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BIOMECHANICAL STUDY OF THE MECHANISMS OF POSTURAL ADJUSTMENT ACCOMPANYING LEARNED AND INDUCED LIMB MOVEMENTS IN CATS AND DOGS

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Abstract. Trajectories of the center of pressure and center of gravity projections were studied in dynamic conditions during learned movement and movement evoked by the motor cortex stimulation (induced movement) in dogs and cats. The learned movement began with initial displacement of the center of pressure towards the limb performing movement. It corresponded often with initial increasing of the performing limb pressure on support and it was a reason of initial acceleration of the center of gravity in the opposite direction. Induced movement began with decrease of the performing limb pressure on support. It could result in the initial displacement of the center of pressure in the wrong direction but usually it was corrected quickly and the general trajectories of the center of pressure and the center of gravity were similar to ones observed during learned movement. Results suggest different programs for movement and appropriate postural adjustment.

Most of human and animal movements are accompanied by the postural adjustments which provide center of gravity (CG) displacement and equilibrium persistence during movement (1, 16, 20). The pattern of postural adjustment in animals is usually diagonal: limb diagonally opposite to a moving limb is unloaded, whereas two other limbs are loaded (5, 10, 15). But it was shown recently (11) that the degree of diagonality is different in learned movements and in movements evoked by motor cortex stimulation (so-called induced movements). Some authors (7) believe that there are two different postural patterns in different kinds of movements (diagonal pattern in induced movements and non-diagonal in learned ones). Therefore it would be interesting to analyse the trajectories of CG in postural adjustments accompanying learned and induced movements.

In some papers (4, 15) projection of CG was identified with the position of center of pressure (CP). But CG projection coincides with CP position only if the frequency of fluctuations of the CP is low enough (19). In particular, for frequency about 0.5 Hz amplitude of the CG fluctuations is about a half the amplitude of the CP ones. So, in dynamic conditions CG displacements are not identical to the CP ones. But usually the direct determination of the CG position is not easy and requires either measuring both vertical and horizontal forces of pressure (3) or recording displacement of special mark of the CG on the body of human or animal (21). It was shown recently (9) that it is possible to calculate the position of CG of animal only by measuring vertical forces of pressure neglecting rotation of the animal body around the CG. For humans a similar approach to the analysis of the horizontal displacements of CG was also described (17). Analysis of vertical CG displacements during locomotion was made both for humans (2) and for animals (13).

In our previous work (6) vertical displacements of the CG in induced movement were described. The present work is devoted to analysis of horizontal dynamic displacements of the animal CG and comparison of CG and CP trajectories in learned and induced movements.

METHODS

Experiments were performed on standing cats and dogs. In cats induced movement of one limb was evoked by monopolar stimulation of appropriate point of the motor cortex with the train of square negative pulses (pulse duration 0.5 ms, frequency 300 Hz and intensity up to 150 μA, the range of train duration was from 50 to 100 ms). Analysis time during which postural changes and limb displacement were performed and finished was about 1.0–1.5 s. The movement was a fast lift of a limb. In dogs the avoidance conditioned reflex (learned movement) was elaborated. In response to sound (CS) (200 Hz, duration 5 s, delay from onset of CS to beginning of US about 0.5 s), dogs had to lift one limb above a certain level and keep it lifted for 4.5–5.0 s to avoid electrical stimulation of skin of this limb. The posture was also analysed during 1 s preceeding the CS. Time of analysis was 6 s in this case. The next kind of movement studied in dogs was an induced lifting movement evoked by an unexpected electrical stimulation of skin of the limb.

In all cases an animal stood at 4 independent platforms with strain-gauges, which made it possible to measure vertical forces of pressure (8, 12). The data were recorded on ink-writer and on magnetic tape with following analysis by computer ES-1020 (for dogs) or digitized and stored on disc of a digital computer PDP 11/40 (for cats). Calculations of the space displacements of CG were made under the assumption that the movement of animal body was a translational one i.e., that resultants of all vertical and horizontal forces passed through the CG (Fig. 1). It permited to calculate horizontal displacement of the CG having only vertical forces according to the following equations system.

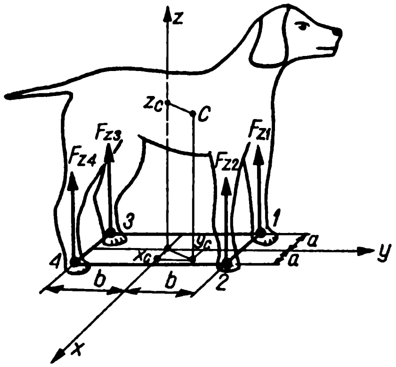

Fig. 1. Scheme of center of gravity projection and distribution of vertical forces. Explanations are in text.

$$Z_c m \ddot{x}_c = x_c \sum_{i=1}^{4} F_i - a(F_2 - F_1 - F_3 + F_4), \tag{1}$$

$$Z_c m \ddot{y}_c = y_c \sum_{i=1}^{4} F_i - b(F_1 + F_2 - F_3 - F_4), \tag{2}$$

$$m \ddot{z}_c = \sum_{i=1}^{4} F_i - mg, \tag{3}$$

where m is mass of animal; g — acceleration of grafity; F_i are experimentally measured appropriate means of vertical forces to the horizontal support; x_c, y_c, z_c — coordinates of CG, 2a and 2b — distances between limbs.

These equations were solved for the cases when initial and final positions of animal were close to static ones. This corresponds to the following variants of the boundary conditions (for example for x (t)):

$$\begin{array}{ll} x_c(0)=x_p(0), & x_c(T)=x_p(T), \\ x_c(0)=x_p(0), & \dot{x}_c(T)=0, \\ \dot{x}_c(0)=0, & x_c(T)=x_p(T), \\ \dot{x}_c(0)=0, & \dot{x}_c(T)=0, \end{array}$$

where x_p is a coordinate of CP. The same is for $y(t)$.

The equations could be principally solved either forward from initial to final point (with conditions x_c $(0) = x_p$ (0) and $\dot{x}(0) = 0$) or backward from final to initial point (x_c $(T) = x_p(T)$ and $\dot{x}_c(T) = 0$. But practically such direct solving was too inaccurate because small errors of measurement on one border of time interval increased to exp (T $\sqrt{g/Z_c}$) times on the other one. Similar effect could be produced by some animal body rotations assumed to be negligible. Therefore the method of calculation allowing for boundary conditions on both borders simultaneously was used (19A). It permitted to compensate for the errors but could result in artifacts in calculated time course of CG trajectory in the beginning and in the end of dynamic phase of movement.

RESULTS

Analysis of CP and CG displacements of the rigid mechanical model

To explore some peculiarities of the animals CP and CG displacements let's consider at first the support forces changes and also CP and CG displacements of the rigid mechanical model standing on four "limbs" presented in Fig. 2. There is a heavy weight fixed inside the construction by two elastic tractions (a and b). Cutting the traction a causes the displacement of the weight from "hindlimbs" (3 and 4) to forelimbs (1 and 2) and consequently the position change of the model CG. The measured changes of vertical forces and the trajectories of CP and CG of the model obtained by solving the Eqs. 1 and 2 (see Methods) are shown in Fig. 3. In Fig. 3*D* the models support area is represented. Schemes of force changes at appropriate "limbs" are given in the corners. Small rectangle inside the rectangle D is the area in which

CP and CG moved. The same rectangle is represented enlarged in Fig. 3*A*. Point *a* corresponds to initial position of CP and CG before cutting the traction (CP coincides with CG in static situation), point *b* — final static position of CP and CG after the end of CP and CG displacement caused by the traction cutting. So, in Fig. 3*A* the general trajectories of CP (thin line) and CG (thick line) from *a* to *b* are represented. Only main big loops of CP trajectory are given in Fig. 3*A*. Other fluctuations of CP near initial and final positions are marked by shadows around points a and b. Figure 3*B* and *C* show the time course of CP and CG during 6 s (time of analysis) in antero-posterior and lateral directions, correspondingly.

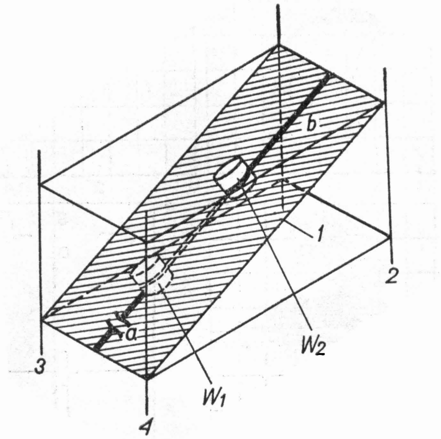

Fig. 2. Scheme of the mechanical model. 1, 2, 3, 4, fulcra ("forelimbs": 1 and 2, "hindlimbs": 3 and 4). *a* and *b*, tractions (traction *a* is cut). W_1 and W_2, initial and final positions of the heavy weight.

Analysing Fig. 3 it is possible to see that cutting one of tractions followed by the displacement of the weight from "hindlimbs" to "forelimbs" at first causes increase of the pressure at the "hindlimbs" and decrease at "forelimbs". The reason of this phenomenon is the following: the force of elastic traction moving the weight forward evokes reactive force applied to the construction and directed backward. It means that in the initial moment after traction *a* cutting the pressure at "hind-limbs" increases, i.e., CP is also displaced backward, in the direction opposite to the displacement of CG. This also can be seen from the trajectories of CP and CG. The picture also shows that in the following period of time CP moves in the same direction as CG, leaves CG behind and finally it moves towards CG. It results in slowing CG displacement and stopping it. At the end of dynamic phase CP coinci-

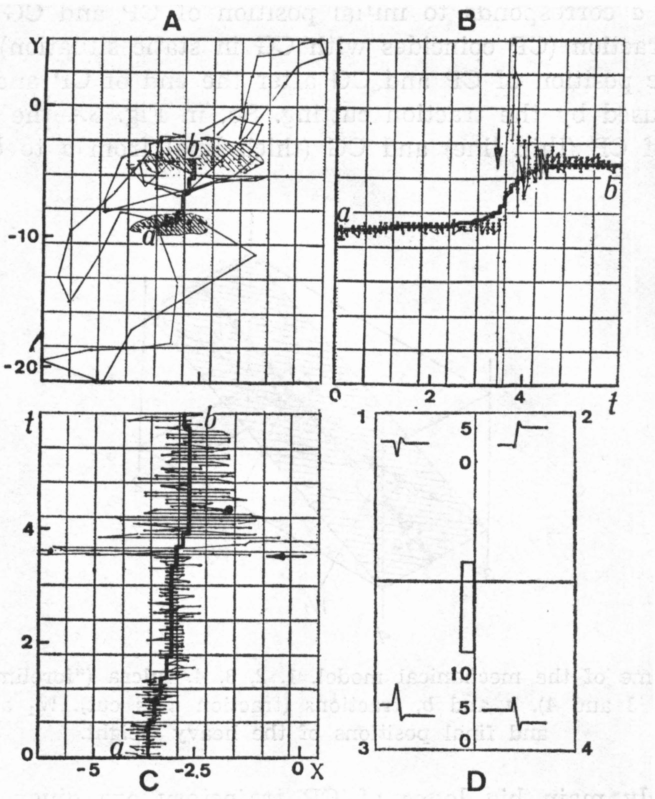

Fig. 3. Horizontal trajectories of the center of gravity (thick lines) and the center of pressure (thin lines) of the mechanical model after cutting one of the tractions (*a* in Fig. 2). D, rectangle corresponding to the area of support (1 and 2, points of "forelimbs" support, 3 and 4, the same for "hindlimbs"). Small rectangle inside it corresponds to the area in which center of gravity and center of pressure moved. The same rectangle is represented in A. B, time course of center of gravity and center of pressure position changes in the antero-posterior direction. C, the same in the lateral direction. In A: abscissa, lateral coordinates, ordinate, antero-posterior ones. In B: abscissa, time of analysis, ordinate, antero-posterior coordinates. In C: abscissa, lateral coordinates, ordinate, time of analysis. Coordinates are represented in percentage of the distances between appropriate "limbs". Zero coordinates correspond to the middle of these distances. Time mark (distance between lines in time scales) in equal 0.6 s (total time of analysis is 6 s). Initial and final positions of the center of gravity are denoted as *a* and *b* correspondingly. On the corners of the rectangle D the schemes of pressure changes to appropriate limbs are represented (0–5 — calibration of forces, kg). Moment of cutting the traction is marked by the arrows in B and C.

des with CG. So, in dynamic situation initial displacement of CP evokes displacement of CG in the opposite direction and final displacement of CP stops the CG displacement. In the other words, CP "pushes" CG.

It is necessary to note some artifacts of CG time course depending on the method of calculations (see Methods) which are seen in Fig. 3*B*, namely, false initial displacement of CG before the real start of the weight movement noted by the arrows. Such artifacts could be also found in some other Figures.

Measuring the real displacement of the weight inside the construction and knowing the weight of the construction it was also possible to calculate real displacement of the model CG. It proved to be in good agreement with the values of the model CG horizontal displacement measured and calculated directly and calculated by the computer program using Eqs. 1 and 2. The maximal error was about 12%. It means that this method can be used in real calculations.

Horizontal displacements of center of pressure and center of gravity in learned and induced movements

Let's consider the trajectories of the CG and CP in the case of learned movement i.e., conditioned movement of the right hindlimb of the dog (Fig. 4). As is seen from the picture, at first the CP moves backward and to the right, that is to the performing limb. This corresponds to the initial displacement of the CP in the mechanical model. Such initial displacement of the dogs' CP can be evoked either by increasing the pressure on the performing limb or by large decreasing the pressure on the diagonal limb. This displacement of the CP is the reason for displacement of the CG in the opposite direction. Usually postural displacement would begin by increasing the pressure to the performing limb if before the onset of CS the CG was outside the triangle formed by the other limbs (so-called support triangle), and it was necessary to place it there quickly. In this case CG was near the border of the support triangle. The following displacements of the CP correct the CG displacement and as in the case of the mechanical model CP moves the same way as CG, leaves CG behind and then shifts towards the CG and stops it. In the cases without an initial increasing of pressure on the performing limb, CP also moves at first to the performing limb by decreasing the pressure on the diagonal limb. The further course of the curves is usual.

Let's consider now the trajectories of the CG and CP in the case of induced movement evoked by stimulation of the motor cortex in the cat. This situation is somewhat different from the previous one. Usually there was no increase of the pressure on the performing limb. In Fig. 5

the averaged (15 trials) trajectories of CP and CG are represented. Right hindlimb was the performing one. It is possible to see that at first the CP moves forward that is to the side opposite to the performing limb, but later there is the displacement toward the performing limb. This loop corrects the trajectory of the CG in the right direction. Finally the CP shifts as usually and stops the displacement of the CG. In some other cats CP moved at first to the performing limb. It was evidently a result of decreasing the pressure on the diagonal limb. Then we could see the usual trajectory of CP correcting that of CG. Thus, in the case of the cortical stimulation, which evokes lifting the limb without initial increase of pressure of this limb, some compensatory postural mechanisms are switched on and general evolutions of CP also cause the displacement of CG into the support triangle.

To analyse in detail a process of the beginning of postural displa-

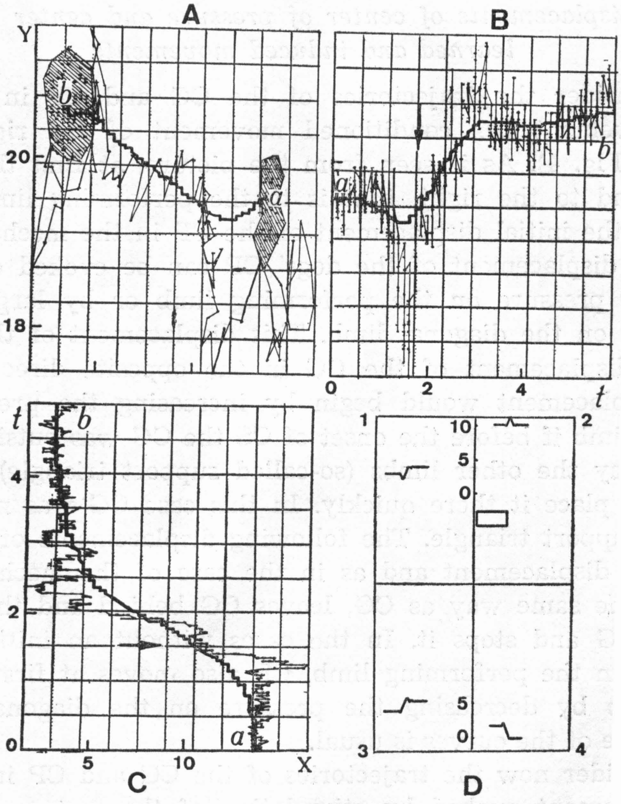

Fig. 4. Horizontal trajectories of the center of gravity and the center of pressure of the dog during learned movement. Designations as in the Fig. 3. The starting moment of limb lifting is marked by the arrows in B and C.

cement in induced movements one more kind of such movement was studied in dogs, namely, a movement of a limb evoked by unexpected electrical shock applied to the limb. The appropriate pictures are presented in Fig. 6 and 7. It is seen that the first reaction of the left forelimb to the electrical stimulation is a decrease of the pressure of this limb, i.e., a flexor reflex (inborn reaction). In this case the initial projection of CG was outside the support triangle. Such decrease in the pressure of the limb evoked acceleration of CG directed to this limb, i.e., the dog could fall. It resulted in the inhibition of the flexor reflex and in increasing the pressure of the limb for the CG displacement to the support triangle. And only then the lifting of the limb was performed. (Actually, CG is inertial and as it is possible to see in

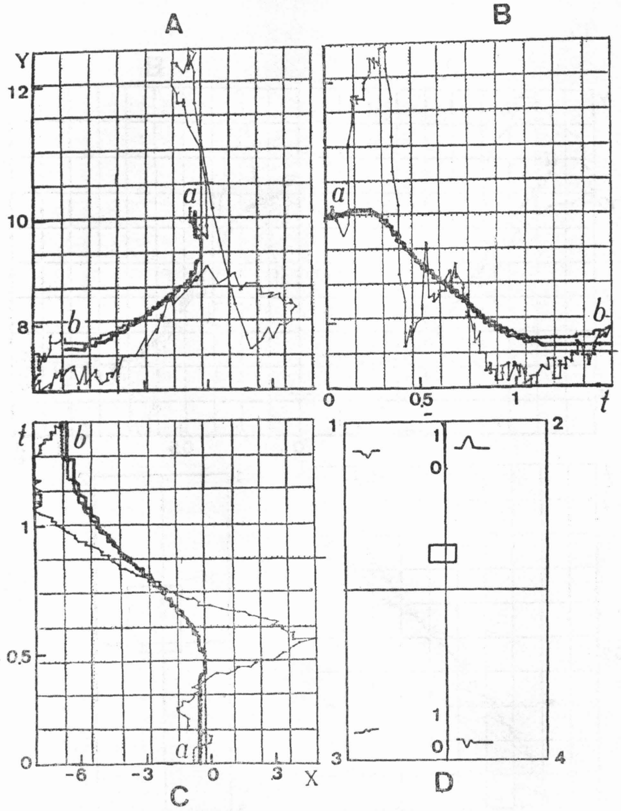

Fig. 5. Horizontal trajectories of the center of gravity and center of pressure of the cat during induced movement. Average curves from 15 trials. Time mark is equal 0.15 s (total time of analysis — 1.5 s). The other designations as in the Fig. 3. Two curves of CG trajectories are obtained using different variants of boundary conditions (see Discussion).

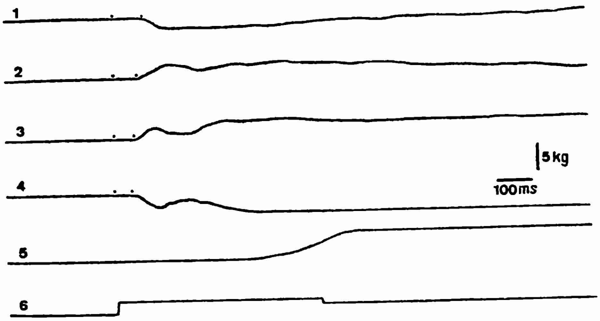

Fig. 6. An example of the movement induced by sudden electrical stimulation of the left forelimb. 1, 2, 3, 4, pressure of right and left hindlimbs and right and left forelimbs, respectively, 5, the left forelimb movement, 6, electrical stimulation.

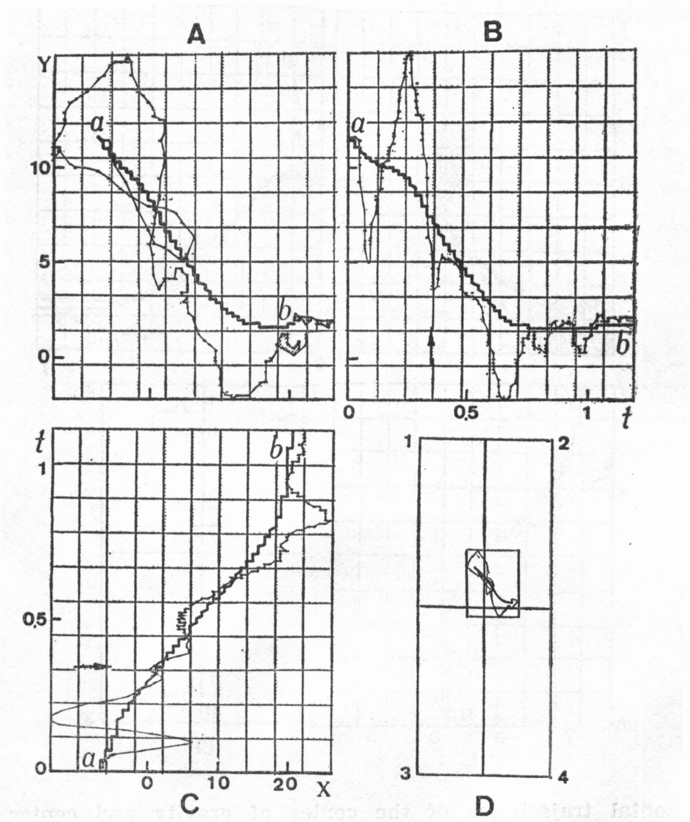

Fig. 7. Horizontal trajectories of the center of gravity and the center of pressure of the dog during induced movement (the same trial as in Fig. 6). The analysis begins just before onset of first changes of the limbs pressure. Time mark is equal 0.12 s (total time of analysis — 1.2 s). Designations as in Fig. 3 and 4.

Fig. 7, CG is not yet displaced to the performing limb before the correction of this position by appropriate displacement of CP). So, one of the compensatory postural mechanisms in induced movement is, probably, a temporary inhibition of an inborn flexor reaction to the electrical stimulation.

DISCUSSION

First of all it is necessary to evaluate the errors which could produce some artifacts in the curves presented above. The artifacts depended on the chosen variant of the boundary conditions. If we postulated the coincidence of initial and final positions of CP and CG we could obtain non-zero values of initial or final velocity (see initial point of Fig. 7C). But, if we postulated that initial or final velocity was equal zero, we could obtain the difference of initial or final positions of CP and CG (see final point of Fig. 7C). In the last case such difference was about 5% of the whole CG displacement. In Fig. 5 two variants of CG trajectories were calculated using different boundary conditions. It is seen that differences of the curves are very small. Usually we analysed the data in which such difference was about (or less) than 10% of the whole CG displacement, so the accuracy of the method was sufficient. On the other hand, this method had advantages because it allowed to analyse a dynamic CG trajectory using only values of vertical forces of pressure, without measuring the horizontal forces.

From the data obtained, it is possible to draw some conclusions about dynamics of postural adjustment accompanying different kinds of movements. Comparing trajectories of CP and CG we can see that CP is much more mobile while CG is very inertial. It is evident when we consider that CP has no inertia, because its position depends only on instantaneous values of the forces, while the changes of CG position depend also on the animal's mass. Changing CP position causes changing position of CG and dislacement of CP in one direction is a reason of CG acceleration in the opposite direction. In other words, to displace CG in definite direction it is necessary to displace CP in the opposite one. It is a way used by an animal to change the position of CG for lifting a limb: increasing a pressure on this limb (or decreasing it on diagonal one) to displace CG in the support triangle. It is interesting that similar relations between CP and CG trajectories are also present in the rigid mechanical model.

The comparison of postural adjustments in the learned and induced movements shows their general similarity, although there are some differences. One of them is the initial decreasing of the pressure of the performing limb in all cases of induced movement and the initial increasing of the pressure in the majority of cases of learned movement. Such differences allow to discuss the question of the movement and postural adjustment program.

Earlier data on stimulation and ablation of sensorimotor cortex (14, 16, 18, 20, 22, 23) showed the difference between the control mechanisms of local movement and postural adjustment. In particular, it was shown that the motor cortex stimulation involves movement of the appropriate limb without postural displacement, which could result in the animals' falling (22, 23). Recently, both the postural displacement and the local movement were observed after motor cortex stimulation (10). It would be reasonable to think that there is the same program for the movement and the postural displacement.

But the data presented suggest that the program of the postural displacement is rather a separate program of the equilibrium preservation during movement. It is rather complicated and includes some evolutions of the CP to change the CG position in a desirable direction. Of course, it is closely integrated with the program of the local movement and, probably, is a "sub-program" of the movement but presumably is controlled by the other structures. In learned and induced movements mechanisms of activation of this program may be different. In the learned movement the switching on of the postural program anticipates the local movement. But in the induced movement the postural program is, probably, switched on by the motor command simultaneously with the command for the movement. It may result in temporary disagreement of the parameters of movement and postural displacement. Probably, estimation of CG acceleration by vestibular system and estimation of CP position on the ground of proprioception are very important in order to analyse and to eliminate this disagreement.

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