

# Postural Control in the Rabbit Maintaining Balance on the Tilting Platform

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**Beloozerova, I. N., P. V. Zelenin, L. B. Popova, G. N. Orlovsky, S. Grillner, and T. G. Deliagina.** Postural control in the rabbit maintaining balance on the tilting platform. *J Neurophysiol* 90: 3783–3793, 2003. First published August 20, 2003; 10.1152/jn.00590.2003. A deviation from the dorsal-side-up body posture in quadrupeds activates the mechanisms for postural corrections. Operation of these mechanisms was studied in the rabbit maintaining balance on a platform periodically tilted in the frontal plane. First, we characterized the kinematics and electromyographic (EMG) patterns of postural responses to tilts. It was found that a reaction to tilt includes an extension of the limbs on the side moving down and flexion on the opposite side. These limb movements are primarily due to a modulation of the activity of extensor muscles. Second, it was found that rabbits can effectively maintain the dorsal-side-up body posture when complex postural stimuli are applied, i.e., asynchronous tilts of the platforms supporting the anterior and posterior parts of the body. These data suggest that the nervous mechanisms controlling positions of these parts of the body can operate independently of each other. Third, we found that normally the somatosensory input plays a predominant role for the generation of postural responses. However, when the postural response appears insufficient to maintain balance, the vestibular input contributes considerably to activation of postural mechanisms. We also found that an asymmetry in the tonic vestibular input, caused by galvanic stimulation of the labyrinths, can affect the stabilized body orientation while the magnitude of postural responses to tilts remains unchanged. Fourth, we found that the mechanisms for postural corrections respond only to tilts that exceed a certain (threshold) value.

## INTRODUCTION

A basic body posture—upright in bipeds and dorsal-side-up in quadrupeds—is maintained due to the activity of the postural control system (Magnus 1924). This closed-loop system operates on the basis of sensory inputs of different modalities—somatosensory, vestibular, and visual. When these inputs signal that the posture has deviated from the normal one, specific motor responses are generated; they are aimed at restoration of the initial posture (for review, see Horak and Macpherson 1995; Massion 1998).

A common method for investigation of the postural system is the observation of its responses to perturbations of posture. Most often, the perturbations are caused by a movement (translation or tilt) of the support surface (see e.g., Nashner 1977). The activity of postural mechanisms is usually monitored by

recording the kinematics and electromyographic (EMG) responses as well as the ground reaction forces. An extensive study of the postural system in a quadrupedal animal (cat) was carried out by Macpherson and her colleagues. These investigators have analyzed in detail the motor responses elicited by horizontal translation of the supporting platform. They characterized the muscle synergies activated in response to a perturbation of posture and the contribution of different limbs to the generation of the resultant force causing postural corrections (Jacobs and Macpherson 1996; Macpherson 1988a,b; Macpherson et al. 1997a). It was additionally found that postural mechanisms are driven primarily by somatosensory input (Inglis and Macpherson 1995; Stapley et al. 2002). The corrective postural responses were only slightly affected by changes in the head position (Barberini and Macpherson 1998), suggesting that there is an independent control of head and trunk position. After spinalization, postural responses in the hindlimbs decreased dramatically, suggesting their supraspinal origin (Fung and Macpherson 1999; Macpherson and Fung 1999; Macpherson et al. 1997b).

When maintaining balance on the translated platform, the body configuration is the same before perturbing equilibrium and after correcting the posture. Thus with this experimental design, the task of maintaining balance and that of stabilizing the body configuration coincide with one another. The situation is different when the animal maintains balance on the inclined surface, which often occurs in natural habitats. In this case, the configuration of limbs necessary for keeping balance is different for different tilt angles and will require operation of special control mechanisms altering the limb configuration. Here we describe postural corrections in the rabbit standing on the platform and maintaining balance when the platform was periodically tilted in the frontal (transverse) plane. Because a transverse dimension of the base of support in quadrupeds is much smaller than its longitudinal dimension, maintaining balance in the transverse plane is the most demanding postural task.

The pattern of postural corrections in this task was partly characterized earlier (Deliagina et al. 2000a). It was shown that tilt of the platform elicited extension of the limbs on the side moving down and flexion on the opposite side. *The first aim* of this study was to continue this analysis and to characterize in more details the kinematics and EMG pattern of postural responses to lateral tilts.

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The system for maintenance of the basic body posture is often considered as a servo-mechanism stabilizing a certain value of the regulated variable, e.g., the position of the center of mass or the orientation of the body axis (see e.g., Ghez 1991; Massion 1994; Massion et al. 1997). The second aim of the present study was to test this hypothesis. For this purpose, we used complex postural stimuli, that is, asynchronous tilting of the anterior and posterior parts of the body. It was found that rabbits could effectively solve these complex postural tasks. That makes the idea of a single regulated variable unlikely in relation to quadrupeds. We suggest instead that the positions of the fore and hind limb girdles are stabilized by two independent controllers.

In the experiments on cats (Inglis and Macpherson 1995), rabbits (Deliagina et al. 2000a) and rats (Deliagina et al. 1997), it was shown that bilateral removal or inactivation of the vestibular organs strongly affects the head position and much less affects the trunk posture. Unilateral removal of a vestibular organ, however, produces a dramatic effect on both the head position and trunk posture (Deliagina et al. 1997; Smith and Curthoys 1989). We further investigated this issue in the present study and developed a special technique for a temporary abolishment or amplification of the tilt-related visual and vestibular inputs. For this purpose, the head of the animal was either rigidly fixed in space or moved together with the tilting platform. Another technique employed in this study was a galvanic stimulation of the labyrinths (Swaak and Oosterveld 1975), which allows the induction of a temporary asymmetry in the tonic activity of the left and right labyrinths. The third aim of this study was, by using the preceding techniques, to investigate the effect on the postural responses to tilt produced by up- or downregulated vestibular input and also the effect produced by asymmetry in the inputs from two labyrinths.

A brief account of part of this study has been published (Deliagina et al. 2002).

## METHODS

Experiments were carried out on nine New Zealand adult rabbits. All experiments were conducted with the approval of the local ethical committee (Norra Djurförsöksetiska Nämnden) in Stockholm.

### Surgical procedures

The surgery was performed under Hypnorm-medazolam anesthesia, using aseptic procedures. The skin and fascia were removed from much of the dorsal surface of the rabbit's skull. Bones of the dorsal surface of the skull were fused together with stainless steel screws and acrylic cement. An aluminum circular base (ring) with a steel rod directed backward was cemented to the screws. The rod was later used for temporary fixation of the head to affect the visual and vestibular inputs (see following text). For EMG recordings, four bipolar electrodes (0.2 mm flexible stainless steel Teflon-insulated wires) were implanted bilaterally into m. triceps (elbow extensor) and m. gastrocnemius (ankle extensor). In addition, in a part of the animals, the electrodes were also implanted into m. biceps brachii (elbow flexor), m. vastus (knee extensor), m. abductor femoris (hip extensor), m. tibialis (ankle flexor), and m. biceps femoris (knee flexor). The wires were led subcutaneously toward the circular base and soldered to a connector fixed on the base.

### Experimental design

No special training of the animals was performed prior to testing. For testing, an animal was positioned on a tiltable platform (P in Fig.

1, A and C). The surface of the platform was covered with sandpaper to prevent sliding of the animal during tilts. The sagittal plane of the animal was aligned with the axis of the platform (Fig. 1A). When standing, rabbits can adopt a variety of postures differing in the distance between the fore and hind limb feet ( $f$  in Fig. 1C). In the present experiments, the animals kept this distance within a range of 7–12 cm. At such distances, the spine was not bent, and there was a clearance of ~1–2 cm between the belly and the ground (Fig. 1C). If the distance differed from its optimal value, we repositioned the limbs.

The platform with the animal was tilted periodically in the frontal (transverse) plane of the animal (roll tilt  $\alpha$ , Fig. 1B). Two major types of tilt trajectories were used: a sine-like trajectory with the frequency of 0.5 or 1 Hz and the amplitude of  $\pm 20^\circ$  and trapezoid trajectory with the transitions between  $-20$  and  $+20^\circ$  positions lasting for ~1 s, and each position being maintained for ~3 s. The tilting was performed manually and timed by a metronome. Due to this timing, the frequency of sinusoidal tilts was rather stable ( $1.02 \pm 0.04$  Hz). The amplitude of tilts was maintained with the accuracy of  $\sim 1-2^\circ$ .

The position of the animal in the transverse plane was monitored by means of mechanical sensors. Each sensor consisted of a variable resistor whose axis was rotated by means of a long lever; the latter was touching the lateral aspect of the body. The sensor S was positioned in the mid-body area, at the half-height of the body (Fig.

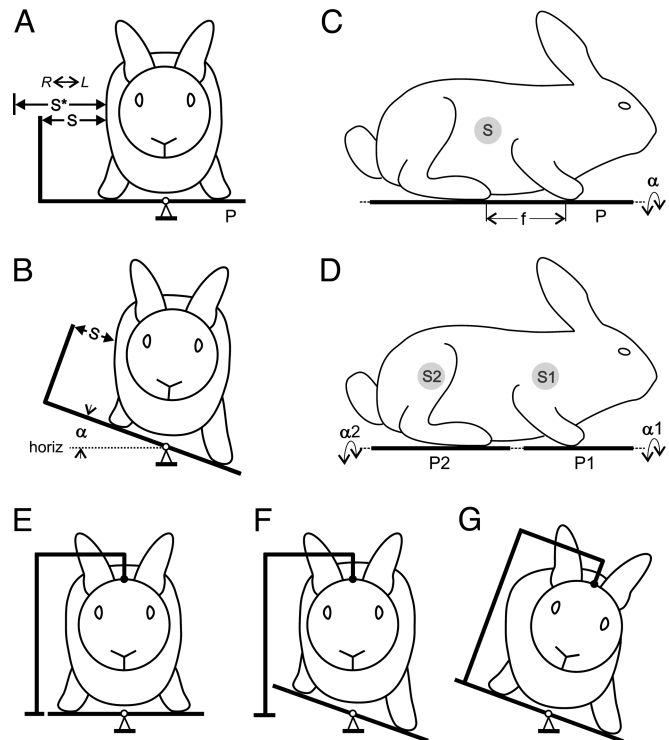


FIG. 1. Experimental design for testing postural responses to tilts. A–C: design with a single platform. The animal was standing on a platform (P) so that its sagittal plane was aligned with the axis of platform rotation ( $\alpha$ , tilt angle). Mechanical sensors S and S\*, positioned at the half-height of the body, measured lateral displacements of the mid-body area in relation to the platform and to the external space, respectively. The distance between feet in rabbits positioned on the platform was 7–12 cm ( $f$  in C). D: design for testing postural responses to complex stimuli, that is separate tilts,  $\alpha_1$  and  $\alpha_2$ , of the anterior and posterior platforms, P1 and P2, respectively. S1 and S2 indicate the position of sensors that measured lateral displacements of the anterior and posterior body parts in relation to the corresponding platforms, P1 and P2. E–G: design for tilting the rabbit with the head fixed to a frame. The frame was motionless in space (F), or moved together with the platform (G). In F and G, a simultaneous tilt of both P1 and P2 platforms is shown for simplicity, but each of the platforms could be tilted individually.

1C). This sensor measured the mediolateral displacements of the lateral aspect of the trunk in relation to the platform (Fig. 1, A and B). In addition, in two animals, the lateral displacements of the trunk in relation to the external space were measured by the sensor S\* (Fig. 1A).

To examine motor responses in complex postural tasks, the rabbit was positioned on two platforms, one under the fore limbs and the other under the hind limbs (P1 and P2 in Fig. 1D). The platforms could be tilted in the frontal plane of the animal (angles  $\alpha_1$  and  $\alpha_2$ ) either in-phase or in anti-phase, at different frequencies, or with only one platform tilted while another one was kept horizontal. In these experiments, mediolateral displacements of the rostral and caudal parts of the trunk (in relation to the corresponding platform) were monitored separately by two sensors, S1 and S2, located in the middle areas of the corresponding parts of the body (Fig. 1D).

To characterize the role of visual and vestibular inputs for the generation of postural responses to tilts, we manipulated these inputs in the following ways. *First*, visual input was abolished either by blindfolding the animal with a nontransparent plaster or by testing the animal in complete darkness. *Second*, the head of the animal was rigidly fixed by attaching the circular base (cemented to the skull during surgery) to a frame (Fig. 1E). During tilts of the platform(s), the frame remained motionless in space (Fig. 1F). In this test, therefore visual and vestibular inputs were not affected by tilting the platform, and the only input signaling information about tilts was the somatosensory one. *Third*, the head was also fixed to the frame (as in Fig. 1E), but in this case, the frame was moving together with the platform(s) (Fig. 1G). Under this condition, the animal was not able to compensate for the head tilt, and that led to a considerable increase in both visual and vestibular inputs induced by the platform tilt. *Fourth*, to cause an asymmetry in the left/right vestibular inputs, galvanic stimulation of vestibular organs was used, employing the method adapted from Swaak and Oosterveld (1975). Two surface electrodes ( $0.5 \text{ cm}^2$ ) were attached bilaterally against the mastoid processes, and a pulse of constant current (2–3 mA) was passed between the electrodes. In the resting animal, these stimuli evoked a 1–2 cm lateral tilt toward the positive electrode. These stimuli were not painful to the animal—they did not evoke any uneasiness in the animal even when applied for a long time or repeatedly.

To characterize kinematics of postural corrections, video recording (25 frames/s) from the front, side, or top was performed in five rabbits. The fur on the limbs and the back of the animals was shaved, and light reflecting paper stickers were attached to the skin projections of the limb joints (see Fig. 3, A and B). In addition, eight reflecting stickers were attached along the midline of the spine, neck, and head (see Fig. 2E). The video camera was positioned at a distance of  $\sim 2 \text{ m}$  from the rabbit. The recordings were then analyzed frame by frame.

The signals from the EMG electrodes and from the position sensors were amplified, digitized with a sampling frequency of 5 kHz (EMGs) and 1 kHz (sensors) and recorded on a disk of an IBM-compatible computer using the data acquisition and analysis software (Power 1401/ Spike 2, Cambridge Electronic Design, Cambridge, UK). The EMGs were rectified and averaged for each of the 20 bins of each tilt cycle. Then the value of each bin was averaged over 10–30 normalized successive cycles (the peak tilt to the left was taken as the cycle onset, see e.g., Fig. 4).

## RESULTS

### Postural responses to roll tilts

Rabbits were easily engaged in the task of balancing on a platform that was periodically tilted in the frontal plane and exhibited stereotypic postural responses during the entire test that lasted for 20–200 tilt cycles. A tilt of the platform caused an extension of the limbs on the side moving down and flexion

on the opposite side as shown schematically in Fig. 1, A and B. These limb movements made the trunk and head move in the transverse plane in relation to the platform in a direction opposite to the platform tilt. This compensatory trunk movement reduced a deviation of the body from the dorsal-side-up position. The lateral displacements of the trunk in relation to the platform were monitored by the sensor S (Fig. 1, A–C). As shown in Fig. 2A, corrective trunk movements (S) occurred in anti-phase with the platform tilts ( $\alpha$ ). Postural stabilization was not perfect, however. That was reflected in the lateral displacements of the trunk in relation to the external space (S\* in Fig. 2A); these displacements were monitored by the sensor S\* (Fig. 1A).

The degree of postural stabilization increased with the frequency of tilts. At the frequency of 1 Hz (Fig. 2A, right), S was larger and S\* was smaller than at the frequency of 0.5 Hz (Fig. 2A, left). In Fig. 2B, the peak-to-peak value of corrective trunk movements is plotted against the frequency of tilting for one of the rabbits. One can see that corrections increase with the frequency. Similar results were obtained in all animals. When averaged over all animals, the peak-to-peak value of S at 1 Hz was 1.3 times larger than at 0.5 Hz [ $4.5 \pm 0.3$  vs.  $3.3 \pm 0.2$  (SE) cm,  $P = 0.001$ , paired *t*-test]. The dynamic properties of the postural response were also evident in tests with trapezoid tilts (Fig. 2, C and D). At a slow speed of the platform tilting, when the tilt duration  $\tau = 1 \text{ s}$ , the S trajectory mirrored the  $\alpha$  trajectory (Fig. 2C). By contrast, at a higher speed of tilting ( $\tau = 0.5 \text{ s}$ , Fig. 2D), a dynamic component was clearly seen in the S trajectory (Dyn), which is an increased compensatory movement during platform tilting. On the termination of tilting (that is during each period of a constant platform tilt), this dynamic component rapidly diminished and only the static component (St) persisted.

Postural corrections were not the same at different points along the body. The difference could be qualitatively assessed by video recording from above of the rabbits during tilting. Figure 2E shows the body outline and the position of eight midline markers at  $0^\circ$  (no tilt) as well as the position of these markers at the maximal tilt to the right ( $20^\circ\text{R}$ ) and to the left ( $20^\circ\text{L}$ ) in one representative experiment. The arrows indicate the positions of a reference marker that was rigidly attached to the platform above its axis at approximately the height of the top of the rabbit spine and head (see e.g., Fig. 1C). Excursions of this marker show the expected lateral deviations of the spine and head midline that would occur at  $20^\circ\text{R}$  or  $20^\circ\text{L}$  tilt provided that the rabbit would not perform postural corrections (“uncorrected deviations”). One can see that, due to postural corrections, the deviations in the caudal and middle trunk constituted  $\sim 30\%$  of the uncorrected value, whereas in the neck and head areas they constituted only  $\sim 20\%$  of the uncorrected value. Similar results were obtained in all tested animals ( $n = 4$ ). It can thus be concluded that postural stabilization of the anterior part of the body is somewhat better than stabilization of its posterior part.

Corrections of the trunk orientation were caused by specific limb movements. The principal feature of these movements was an extension at all main limb joints on the side moving down—and flexion on the opposite side—as demonstrated by a video recording of the rabbits from the side (Fig. 3). The configurations of the fore and hind limb at the maximal tilt to the right ( $20^\circ\text{R}$ ) are shown as stick diagrams in Fig. 3A and at



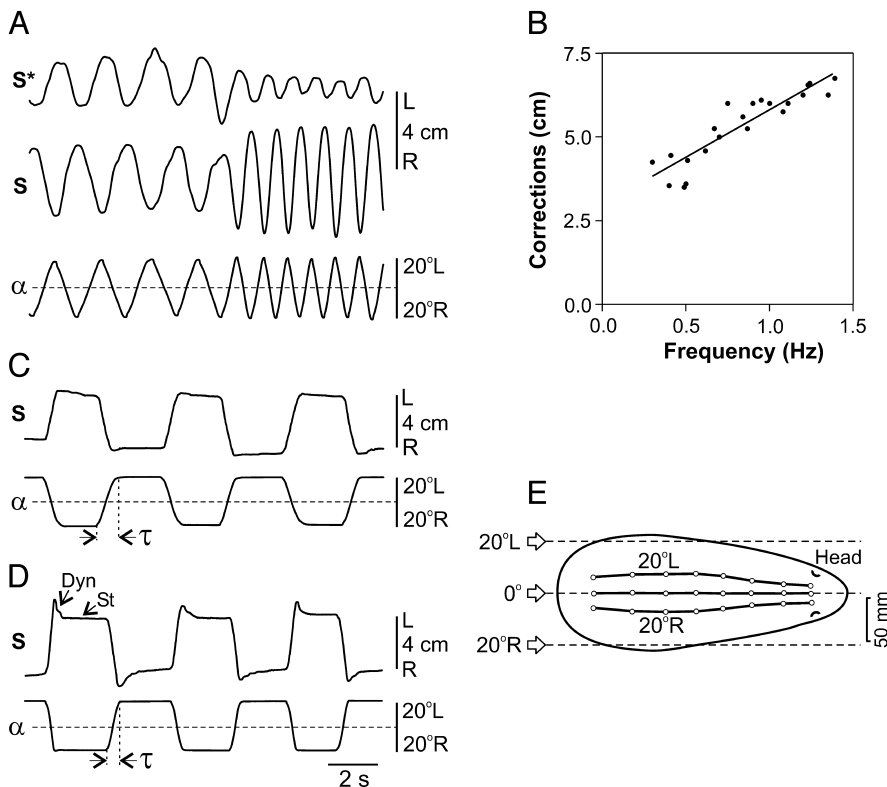


FIG. 2. Postural responses to tilts. *A*: sinusoidal tilts of the platform ( $\alpha$ ) caused lateral displacements of the trunk in relation to the platform (*S*) and to the external space (*S\**). An increase of the frequency of tilting caused an increase of postural responses and a decrease of displacements in space. *B*: peak-to-peak value of postural responses to sinusoidal tilts in 1 of the rabbits is plotted as a function of the frequency of tilting. Linear regression line ( $R^2 = 0.82$ ) is shown. *C* and *D*: responses to slow and rapid trapezoid tilts. Duration of tilting  $\tau$  was  $\sim 1$  s in *C* and  $\sim 0.5$  s in *D*. In *D*, the dynamic (Dyn) and static (St) components of the response are indicated for 1 of the cycles. *E*: postural responses in 8 points along the body dorsal midline. The body outline (view from above) is shown for 0 tilt ( $0^\circ$ ). The position of the body dorsal midline is shown for  $0^\circ$ ,  $20^\circ\text{L}$ , and  $20^\circ\text{R}$  tilts (—). The reference marker was rigidly attached to the platform above its axis at the height of the top of spine and head. Excursions of this marker (shown by  $\rightarrow$  and  $\leftarrow$ ) indicate the deviations of the body back midline that would occur without postural corrections.

the maximal tilt to the left ( $20^\circ\text{L}$ ) in Fig. 3*B*. The stick diagrams are superimposed in Fig. 3, *C* and *D*. Here, one can see that the effective lengths of the limbs on the side tilted down are considerably larger than those on the opposite side. Due to these differences in length, the limbs compensate for the tilts of the platform and maintain the normal body orientation. Different limb joints were involved differently in the compensatory flexion-extension movements. The peak-to-peak movements at the hip and knee joints of the hind limbs were larger than the movements at the ankle joint. Similarly, the

movements at the elbow joint of the forelimb were larger than the movements at the shoulder joint (Fig. 3*E*). These flexion-extension movements were observed in all animals.

The extension of limbs on the side moving down was primarily due to the activation of their extensor muscles. As shown in Fig. 4*A*, sinusoidal tilts of the platform evoked a periodical modulation of the EMGs of *m. triceps* and *m. gastrocnemius* with increased activity during ipsilateral tilting and decreased activity during contralateral tilting. The peaks of activity on the left and right sides alternated. Figure 4*B*, *top four traces*, shows the EMGs of four extensor muscles of the right fore and hind limbs recorded in one of the rabbits and averaged over 20 successive tilt cycles. The EMG pattern in different extensors was similar with a peak occurring slightly before the maximal ipsilateral tilt. This pattern was consistent across all subjects as illustrated in Fig. 4*C* in which the profile of the *m. triceps* EMG in the tilt cycle is presented for three animals. The peak of EMG was usually two to three times larger than the minimal EMG level. Sometimes this modulation of EMG was less pronounced, especially in *m. gastrocnemius*, and the peak was only 1.5 times higher than the minimum.

Among the three flexor muscles studied, a consistent pattern of periodic modulation was observed only in *m. biceps femoris* (knee flexor). In all tested animals ( $n = 5$ ), this muscle had a peak during contralateral tilting (Fig. 4*B*) that is in anti-phase with extensors. No consistent results were obtained when recording the EMG responses to tilt from other flexor muscles—*m. biceps brachii* (elbow flexor) and *m. tibialis* (ankle flexor). Tilts could evoke a rhythmic modulation of the flexor EMG in-phase with the ipsilateral tilt in some cases, or in anti-phase in other cases (not illustrated), or caused no modulation (as in *m. tibialis* in Fig. 4*D*).

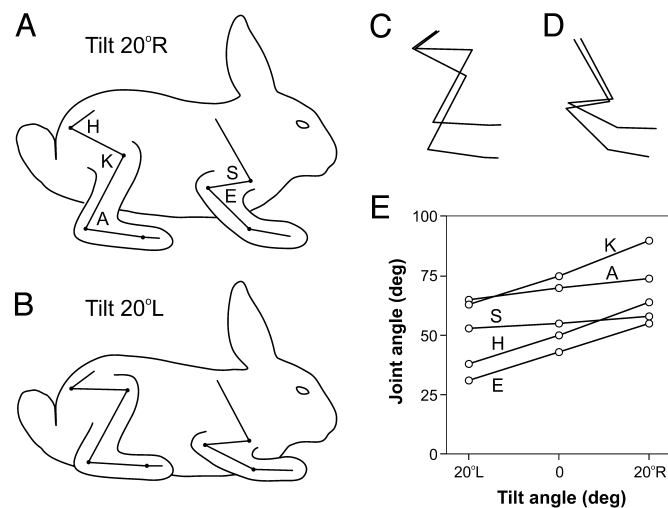


FIG. 3. Corrective limb movements during tilts. *A* and *B*: the body outline (view from the right side) is shown for 2 platform tilts,  $20^\circ\text{R}$  and  $20^\circ\text{L}$ , together with the stick diagrams for the fore and hind limbs. *C* and *D*: superposition of the stick diagrams for  $20^\circ\text{R}$  and  $20^\circ\text{L}$  tilts. *E*: angles in different joints at different platform tilts measured in 1 representative experiment. S, shoulder; E, elbow; H, hip; K, knee; A, ankle.

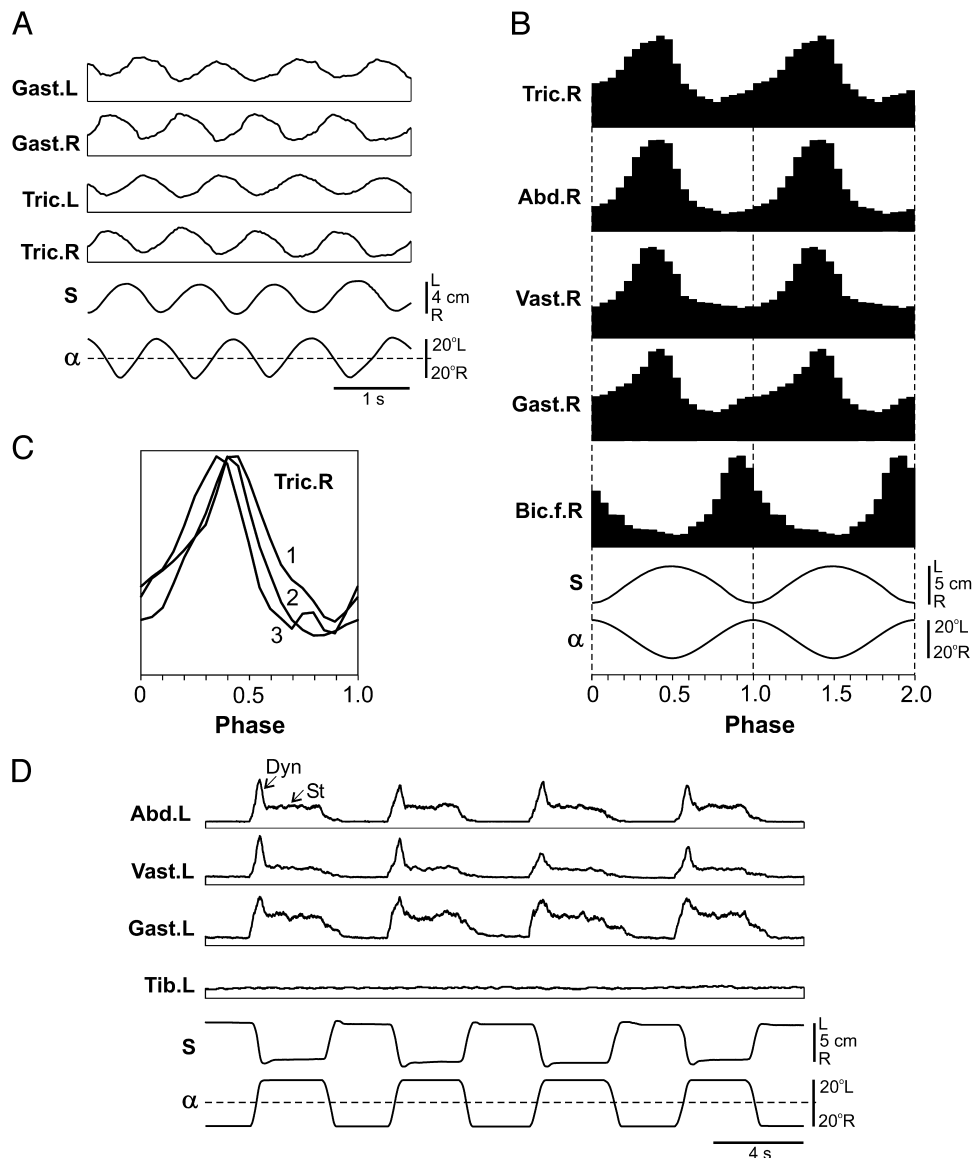


FIG. 4. Electromyographic (EMG) responses to tilts. *A*: a representative recording of body lateral displacements (*S*) along with EMGs of the left and right m. triceps and m. gastrocnemius caused by sinusoidal tilts ( $\alpha$ ). The EMGs were rectified and smoothed (time constant, 50 ms). *B*: summary of EMG responses to tilt in different muscles of the right fore and hind limbs. Each EMG was averaged over 20 normalized successive tilt cycles (20 bins/cycle; the peak tilt to the left was taken as the cycle onset). The cycle is repeated twice. *C*: a profile of m. triceps EMG as a function of the cycle phase observed in 3 rabbits (the curves are normalized to their peaks). *D*: motor and EMG responses to trapezoid tilts. The dynamic (Dyn) and static (St) components of the response in m. abductor are indicated for 1 of the cycles. Muscle name abbreviations in this and following figures: Tric., m. triceps; Gast., m. gastrocnemius; Bic.f., m. biceps femoris; Tib., m. tibialis; Abd., m. abductor.

The dynamic characteristics of postural corrective movements of the trunk (Fig. 2) were reflected in the EMG responses of limb muscles. *First*, the activation of all extensor muscles with ipsilateral tilting was stronger at 1 than at 0.5 Hz (not illustrated). *Second*, tests with trapezoid tilts showed that the EMG activity of all extensors had two components: a dynamic one, that is a peak of activity during tilting, and a static one, that is a sustained activity when a tilted position was maintained (Fig. 4*D*). Typically, the static component was two to three times smaller than the peak of the dynamic component. Similar dynamic properties were observed in the knee flexor m. biceps femoris (not illustrated).

#### Responses to complex postural stimuli

In these experiments, the rabbit maintained balance on two platforms (Fig. 1*D*), one under the fore limbs (*P1*) and the other under the hind limbs (*P2*). The platforms were tilted in the frontal plane of the animal (angles  $\alpha_1$  and  $\alpha_2$ ). Postural responses, that is, lateral displacements of the anterior and posterior parts of the body in relation to the corresponding plat-

form (*S1* and *S2* in Fig. 1*D*), were recorded. Figure 5 illustrates responses to complex stimuli recorded in one of the rabbits. Similar results were obtained in all tested animals ( $n = 6$ ).

First, when both platforms were tilted in-phase, postural responses in the anterior and posterior parts of the body also occurred in-phase with each other but in anti-phase with the platform tilts (Fig. 5*A*).

Second, when only *P1* was tilted while *P2* was kept horizontal (Fig. 5*B*), the rabbit tended to stabilize the dorsal-side-up orientation of the anterior part of the body by performing flexion-extension movements of its fore limbs. These limb movements led to corrective trunk movements in anti-phase to *P1* tilts and with a normal amplitude (compare *S1* traces in Fig. 5, *A* and *B*). The postural stabilization in the anterior part of the body was not perfect, however. Residual, periodic, lateral displacements (as in Fig. 2*E*) through the rigid body probably caused small displacements of the caudal trunk (Fig. 5*B*,  $\downarrow$ ).

Third, when only *P2* was tilted while *P1* was kept horizontal (Fig. 5*C*), the rabbit tended to stabilize the dorsal-side-up orientation of the posterior part of the body by performing

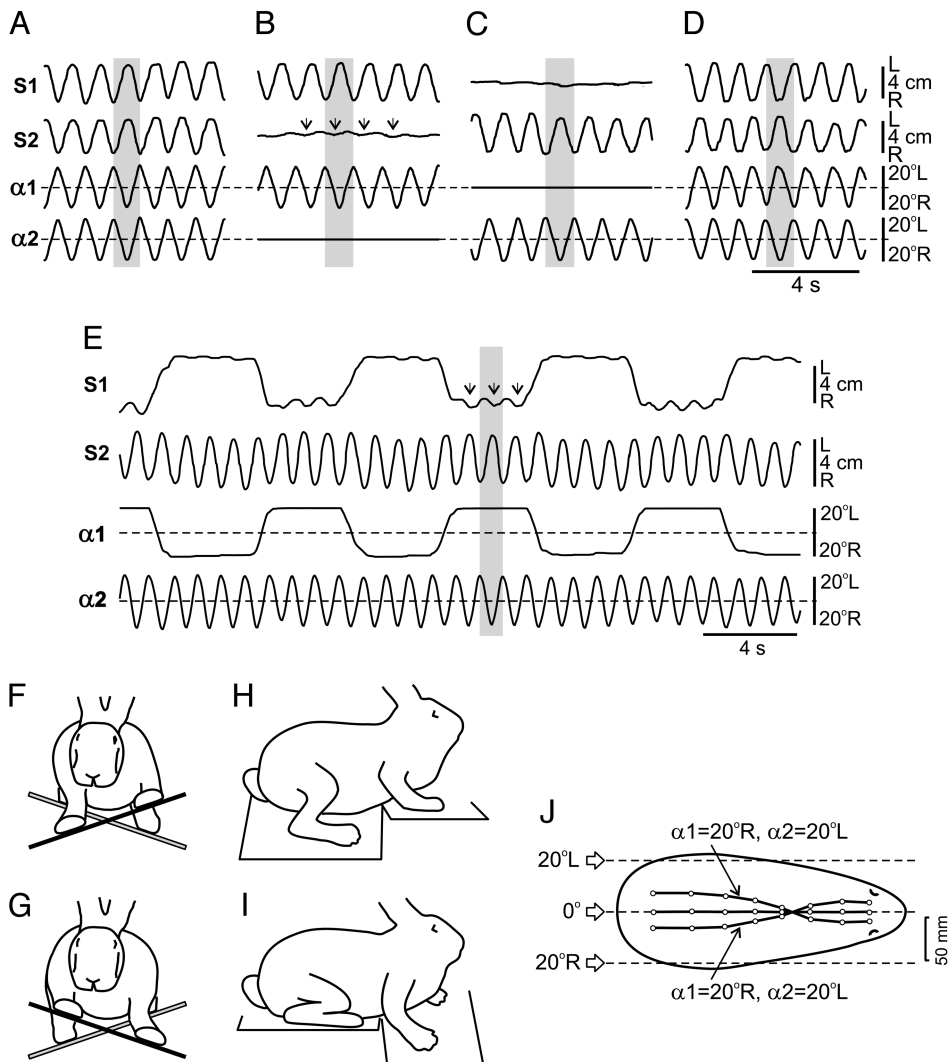


FIG. 5. Postural motor responses on the split platform. A–E: postural responses in the anterior (S1) and posterior (S2) areas of the trunk to different combinations of tilts of the anterior and posterior platforms ( $\alpha 1$  and  $\alpha 2$ ).  $\square$ , 1 of the tilt cycles to facilitate comparison between curves.  $\downarrow$ , responses caused by movements of the “foreign” platform, e.g., by tilts of the anterior platform when recording responses of the posterior trunk. F–I: the body outline for the 2 extreme positions ( $20^\circ\text{L}$  and  $20^\circ\text{R}$ ) of the platforms tilted sinusoidally in anti-phase (as in D). Video recordings were performed from the front (F and G) and from the right side (H and I). J: postural responses in 8 points along the body dorsal midline evoked by anti-phase tilting of the 2 platforms. The body outline (view from above) is shown for  $0^\circ$  tilt that occurred simultaneously in the 2 platforms. The midline position is also shown for this situation as well as for the situation when the platforms were tilted at their extreme positions.  $\rightarrow$ , the midline excursions expected without postural corrections (see legend to Fig. 2E for details).

flexion-extension movements of its hind limbs. These limb movements led to corrective trunk movements in anti-phase to P2 tilts and of a normal amplitude (compare S2 traces in Fig. 5, A and C). The influences of residual oscillations of the hind quarters onto the front part of the body in this particular rabbit were almost absent (see almost linear S1 trace in Fig. 5C). In other animals, these influences could be more pronounced.

Fourth, when P1 and P2 were tilted periodically at the same frequencies but in anti-phase to each other (Fig. 5D), postural responses in the anterior and posterior parts of the body (S1 and S2) occurred in anti-phase to tilts of the corresponding platform (P1 and P2) and therefore in anti-phase to each other. This was due to anti-phase flexion-extension movements of the fore and hind limbs on each side as was clearly seen in the video recording (Fig. 5, F–I). Figure 5J shows the position of the midline of the rabbit's back at  $0^\circ$  and at the maximal tilts of the platforms ( $20^\circ\text{R}$  and  $20^\circ\text{L}$ ) performed in anti-phase. Due to the postural corrections, displacements of the midline were much smaller than would have occurred without compensation ( $20^\circ\text{R}$  and  $20^\circ\text{L}$ ,  $\rightarrow$ ). In contrast to in-phase P1 and P2 tilts (Fig. 2E), when all points along the midline exhibited in-phase displacements, anti-phase P1 and P2 tilts caused the displacements of the midline in the anterior and posterior parts of the body to occur in opposite directions. As a result, displacements

in the mid-body part (where the center of mass is located) were small or absent.

Finally, P1 and P2 were tilted at different frequencies. This allowed us to correlate postural responses with particular postural perturbations. When P2 was tilted sinusoidally at 1 Hz while P1 was tilted trapezoidally at 0.25 Hz, the rabbit compensated well for the tilts of each of the platforms (Fig. 5E). Sinusoidal P2 tilts evoked anti-phase corrective displacements of the posterior trunk (S2) that were of normal amplitude. Trapezoidal P1 tilts evoked anti-phase corrective displacements of the anterior trunk (S1), also of normal amplitude. Also in the S1 and S2 traces, one can see small influences of a foreign platform. [The influences of P2 tilts are marked ( $\downarrow$ ) in the S1 trace.] Similar results were obtained when P2 was tilted at 0.25 Hz and P1 at 1 Hz (not illustrated). The EMG recordings have shown that each of the limbs participated in the compensation for postural perturbations evoked by movements of both platforms. Figure 6, A–D, illustrates the experiment when P1 was tilted sinusoidally at 1 Hz and P2 was tilted trapezoidally at 0.25 Hz. Each panel (A–D) shows the average responses to tilts of P1 in the particular muscle recorded under two conditions: when P2 was tilted to the right ( $\alpha 2 = 20^\circ\text{R}$ ) and when it was tilted to the left ( $\alpha 2 = 20^\circ\text{L}$ ). Both P1 and P2 tilts were reflected in the EMGs of all four muscles. We

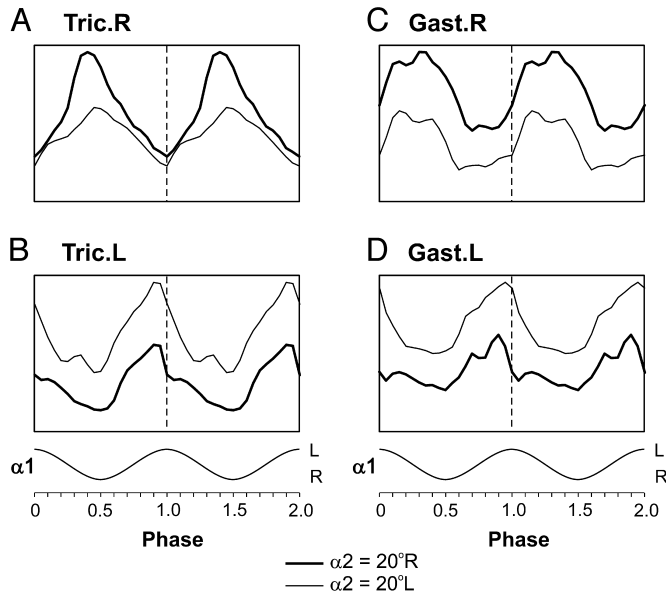


FIG. 6. Postural EMG responses on the split platform. Tilts of the anterior platform (sinusoidal, 1 Hz) were combined with tilts of the posterior platform (trapezoidal, 0.25 Hz). The graphs show profiles of averaged EMGs for different muscles in the normalized tilt cycle of the anterior platform (the cycle is repeated twice) for 2 stationary positions of the posterior platform, 20°R (thick lines) and 20°L (thin lines). In each panel, the 2 EMG responses are presented with the same amplification.

suggest that the tilt of either platform affects the mechanical conditions (loading), not only for the limbs positioned on that particular platform but also—through the rigid trunk—for the limbs of the other girdle, thus evoking reflex responses in their muscles.

#### Role of different sensory inputs

To assess the role of sensory inputs of different modalities for the generation of postural responses to tilt, a number of experimental techniques were used.

First, the significance of visual input was studied by comparing the postural motor responses *S* to tilts in light and in darkness. In a representative animal, the peak-to-peak value of *S* was  $5.1 \pm 0.1$  cm in light versus  $5.0 \pm 0.1$  cm in darkness (means  $\pm$  SE). The difference was not statistically significant (*t*-test). Similar results were obtained in all four animals tested. Also, blindfolding the animals did not affect this value (3 animals tested, 1 of these was also tested in darkness). These results indicate that visual information does not play any significant role for maintenance of the dorsal-side-up body orientation.

Second, in a different set of experiments, both visual and vestibular inputs signaling about tilts were abolished by fixation of the head position in space as shown in Fig. 1*F*. In these experiments, stabilization of the hind quarters was investigated. We used a split platform and performed periodical tilting of only the posterior platform that supported the hind limbs (*P2* in Fig. 1*D*), whereas the anterior platform, which supported the fore limbs (*P1* in Fig. 1*D*), was maintained in the horizontal position. As shown in Fig. 7*A*, tilting the posterior platform elicited postural corrections in the posterior part of the trunk (*S2*), with a peak-to-peak value of 4–5 cm, that did not differ significantly from the corresponding value when the

head was not fixed ( $4.5 \pm 0.3$  cm). The EMG pattern in the hind limbs, that is, activation of *m. gastrocnemius* during ipsilateral tilting (Fig. 7*A*), also did not differ from the normal one (Fig. 4, *A* and *B*). Similar results were obtained in all three animals tested. These results indicate that vestibular and visual signals about tilt are not necessary for the generation of normal postural corrective responses in the hind quarters. Because in these experiments only the posterior platform was tilted, it seems most likely that the responses to tilts in the hind limbs were elicited by somatosensory input from these limbs. We did not investigate the effect of head fixation on postural corrective responses in the fore limbs because this factor could considerably affect mechanical conditions for the anterior part of the body and for the fore limbs.

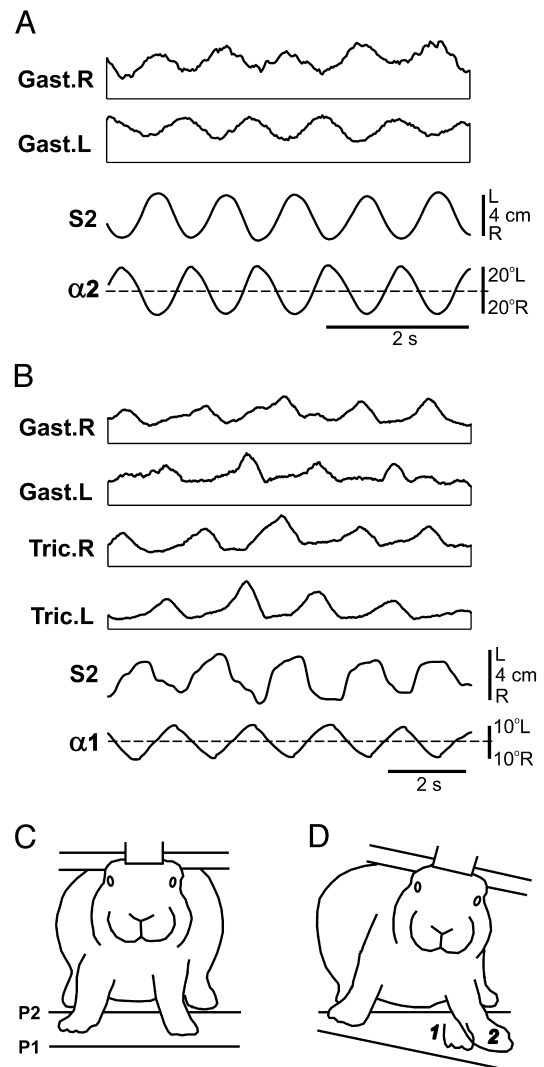


FIG. 7. Effects of restriction of head movements. *A*: the head position was fixed in the external space, and the anterior platform was kept horizontal. Tilting the posterior platform ( $\alpha_2$ ) caused normal EMG responses in the hind limb extensors (*Gastr.R* and *Gastr.L*) and postural corrections in the posterior part of the trunk (*S2*). *B*: the head was fixed to the frame moving with the anterior platform (*P1*), and the posterior platform was kept horizontal. Tilt of the anterior platform ( $\alpha_1$ ) caused EMG responses in both fore and hind limbs as well as lateral displacements of the posterior trunk (*S2*). *C* and *D*: the posterior trunk displacement caused by the *P1* tilt ( $10^\circ$ L) as seen from the video recording. This tilt also evoked a lateral step of the left fore limb, from position 1 to position 2.



Third, fixation of the head to the tilting anterior platform (Fig. 1G) allowed us to increase the tilt-related vestibular and visual inputs considerably. Indeed, without head fixation, postural corrections led to a fivefold reduction of the head deviation as compared with the uncorrected deviation (Fig. 2E). By preventing compensatory head movements, head fixation will therefore lead to a fivefold increase of head movements and to a corresponding increase of the vestibular and visual inputs evoked by the platform tilts of the same magnitude. In Fig. 7, C and D, the head was fixed to the anterior platform (P1) that was periodically tilted, while the posterior platform (P2) was maintained horizontal. Even small tilts of P1 ( $\pm 10^\circ$ ) evoked normal EMG responses in the forelimbs—that is, an activation of m. triceps with ipsilateral tilt (Fig. 7B). (Because of head fixation, the muscle activity in the fore limbs did not cause any significant corrective movements in the frontal part of the body.)

The P1 tilts also evoked strong responses in the hind limbs. These responses include activation of m. gastrocnemius with ipsilateral P1 tilt and large (3–4 cm peak-to-peak) displacements of the posterior trunk (S2) in a direction opposite to P1 tilt (Fig. 7B). The lateral trunk displacement in the direction opposite to tilt is readily seen in the video recording (Fig. 7, C and D). Because P2 was motionless, these responses did not promote the maintenance of the dorsal-side-up orientation but rather deflected the posterior part of the trunk from its normal position. These effects persisted in blindfolded rabbits ( $n = 2$ ), suggesting that they were caused by the tilt-dependent vestibular input. Similar results—that is, strong responses in the hind quarters to small tilts ( $\pm 5$ – $10^\circ$ ) of the P1 and head—were obtained in all animals tested ( $n = 3$ ).

An increase of the tilt amplitude  $\leq 10$ – $15^\circ$  evoked, in some tilt cycles, a different type of response: a lateral step of the fore limb, as illustrated in Fig. 7D. On reaching a tilt angle of  $10^\circ$ , the ipsilateral forelimb was lifted and rapidly (in 150–200 ms) moved from the initial position (1) to a more lateral position (2). Such lateral steps were observed in all animals tested ( $n = 3$ ). An increased tilt-dependent vestibular input most likely triggered this postural reaction with a lateral step aimed at preventing the rabbit from a losing its balance.

Fourth, evidence that an asymmetry in the tonic vestibular input can affect the stabilized body orientation was obtained in experiments with galvanic stimulation of the labyrinths (3 animals tested). In the rabbit standing on the horizontal stationary platform, a current pulse of 3 mA evoked a lateral tilt of the animal toward the positive electrode (Fig. 8A). When the current of the same value was applied during periodical tilts of the platform, the left and right tilts still evoked corrective postural responses of a normal magnitude, but the responses were superimposed on a bias toward the positive electrode (Fig. 8, B and C). This finding suggests that a tonic asymmetrical vestibular input causes a displacement of the set-point of the postural system stabilizing the body orientation in the frontal plane.

#### Threshold and plateau properties of postural responses

The following observations suggest that the mechanisms for postural corrections respond only to postural stimuli (deviations from the stabilized body orientation) that exceed a certain threshold value.

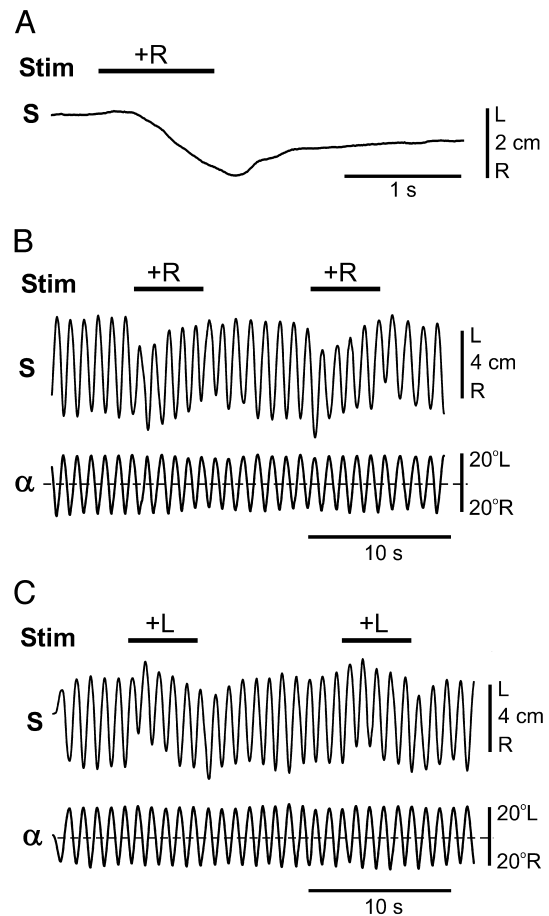


FIG. 8. Effects of galvanic stimulation of the labyrinths. A: in a rabbit standing on a stationary horizontal platform, a pulse of constant current (3 mA) caused a postural response—that is, a lateral displacement of the body (S) toward the positive (right) electrode. B and C: galvanic stimulation during periodical tilts of the platform caused a lateral body displacement superimposed on the periodical compensatory movements. The positive electrode was on the right (B) or the left (C).

First, although a profile of the postural responses to rapid tilts (0.5–1 Hz) was usually rather smooth (see e.g., Fig. 2A), a clear-cut stepwise structure of this response was always observed at a slow speed of tilting. As shown in Fig. 9, A and B, a slow tilt of the platform evoked corrective responses with stepwise profile. In each step, a rapid corrective movement was followed by a plateau. The difference between the tilt angles corresponding to the onset of successive steps was on the order of a few degrees.

Second, further evidence for the threshold properties of postural responses was obtained in a different set of experiments. In the test with sinusoidal (0.5 Hz) tilts of the platform, we changed the tilt amplitude gradually and found that the postural corrections appeared only when the peak-to-peak value of tilts exceeded 3– $5^\circ$  (Fig. 9C).

Third, an indirect piece of evidence for the threshold properties of the postural mechanisms was obtained in experiments with brief and fast tilts (jerks; Fig. 9, D and E). When the platform was rapidly tilted and then returned to the initial position ( $0^\circ$ ), the positions maintained by the animal after jerks in opposite directions differed by 1–2 cm. In some animals,



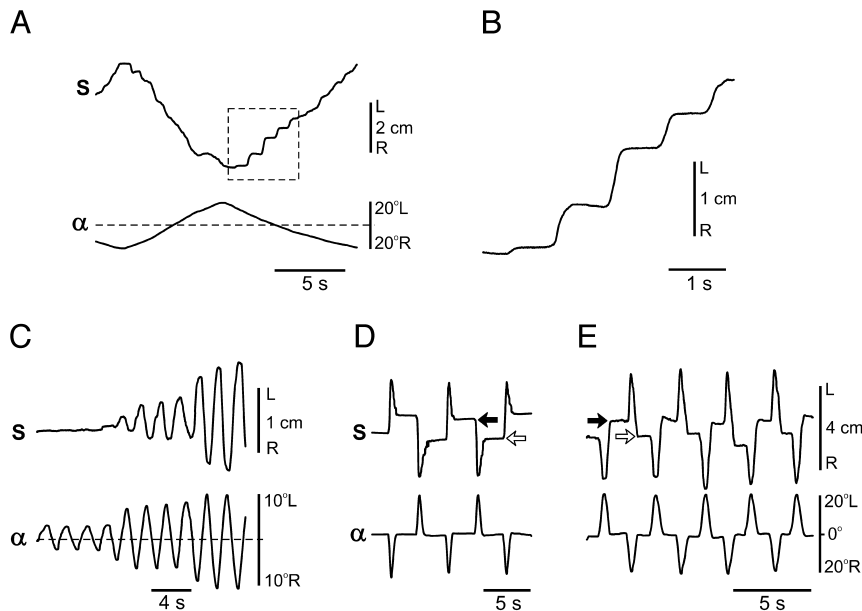


FIG. 9. Threshold and plateau properties of postural mechanisms. *A* and *B*: postural responses evoked by slow tilts. The part indicated by a rectangle in *A* is shown in *B* with a higher resolution. *C*: postural responses to sinusoidal tilts of different amplitudes. *D* and *E*: postural responses to jerk-like tilts recorded in 2 different rabbits. The animals maintained different stationary positions after the jerks in opposite directions (arrows).

there was apparent undercompensation for tilt (Fig. 9*D*) and in others overcompensation (Fig. 9*E*).

#### DISCUSSION

In the present study, we characterized different aspects of postural control in the rabbit maintaining balance on the tilting platform—the pattern of postural corrections caused by tilts of the whole platform or its parts, the role of different sensory modalities in generation of these corrections, and the threshold properties of postural mechanisms.

##### Simple postural task

It was found that the rabbit can easily keep balance on the platform tilted in the frontal plane by  $\pm 20^\circ$  (simple postural task). To maintain equilibrium at different tilt angles, the rabbit modified configuration of its limbs. By recording body displacements, angles in the limb joints, and EMGs of limb muscles, we have characterized the pattern of postural responses to lateral tilts.

In the absence of postural corrections, a tilt of the platform in the frontal plane of the animal would cause a displacement of the projection of the center of mass toward the lateral border of the base of support and thus would decrease the postural stability. It seems likely that postural corrections, in the simple postural task, are aimed at reducing the displacements of the projection of the center of mass. This is achieved by extending the limbs on the side moving down and flexing the limbs on the opposite side (Fig. 1, *A* and *B*). These limb movements move the body in relation to the platform, thereby partly compensating for the platform tilt. Thus the limb movements lead to the maintenance of the dorsal-side-up orientation of the trunk and head. The present study showed that the residual lateral displacements are smaller in the anterior part of the body than in its posterior part (Fig. 2*E*), indicating that postural stabilization in the anterior part is more efficient. This difference could be due to more efficient corrective movements in the fore limbs and additional corrective neck movements that supplement the corrective limb movements.

We found that lateral displacements of the trunk in relation to the platform (postural corrections) had a substantial dynamic component, that is, compensation for rapid tilts was better than compensation for slower tilts (Fig. 2, *A* and *B*) and, also, better than compensation for sustained tilts (Fig. 2*D*). One can suggest that these dynamic characteristics allowed the system to better respond to rapid postural disturbances.

Limb movements that cause corrections of the trunk orientation were relatively simple (Fig. 3). They included extension at all joints on the side moving down, both in the fore and in the hind limb, and flexion on the opposite side. Correspondingly, the activity of all tested extensor muscles increased with ipsilateral tilt and decreased with contralateral tilt (Fig. 4*B*). Of the three tested flexor muscles, a consistent tilt-cycle-related modulation was observed only in *m. biceps femoris* (knee flexor). Thus the corrective flexion-extension limb movements were caused primarily by a modulation of the extensor activity, whereas periodic flexor activity seems to play less important role. This allowed each of the limbs to support the body in all phases of the tilt cycle. This motor and EMG pattern differs from the locomotor pattern in which a limb supports the body only in the stance phase, and the activities of flexor and extensor muscle groups are 100% modulated and alternate with each other (Orlovsky et al. 1999).

Experiments with trapezoid tilts have shown that the extensor activity consists of the dynamic and static components (Fig. 4*D*). The dynamic component is observed during tilting: it causes extension of the limbs on the side moving down and moves the body in the opposite-to-tilt direction. The static component lasts as long as the platform remains tilted. This component is responsible for the maintenance of the compensatory body displacement in relation to the platform. The dependence of the static extensor activity on the tilt angle allows the rabbit to maintain equilibrium on differently tilted surfaces. Receptors signaling the load in the limb (positive force feedback) might be responsible for the activation of extensors with their loading caused by tilt (Deliagina et al. 2000a; Duysens et al. 2000; Pratt 1995).

### *Complex postural tasks*

Our experiments with independent tilting of the anterior and posterior parts of the body have shown that the animals are capable of solving these complex postural tasks (Fig. 5). Especially demanding was the task with different frequencies and timing of the tilts of the anterior and posterior platforms (Fig. 5E) as well as the task with anti-phase tilts of the two platforms (Fig. 5, D and F–J). In the latter task, tilts of the platforms caused either only minor lateral displacements in the mid-body area (where the center of mass is located) or no displacements at all (Fig. 5J). This makes unlikely the hypothesis that postural corrections in quadrupeds are caused by the center of mass displacements (see e.g., Ghez 1991; Massion 1994; Massion et al. 1997).

The more likely explanation for these findings is that the limbs of the hip and shoulder girdles are controlled by their own postural mechanisms driven primarily by somatosensory inputs from the corresponding limbs. These two postural subsystems tend to maintain the dorsal-side-up orientation of the corresponding (anterior and posterior) parts of the body. The capacity of the postural mechanism in a single girdle to operate independently is also suggested by the fact that rabbits can maintain equilibrium during bipedal standing.

Such a functional organization of the postural system is similar to that of the locomotor system in quadrupeds, where the shoulder and hip girdles have their own control mechanisms, and even individual limbs have relatively autonomous controllers that generate stepping movements and interact with each other to secure the inter-limb coordination (Orlovsky et al. 1999; von Holst 1938). It was suggested that a control system consisting of semi-autonomous subsystems can better adapt to complicated environmental conditions as compared with a centralized system (Gelfand and Zetlin 1971).

It is well established that, under certain conditions, the system controlling the head position operates independently from that controlling the trunk posture (Barberini and Macpherson 1998; Berthoz and Pozzo 1988; Boyle 2001; Deliagina et al. 2000a). Given that the trunk posture in quadrupeds is maintained by two mechanisms, one can conclude that, in complex postural tasks, the whole body is stabilized by the simultaneous activity of three principal mechanisms.

### *Double role of vestibular input*

In the previous study (Deliagina et al. 2000a), it was shown that rats and rabbits, after destruction of both labyrinths and being blindfolded, were able to maintain balance on the tilting platform. It was also shown that, in cats, the basic pattern of postural response to a platform translation persisted after bilateral labyrinthectomy (Inglis and Macpherson 1995) but suffered in animals with somatosensory deficit (Stapley et al. 2002). These findings indicate that vestibular and visual inputs are not necessary for the generation of corrective responses in these postural tasks. However, lesion to vestibular organs gives rise to rather rapid compensatory processes (Smith and Curthoys 1989), which may affect the interpretation of experimental results.

We developed a technique (head fixation) to reversibly manipulate the vestibular input. It is known that vestibular signals about head movement are presented as a modulation of the

background tonic discharge of vestibular afferents (Fernandez and Goldberg 1976). In contrast to experiments with destruction of labyrinths (Deliagina et al. 1997, 2000b; Inglis and Macpherson 1995), head fixation allowed us to affect only the component of sensory input that signals the head movement without affecting its tonic component. Also, by fixing the head in space or in relation to the moving platform, we were able to either abolish or considerably increase the tilt-related vestibular and visual signals. These experiments showed that a removal of vestibular and visual information concerning postural perturbations did not affect significantly the quality of postural stabilization (Fig. 7A), thus corroborating previous findings (Deliagina et al. 2000a; Inglis and Macpherson 1995). In contrast, a large increase of the tilt-related vestibular signals produced a dramatic effect, that is, a considerable increase of postural responses and even a lateral compensatory step toward the side moving down (Fig. 7, B–D). These findings suggest that phasic vestibular input (signaling head movement) does not play any significant role for trunk stabilization under ordinary conditions; under these conditions, postural mechanisms are driven almost exclusively by somatosensory input. The phasic vestibular input, however, becomes of crucial importance when ordinary postural corrections are not effective and there is a danger of losing balance as was also demonstrated for falling cats (Watt 1976).

It is known that a unilateral removal of a vestibular organ produces dramatic effects on both the head position and the trunk posture (Deliagina et al. 1997; Smith and Curthoys 1989). It was suggested that these effects were caused by an asymmetry in the tonic component of vestibular inputs on the two sides. This asymmetry elicits a shift of the set-point in the somatosensory-driven postural control system (Deliagina et al. 1997). In the present study, we caused an asymmetry in the tonic vestibular input by means of a galvanic stimulation of the labyrinths (Swaak and Oosterveld 1975). It was found that this stimulation did not affect the magnitude of responses to tilts, but it affected the stabilized body orientation (Fig. 8). These data support the notion that a tonic vestibular drive may affect the set-point of the postural system.

### *Stepwise pattern of postural responses*

The present study has shown that postural mechanisms in the rabbit possess both threshold and plateau properties. We observed threshold properties in the responses to both slow and fast postural stimuli, whereas plateau properties were observed in responses to slow tilts only (Fig. 9). Plateau properties of postural mechanisms were first demonstrated by Mori (1987, 1989), who reported that a brief stimulation of the dorsal or ventral tegmental field in the brain stem of the decerebrate cat elicited long-lasting (plateau-like) changes in the tone of extensor muscles. One can therefore conclude that a stepwise pattern of postural responses is not a unique characteristic of the rabbit postural system. The functional role of these properties and their biological expedience are not clear, however, neither the location of the corresponding neuronal mechanisms.

In the present study, some aspects of functional organization of the postural control system in quadrupeds were characterized. Very little is known, however, about neuronal mechanisms involved in postural control. These mechanisms reside in

different parts of the brain and in the spinal cord (for review, see Deliagina and Orlovsky 2002; Horak and Macpherson 1995). Recently it was shown that the neuronal activity in the motor cortex correlates with postural corrections (Beloozerova et al. 2003; Deliagina et al. 2000b).

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## DISCLOSURES

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