the head and trunk backwards when the arms
are raised. There, also, the backwards shift of the trunk and neck compensates for the forward shift of the arms.

2. Dynamic factors intervene during the performance of fast movements, which explains the need for an adjustment of posture. The forces that are at the origin of the movement are accompanied by equal forces in opposite directions exerted on the body segment that serves as a support for the movement. For example, raising the arm upwards results from forces directed forwards and upwards and is accompanied by forces of equal amplitude exerted backwards and downwards on the trunk. The thrust on the trunk will tend to bend the joints and to disrupt the equilibrium. A postural adjustment will increase the stiffness of the shoulder and trunk joints and also minimize the equilibrium disturbance. These interpretations of the role of the postural adjustment associated with the movement were previously proposed by Hess (1943) and by Jung and Hassler (1960). Two aspects of any given movement were described: the teleokinetic aspect, that is the displacement oriented towards a goal, and the eiesmatic aspect, that is the support provided to the movement by the postural fixation and also by the postural adjustment that maintains the equilibrium.

3. The voluntary movement is also a source of perturbation of posture and equilibrium when it is used to load or unload another body segment, as for example when weighing objects are manipulated and moved from one hand to the other. In this situation, rather frequently seen during the performance of manual tasks, adjustment of posture of the loaded and unloaded segments is seen.

Main features of the postural adjustments associated with movement

The main features of the postural adjustments associated with movement are: (1) their anticipatory nature, which minimizes the perturbation provoked by movement on posture and equilibrium; (2) their adaptive character, in the sense that the postural pattern is not fixed but changing as a function of the offered possibilities to perform the adjustment with efficiency; and (3) the influence of the "instructions" which modifies the pattern as a function of the requirements of the task ordered to the subject.

Anticipatory nature of the postural adjustments

It was a common observation made first by Belenkiy et al. (1967) and later by several authors (Alexelev and Naidel 1973; Cordo and Nashner 1982; Bouisset and Zattara 1981; Clement et al. 1983) that with a voluntary arm movement, the first muscle to be activated was not the prime mover such as deltoid or biceps, but muscles located in remote segments involved in postural control such as triceps suralis or biceps femoris. The anticipation of leg muscle myographic changes, with respect to arm muscles is of 50 ms or more. Gurfinkel had proposed that the purpose of the anticipation of the postural adjustment with respect to the movement is to minimize the perturbation of posture and equilibrium provoked by the movement. This interpretation was recently confirmed by Bouisset and Zattara (1983) who placed ac-
celerometers on various body segments and observed that the early postural changes are performed in a direction opposite to that of the forces exerted by the moving arm on the trunk and legs. In the same way, Hugon et al. (1982) have investigated with a bimanual task the effect on the position of one arm loaded with a weight of 1 kg, of unloading exerted by the active movement of the other hand. As can be seen in Figure 2, the position of the postural forearm changes very little with unloading; this results from an anticipatory inhibition of the biceps of the postural arm (Fig. 2).

Another type of postural adjustment, very similar to those that are associated with voluntary movement and which also shows an anticipatory character is that which is associated with a perturbation applied to a localized body segment, such as the thumb (Marsden et al. 1981). These local perturbations are accompanied by remote myographic responses of body parts involved in the postural maintenance (latency 40–80 ms after the onset of perturbation); since the responses precede the remote mechanical changes resulting from the local perturbations, they were considered to be anticipatory. They tend to reduce the disturbance of posture in the same way as the postural adjustment associated with voluntary movements. It is not excluded that parts of the central network responsible for these two types of postural adjustment are common as shown in Figure 3.

**Adaptive character**

A second feature of the postural changes associated with movement is their short term adaptation to the conditions of the postural support offered at a given time. Thus when the standing man takes support on a horizontal bar placed at the level of the trunk, the leg postural adjustments are reduced or even disappear (Cordó and Nazhner 1982). If the standing subject takes support on one arm the postural adjustments that were previously seen in leg muscles will be observed in the arm (Marsden et al. 1981). A preselection of the postural circuits is observed as a function of their ability

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**Fig. 2a and b.** Anticipatory postural activity with a bimanual task. A Two experimental situations were utilized: Active unloading is performed by the subject with its other arm. Passive unloading is made by the experimenter. A force platform (F) is loaded by a weight. The potentiometer (P) measures the joint position, b Recording of forces (load), joint position of the elbow (Pot) rectified and integrated myogram of biceps (Bi) left (l) and right (r). Mean value of 15 trials. Notice, under active conditions, the lack of displacement of the elbow joint with an inhibition of biceps preceding the onset of unloading (from Hugon et al. 1982)
to ensure an appropriate support. The preselection is made unconsciously. In addition to short term adaptation, long term adaptations are also seen. For example, when a normal subject remains for several days in bed, the postural adjustments are reduced or lost and reappear after some retraining (Gurfinkel and Elner 1973).

**Influence of instruction**

The “instruction” given to the subject may change the preselected postural circuits. As shown by Marsden et al. (1981), in a situation when part of the body weight is supported by an arm, a local perturbation of the thumb of the other arm will result in a postural reaction of the supporting arm with increased contraction of the arm extensors and hence an increased thrust on the supporting surface. If the instruction given to the subject is that the thrust on the supporting surface should remain constant, then the response of the supporting arm to the local perturbation is modified and a response in flexors is seen that prevents the appearance of the increased thrust.

**Central organization of the postural adjustment associated with movement**

The reports in the clinical literature concerning the pathology of the postural adjustment associated with voluntary movement are not very abundant. Since the description by Babinski (1899) of cerebellar patients with asynergy, very few papers can be mentioned. Thomas (1940) as well as Holmes (1939) cast some doubt on the cerebellar function in motor synergies and this problem remains controversial (see Rondot et al. 1979). Pattev and Elner (1967) observed abnormalities of the postural changes associated with respiratory movements in patients with cerebellar and frontal lesions. Martin (1967) described abnormalities in coordination between posture and movement in Parkinsonian patients as did Traub et al. (1980) for the adjustment associated with local perturbations. In a recent work, Nashner et al. (1983) compared the postural adjustments of normal children with those of children with cerebral palsy. They noticed that in the spastic hemiplegic or diplegic children the stereotyped disto-proximal pattern of leg muscles’ responses to imposed platform perturbation was lost as well as the anticipatory leg muscles’ myographic responses with voluntary movement. In contrast, with atactic children, the main trouble was in the sensory side, bearing on a wrong evaluation of verticality with conflicting sensory information. As a whole, the mechanisms that are involved in the coordination between posture and movement are still little known or understood.

Animal experiments as well as data from the normal human have shed some light on the central organization of postural adjustment. They suggest that a repertoire of postural adjustment might exist that would be accessible to sensory or central command inputs.

**Is there a repertoire of postural adjustments?**

The quadruped has the advantage over man of having a more stable posture due to the quadrupedal stance. By placing a cat on four force platforms, and by observing the force changes with single limb movements, the pattern of the postural changes can be inferred from the analysis of the force changes. Additional myographic recordings and photographic images of the back position make the pattern more precise.

Two patterns of postural adjustment were identified with single limb movement, a diagonal one (Ioffe and Andreyev 1969) and a non-diagonal one (Dufosse et al. 1982), both of them being associated with myographic changes preceding the force changes and indicating a phasic contribution of the central nervous system to the pattern (Dufosse et al. 1982). One of the patterns is observed as the result of an external perturbation of the limb and is also seen with electrical stimulation of motor cortex (Gahery and Nieoullion 1978) that provokes a contralateral limb movement. From these data and from other experiments, it was proposed (Gahery and Massion 1981) that a repertoire of postural adjustments was located somewhere in the pathways responsible for the execution of movement and that the central command could have access to this repertoire in order automatically to provide the appropriate postural adjustment (Fig. 4). How the selection of the pattern would be made is not yet clear and several hypotheses can be proposed.

The possibility that a repertoire of postural patterns exists in man was proposed by Nashner et al. (1979) on the
basis of the reactions provoked by external perturbations of the legs. According to the type of perturbation, quite different patterns were seen each one specific for a given type of perturbation. The possibility that these patterns might be used in association with voluntary movements does exist.

Where are the stereotypes located?

In this domain, the proposed sites are still mainly hypothetical. During the following analysis two main aspects are considered: (1) Is a given structure a possible site for a repertoire of postural patterns? (2) Could that structure account for an anticipatory command of the postural adjustments?

Spinal cord. One of the first sites where the postural stereotypes might be located is the spinal cord or at the bulbo-spinal level. Loffe (1973) had already proposed this site for the diagonal postural pattern observed in the standing quadraped with single limb movement. It has been known since Sherrington (1906) that this pattern can be elicited in an animal transected at the bulbo-pontine level.

The existence of bulbo-spinal postural circuits could account for a simultaneous command of movement and its associated postural adjustment by way of collaterals of the descending command pathway to specialized propriospinal neurons (Gahery and Massion 1981). However, it is more difficult to understand how the postural adjustment can precede the movement, except if one admits that two parallel commands are put into action at the same time, one for the posture, the other for the movement, and that some interaction between the two systems could take place (Cordo and Nashner 1982).

Neocerebellum. According the early work of Babinski (1899) on asynergia, one important function of the cerebellum is to provide synergistic action of muscles distributed among different body segments in order to organize a complex movement or to coordinate the adjustment of posture and the movement. This aspect of cerebellar function has been neglected for a long time. However, stimulation experiments of Schultz et al. (1979) and lesion experiments of Growdon et al. (1967) have suggested that the neocerebellum might be important in providing a coordination between posture and movement.

Recent data from Rispal-Padel et al. (1981, 1982) resulting from stimulation experiments in monkey, indicate that the dentate nucleus (or the efferent pathways from this nucleus) could contain a repertoire of stereotypes. The rostro-medial zone of this nucleus is at the origin of motor synergies concerning different segments of the same limb or segments located in remote body parts, such as shoulder-hip or head-hand. A caudalateral zone of this nucleus is the source of single joint movements of the arm or of the face. These simple movements are accompanied by a co-contraction of the proximal joint, providing altogether a postural fixation of the joint supporting the more distal movement. Thus within the two subdivisions of the nucleus, an organization of caudorostral or proximo-distal synergies able to provide postural adjustments for various types of movement appears to exist.

The schema of Figure 5 shows how neocerebellar postural patterns might be used when a movement is initiated and how the postural change could precede the movement onset.

DENTATE AND ADJUSTMENT OF POSTURE

Association areas

Motor Cortex

Sensory areas

Dentate nucleus

Movement

Fig. 5. Possible role of neocerebellum in adjustment of posture with fast movements

The neocerebellum is mainly under the control of cerebral cortex. By the intermediation of the pontine nuclei, it receives projection from three types of areas: the sensory areas, somesthetic and visual, the associative areas, mainly the premotor area and the supplementary motor cortex, and the motor cortex (Wiesendanger et al. 1979). When a sensory input that triggers the movement is delivered, it provokes a short latency response at the level of the sensory or associative areas but not at the motor cortex. A short latency response is also seen at the level of the dentate nucleus (Lamarre et al. 1983). By these circuits, there is a possibility that an early postural command would take place and precede the movement; the postural command might be executed through the dentato-reticulospinal pathway (Bantli and Bloedel 1976) or through the thalamocortical pathway. This possible action of neocerebellum on posture has been recently suggested by Schultz et al. (1979) and Beaubaton et al. (1983).

Other sites. Deficits in postural adjustments associated with movement were observed in Parkinsonian patients and in patients with frontal lesions. Are the basal ganglia a possible site for postural stereotypes inborn or learned? Is the frontal cortex, and possibly the supplementary motor area, which is related to the neocerebellum, another place where the postural adjustments could be organized? Are these structures activating centers containing the stereotypes? These questions remain open and unsolved at the present time.

Levels of organization for the coordination between posture and voluntary movements

The simultaneous control of two different functions such as movement and adjustment of posture raises the general prob-
lem of the coordination of two different aspects of a given motor act.

In his synthesis of the problem, Arbib (1981) proposed that a higher coordinating structure intervened for the coordination of simultaneous actions. One of the examples given was arm transportation and hand shaping during a prehension task (Jeannerod et al. 1980). Each of these aspects of the task was associated with its own sensory analysis, which resulted in an appropriate motor command, the coordinating structure providing mainly a timing that synchronized the onset of the commands and the onset of their terminal adjustment.

In the coordination between posture and movement, the coordination could take place in different ways. A first possibility is a hierarchical dependence of the postural adjustment on the movement control pathways as in Figure 4. In that case, execution of movement could be associated with a feed-forward command of posture by way of collaterals of the movement command pathways to the postural circuits. Experiments with motor cortical stimulation in man suggested that this actually exists. In such a process, the selection of the appropriate postural pattern might intervene through a distinct control process. Alternatively, the link between a given movement and its postural support could be the result of learning, giving rise to a specific connection between the movement pathway and a postural network. The two aspects of the motor act could then be part of a specific motor program, in the sense of a complex prewired network partly modified by learning, coming automatically into action with a command signal.

A second possibility would be the parallel command of the movement and the postural adjustment under the control of a higher coordinating center. Recent results from Woolacott et al. (1983) are in favor of this possibility. In his review on the problem of motor programs, Mac Kay (1980) proposed that they were organized as a sequence of conditional loops, central and/or peripheral, evolving when the start signal is given and giving rise to the different aspects of the motor act. In the example of the coordination between posture and movement, the fact that the postural adjustment often precedes the onset of movement could be explained by the sequential involvement of cerebellum-cortical internal loops (Masiion 1973) and the early involvement of neocerebellum after the sensory command signal also suggests the possibility of a sequential action on posture and movement by the way of these internal loops (Fig. 4). Here, the selection of the appropriate internal or external loops would reflect the result of learning, and interestingly, the early involvement of the cerebellum-cortical pathway after a sensory command signal only appears at the end of the learning of a given motor task (Sasaki and Gemb 1983).

Must a higher coordinating ensemble be postulated for the selection of the appropriate postural command as a function of the movement to be executed? It is generally proposed that prefrontal cortex together with basal ganglia are very important in the planning task which consists of preselecting the appropriate circuits for a given motor task (Allen and Tsukahara 1974; Brooks 1979; Pallard 1982; Requin 1980; Rolls 1983). Concerning the basal ganglia, Marsden (1982) suggested that one of the major deficits in Parkinsonian patients was in the ability to combine two motor acts at the same time. This would also apply for the coordination between posture and movement and would explain the loss of the adjustment of posture in these patients.

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