Activity of pyramidal tract neurons in the cat during postural corrections

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Beloozerova, I. N., M. G. Sirota, G. N. Orlovsky, and T. G. Deliagina. Activity of pyramidal tract neurons in the cat during postural corrections. J Neurophysiol 00: 000-000, 2004. The dorsal side-up body orientation in quadrupeds is maintained by a postural control system. We investigated participation of the motor cortex in this system by recording activity of pyramidal tract neurons (PTNs) from limb representations of the motor cortex during postural corrections. The cat was standing on the platform periodically tilting in the frontal plane, and maintained equilibrium at different body configurations: with the head directed forward (symmetrically alternating loading of the left and right fore limbs), or with the head voluntary turned to the right or to the left (asymmetrical loading). We found that postural corrective responses to tilts included an increase of the contact forces and activity of limb extensors on the side moving down, and their decrease on the opposite side. The activity of PTNs was strongly modulated in relation to the tilt cycle. Phases of activity of individual PTNs were distributed over the cycle. Thus, the cortical output mediated by PTNs appeared closely related to a highly automatic motor activity, the maintenance of the body posture. An asymmetrical loading of limbs, caused by head turns, resulted in the corresponding changes of motor responses to tilts. These voluntary postural modifications were also well reflected in the PTNs activity. The activity of a part of PTNs well correlated with contact forces, in some others with the limb muscle activity; in still others no correlation with these variables was observed. This heterogeneity of the PTNs population suggests a different functional role of individual PTNs.
INTRODUCTION

The dorsal side-up body orientation in quadrupeds is maintained due to the activity of a postural system. This closed-loop control system operates on the basis of sensory feedback signals and generates a corrective motor response when a posture differs from the desired one (for review, see Deliagina and Orlovsky 2002; Horak and Macpherson 1995; Macpherson et al. 1997a; Massion 1998). Animals are able to maintain the normal body orientation and keep equilibrium when standing on an inclined or tilting surface (Deliagina et al. 2000; Maioli and Poppele 1991; Lacquaniti et al. 1984). They can also combine maintenance of the normal posture with voluntary limb or head movements (Barberini and Macpherson 1988; Gahery et al. 1980; Massion 1994).

Lesion experiments indicate that basic nervous mechanisms for feedback postural control reside in the brainstem, cerebellum, and spinal cord. First, chronic decerebrate animals are able to maintain the dorsal side-up posture (Magnus 1924; Bard and Macht 1958). Second, after inactivation of the motor cortex, which is the main motor output of the forebrain, the animals are able to maintain equilibrium when standing or walking over a flat terrain (Chambers and Liu 1957; Adkins et al. 1971; Dubrovsky et al. 1974; Beloozerova and Sirota 1988, 1993). These experiments, however, did not answer two important questions regarding the role of the motor cortex in postural control: (1) Do the cortical mechanisms supplement the principal, brainstem-spinal postural mechanisms when maintaining the basic, dorsal side-up body posture? (2) Do the cortical mechanisms participate specifically in voluntary modifications of the basic posture?

The first one of these two questions was addressed in our recent study (Beloozerova et al. 2003b). We have examined the activity of cortical neurons in the rabbit maintaining balance on the periodically tilting platform. It was found that the activity of two classes of
neurons from the limb representation of the motor cortex (efferent neurons of layer V and putative inhibitory interneurons) was modulated in relation to the tilt cycle. This finding suggests that the motor cortex participates in the generation of postural corrective responses.

To further investigate these problems, in the present study we have examined the activity of the main cortical output – pyramidal tract neurons (PTNs) from the limb representation of the motor cortex – in the awake cat standing on a periodically tilting platform. The experimental design for postural tests was similar to that used in our recent studies of the postural mechanisms in rabbits (Deliagina et al. 2000; Beloozerova et al. 2003b); the technique for recording cortical neurons was also similar to that used in the experiments on rabbits (Beloozerova et al. 2003c). Two postural tasks were employed: (a) Maintenance of equilibrium with a straight (symmetrical) body configuration, i.e., with the head directed forward. (b) Maintenance of equilibrium with voluntary modified body configurations, i.e., with the head turned to the right or to the left toward the source of food. The main goals of these experiments were to determine: (1) whether the activity of PTNs correlates with reflectory postural responses, and (2) whether this activity reflects voluntary modifications of posture. In addition, we attempted to correlate the PTNs postural responses with some specific characteristics of motor responses (forces, EMGs).

We have found that the activity of PTNs well reflects the platform tilts and the postural corrections caused by these tilts. Modifications of body configuration accompanying voluntary turns of the head are also well reflected in the activity of PTNs. A possible role of different groups of PTNs in the elicitation of postural corrections is discussed.

A brief account of this study was published in abstract form (Deliagina et al. 2003).
MATERIALS AND METHODS

Recordings were obtained from three adult cats (#1 and #2 females, and #3 male, weighting 3.2, 3.0, and 3.8 kg, respectively). Some of the methods have been described (Beloozerova and Sirota 1993; Beloozerova et al. 2003b) and will be reported briefly here. All experiments were conducted with the approval of the Barrow Neurological Institute Animal Care and Use Committee.

Surgical procedures

Surgery was performed under Isoflourane anesthesia using aseptic procedures. The skin and fascia were removed from much of the dorsal surface of the skull. At ten points around the circumference of the head, stainless steel screws were screwed into the skull and connected together with a wire; the screw heads and the wire were then inserted into a plastic cast to form a circular base. Later, awake cats were rigidly held by this base while searching for neurons before postural tests. The base was then used also for fixation of connectors, a miniature microdrive, a pre-amplifier, contacts for EMG wires, contacts for stimulating electrodes, and a protective and electrically shielding cap.

A portion of skull and dura above the left motor cortex, over approximately 1 sq cm, were removed. The area of the motor cortex was visually identified by the surface features and photographed. The aperture was then covered by a plastic plate 1 mm thick, in which approximately 100 holes (0.3 mm in diameter) had been drilled and filled by sterile wax. The plate was fastened to the surrounding bone with orthodontic resin (Densply Caulk).

A pair of EMG recording electrodes, separated by 10 mm and constructed from teflon-insulated multi-strand stainless-steel wire (0.2 mm outer diameter, AS633, Cooner Wire), was implanted bilaterally into the lateral head of m. triceps (elbow extensor), and into the lateral head of m. gastrocnemius (ankle extensor). In addition, the electrodes were
implanted unilaterally into *m. soleus* (ankle extensor) and *m. brachialis* (elbow flexor).

Electrode placement was verified by stimulation through the implanted wires before closure of the incision. The wires were positioned under the skin and soldered to the connectors on the head base.

Two 26 gauge hypodermic guide tubes were implanted vertically above the medullary pyramid at the Horsley and Clarke coordinates (P 10, L 0.5) and (P 10, L 1.5), at the depth of H 0 for insertion of stimulating electrodes into the pyramidal tract later in the awake state.

**Identification of fore- and hind limb motor regions**

After several days of recovery, experiments were initiated by placing the animal in a head-restraining device and restraining its head by the base that was attached to the skull during surgery. Over several days, a number of sessions of increasing duration were used to accustom the cat to the head-restrainer. Methods ensuring the humane treatment of subjects during immobilization of the head have been described (Beloozerova and Sirota 1993; Beloozerova et al. 2003a).

In the cat, the area immediately adjacent to and inside the lateral half of the cruciate sulcus is considered to be the motor cortex. This is based on considerable body of data obtained by means of inactivation, stimulation, and recording techniques (Nieoullon and Rispal-Padel 1976; Phillips and Porter 1977; Vicario et al. 1983; Armstrong and Drew 1984, 1985; Drew 1993; Beloozerova and Sirota 1993; Martin and Ghez 1985, 1993), as well as on histological considerations (Hassler and Muhs-Clement 1964; Myasnikov et al. 1994; Ghosh 1997). The fine mapping of the body parts in the cortex varies in different subjects, however (e.g. Myasnikov et al. 1997). In order to identify the fore- and the hind limb representations of the left motor cortex in each subject, three approaches have been used: (1) somatic receptive fields mapping, (2) observation of neuronal activity during voluntary movements,
and (3) intracortical micro-stimulation.

First, in the animal resting with its head restrained, multiunit recording electrode was inserted in the motor cortex through a hole in the plastic plate implanted above it. A miniature manual micromanipulator, rigidly fixed to the skull, was used to lower the electrode. After amplification and filtering (0.3–10 kHz band pass; Power-1401/Spike-2 System, Cambridge Electronic Design, Cambridge, UK), neuronal activity was displayed on the screen of an IBM compatible computer and also led to an audio monitor. Somatic receptive fields were mapped by manual application of stimuli to the skin and fur, by palpation of muscles and their tendons, and by passive movements of joints while simultaneously listening to the multiple-unit neuronal responses and observing them on the computer screen. Second, activity of the neurons during active withdrawal and reaching movements of the animal was noted. Third, in selected tracks micro-stimulation (trains of ten 50 µA cathodal pulses at 200 Hz, with each pulse of 0.2 ms) was applied. Effects of micro-stimulation were evaluated by observation of evoked movements, by body parts palpation, and/or by recording responses from muscles with implanted EMG electrodes.

The area just rostral to the lateral half of the cruciate sulcus, where (1) the neurons responded to somatic stimulation of the forelimb, (2) the neurons were active during active movements of the forelimb, and (3) in which micro-stimulation resulted in movements of the forelimb – was considered to be the forelimb area (I in Fig. 4A). Analogous judgment was made regarding the area just caudal to the middle portion of the cruciate sulcus in connection with hind limb sensitivity/movements (hind limb motor representation, 2 in Fig. 4A). The only difference from the forelimb motor representation was that, because of the fold of the sulcus, different penetrations in this area reached the hind limb representation at different depths in the bank of the sulcus. During recording experiments, the microelectrode tracks
were made inside these two (fore- and hind limb) identified regions, covering predominantly elbow/shoulder and ankle/knee areas in the fore- and hind limb representations, respectively. In addition, postmortem positions of recording tracks in the motor cortex were estimated in relation to the reference lesions; they were found to be grouped in the area 4γ.

**Cell recording and identification**

Single neuron activity was recorded extracellularly using either platinum-tungsten quartz insulated microelectrodes (40 μm outer diameter) pulled to a fine tip and mechanically sharpened (using a diamond grinding wheel, Reinbeck 1983), or commercially available tungsten varnish insulated electrodes (Frederick Haer & Co). The impedance of both types of electrodes was 2-4 MΩ at 1000 Hz. After the electrode reached the depth of the cortex where clear responses of many neurons to limb movements could be observed (presumably layer V), a bipolar stimulating electrode was slowly lowered into the pyramidal tract. This electrode consisted of two platinum-iridium wires (200 μm outer diameter, insulated with Teflon to within 0.4 mm of the tip) separated by 1 mm in the medio-lateral direction. It was inserted using a micromanipulator, with each of the wires going down through a separate guide tube in a two-26 gauge tubes arrangement that was stereotaxically implanted during the surgery above the pyramidal tract at the medullar level. Pulses of graded intensity (in the range of 0.1-0.5 mA, 0.2 ms duration) were delivered through this bipolar electrode. The electrode was stopped in the position that was most effective in eliciting antidromic responses in neurons in the motor cortex, fixed to the guide tubes by acrylic cement, and served as the pyramidal tract-stimulating electrode for the duration of recordings in the cat.

The criterion for identification of antidromic responses was the test for collision of spontaneous and evoked spikes (Bishop et al. 1962; Fuller and Schlag 1976; Swadlow 1998). First, a spike response in the motor cortex to stimulation of pyramidal tract that would have a
stable latent period was searched for. The latent and the refractory periods were measured, and the stability of the latent period and the refractory period of < 3 ms were taken as suggestive of the antidromic nature of the response. Then, stimulation of the pyramidal tract was triggered from spikes of a similar waveform from the motor cortical record (spike waveforms were analyzed using the Power-1401/Spike-2 system waveform-matching algorithm). Spike responses to stimulation were observed as the time delay between the trigger spike and the stimulus was diminished from much longer than the evoked response latent period to a shorter one. If at the appropriate time delay (latent period plus refractory period) and shorter, the evoked spike was ceasing to occur, it was considered to be the sign of collision of the evoked and spontaneous spikes. Since collision may occur inside the same axon only, the collision of the evoked and spontaneous spikes was taken as indicative of the projection of the neuron to the medullar pyramidal tract. Before and after testing in postural tasks, all encountered neurons were tested for antidromic activation using the test for collision described above.

The somatic receptive fields were examined in the resting animals under conditions of head restraint. The size of receptive fields was determined by listening to the audio monitor and measuring the entire area from which action potentials could be elicited. A directional selectivity was assessed by comparing the number of spikes elicited by stimulation in the optimal direction with the direction opposite from optimal. Occasionally, micro-stimulation was used to ensure that the sampling is made indeed from the limb representation of the motor cortex.

Signals from the microelectrode pre-amplifier, as well as those from the EMG electrodes and from the body position and force sensors were amplified, digitised with a sampling frequency of 30 kHz (microelectrode), 3 kHz (EMGs), and 400 Hz (sensors),
displayed on the screen, and recorded to the disk of a computer by means of data acquisition software (Power-1401/Spike-2). After digitization, the EMG signals were rectified and smoothed by filters with a time constant of 50 ms.

**Postural tests**

After a neuron was identified, the animal was transferred to a setup for postural tests, and stimuli were applied (1) to induce a specific body configuration and (2) to examine postural corrective responses at this configuration. Cats were trained to quietly stand on a platform (covered by a thin rubber pad), and were rewarded by a paste-like food slowly ejected from a feeder. The feeder (plastic tube of 18 mm outer diameter and 6 mm inner diameter) was positioned in front of the cat at a height of 21-23 cm (Fig. 1A). The lateral position of the feeder could vary. First, we positioned the feeder in the sagittal plane of the cat, so that the animal, when licking food, assumed a symmetrical body posture with the head directed forward and aligned with the trunk (Fig. 1A,B). Second, we periodically changed the position of the feeder by moving it horizontally in the frontal plane (Fig. 1F,G). A "trapezoid" trajectory of the feeder displacement versus time, symmetrical in relation to the sagittal plane, was used. The period of feeder movement was 8 s, the distance between the two extreme positions was 14 cm, the transition between these positions lasted for ~1 s, and each stationary position was maintained for ~3 s. At such a speed of feeder displacement (~14 cm/s), all cats were able to easily follow the feeder, without interrupting the licking (see Results). By moving the feeder laterally, we provoked cats to voluntary change the head position and, correspondingly, to change the body configuration. Thus, the animals maintained sequentially two different, highly asymmetrical postures (Fig. 1F,G), strongly differing in a relative loading of the left and right fore limbs (see Results).
To examine the motor and neuronal responses to externally applied perturbations of posture, the platform under the standing cat was periodically tilted in the frontal (roll) plane of the animal (Fig. 1A-C). A sine-like tilt trajectory was used, with a period of 1 s and amplitude of ±15°. This was done both for the symmetrical body configuration, when the head was aligned with the trunk (Fig. 1A-D), and for the asymmetrical body configurations, when the head was turned to the right or to the left (Fig. 1F). All cats were easily engaged in these postural tasks. They tended to compensate for the platform tilts by performing postural corrections (see Results), which allowed them to keep licking food from the feeder. No foot slippage occurred during tilts.

The following values were continuously measured during postural tests by the corresponding sensors, along with neuronal recording: (1) A tilt angle of the platform (Tilt in Fig. 1A,C). (2) A lateral displacement of the feeder (Fd in Fig. 1F). (3) A lateral displacement of the upper point of the anterior part of the trunk in relation to the platform (body displacement, Bd in Fig. 1A-C). (4) To be sure that the position of the head was stabilized and determined by the feeder position, a contact of the tongue and lips with the feeder was continuously monitored by measuring an electrical resistance between the feeder and the animal.

In addition to these values, in selected experiments with each cat, contact forces produced by the feet were measured by means of two force plates positioned either under the fore limbs or under the hind limbs. Each force plate measured separately the normal and tangential (lateral, directed outward) components of the force (F_N and F_T in Fig. 1C). All paws, standing and not standing on the force plates, were level. The body configuration induced by feeder movements and by platform tilts was recorded using Visualeyer 3-D Motion Capture and Analysis System (Phoenix Technologies Inc.) (60 frames/s), and/or a
video camera (30 frames/s). The fur on the lateral aspect of legs and along the vertebral column was shaved, and light-emitting photodiodes (for Visualeyer System), or light-reflecting markers (for video recordings) were attached to the skin projections of the main limb joints (Fig. 1A), as well as along the midline of the dorsal aspect of trunk and head (Fig. 1D,F).

**Experimental protocol**

Each identified pyramidal tract neuron (PTN) was recorded during an experimental session that included two tests:

**Test 1.** The animal was maintaining balance on the sinusoidally tilting platform while its head was oriented towards the centrally positioned feeder. The test included 50-70 tilt cycles.

**Test 2.** The animal was maintaining balance on the sinusoidally tilting platform while its head was oriented towards the feeder which was moving trapezoidally, and repeatedly occurred at the extreme right and left positions. For each of these positions, about 20 platform tilt cycles were performed. The test included 4-5 feeder movement cycles.

Usually during the session, the cat was quietly standing on the platform, and the sagittal plane of its trunk was aligned with the platform axis. In the rare cases, when a cat significantly changed its orientation during a test (for example, by performing a step), the animal was returned to the initial position by an experimenter, and the test was repeated.

In addition to tests 1 and 2 of the present study, during the same experimental session the PTN responses to trapezoid tilts and to a hampering of the voluntary head movement were examined. This study will be reported separately.
Data processing

In both tests 1 and test 2, each of the tilt cycles was divided into 10 equal bins, the peak of the right tilt being taken as the cycle onset. The EMG and force signals were averaged for each bin, and then over all successive cycles of a given test (as in Fig. 2C-F). In test 2, these calculations were performed separately for the left and right stationary positions of the feeder (as in Fig. 3B-E).

For each PTN, a phase histogram of spike activity in the tilt cycle was generated. Then the activity was averaged over all successive cycles of a given test (as in Fig. 4E). In test 2, these calculations were performed separately for the left and right positions of the feeder (as in Fig. 7A). Using the histogram, the portion of the cycle where the activity level exceeded 25% of the difference between the maximal and minimal frequencies in the histogram was defined as a "burst", and the remaining portion, as an "inter-burst period" (as illustrated in Fig. 4E). For the burst and inter-burst periods, average frequencies were calculated. A degree of periodic changes in a PTN activity caused by tilts were characterized by a coefficient of frequency modulation: \( M = 1 - \frac{F_{\text{INTER}}}{F_{\text{BURST}}} \), where \( F_{\text{BURST}} \) and \( F_{\text{INTER}} \) are average frequencies during the burst and inter-burst periods, respectively. The "preferred phase" of the discharge of each neuron in the tilt cycle was assessed using circular statistics. The occurrence of each spike was presented as a vector of a unit length. The angle of this vector was calculated by multiplying the phase of the spike in the cycle (in portions of the cycle) by \( 2\pi \). The preferred phase was then calculated as the phase of the mean vector, i.e., the angle of the vector divided by \( 2\pi \).

The population activity of PTNs was characterized separately for the neurons from the fore limb and the hind limb representations in the motor cortex. First, the bursts of all individual neurons of a given group were plotted against the phase of the tilt cycle to show
their phase distribution (see Fig. 6A,D). Second, a dependence of the cell group activity on the phase of the cycle was characterized by a histogram of the mean frequency of all neurons in the group (see Fig. 6C,F).

All quantitative data in this study are presented as the mean ± SEM. The t-test was used to characterize the statistical significance when comparing different means; the significance level was set at p = 0.05.

**Histological procedures**

At the termination of the experiment, cats were deeply anesthetized with pentobarbital sodium. Several reference lesions were made in the region of motor cortex from which neurons were sampled. Positions of EMG electrodes in the muscles were verified. Cats were then perfused with isotonic saline followed by a 10% Formalin solution. Frozen brain sections of 50 µm thickness were cut in the regions of recording and stimulating electrodes. The tissue was stained for Nissl substance with cresyl violet. Position of stimulation electrodes in the medullar pyramids was verified by observation of electrode track gliosis. Positions of recording tracks in the motor cortex were estimated in relation to the reference lesions.

**RESULTS**

**Postural motor responses**

*Responses to tilts of the platform with symmetrical body configuration*

In all three cats, tilt of the platform (*test 1*) elicited a stereotypic postural response – an extension of the limbs on the side moving down, and flexion on the opposite side (see Fig. 1C, and below). The limb movements made the trunk and head displace laterally in relation to the platform, in the direction opposite to tilt. These compensatory (corrective) body
movements reduced deviation of the trunk and head from the dorsal side-up position. By means of a sensor \textit{Bd} (Fig. 1A-C), we recorded lateral displacements of the upper point of the anterior part of the trunk in relation to the platform. These corrective trunk movements occurred in anti-phase with the platform tilts (Fig. 2A), and their peak-to-peak value, averaged over all \textit{test 1} trials, was 11.3 ± 0.2 cm, 11.6 ± 0.3 cm, and 10.6 ± 0.3 cm for cats # 1, 2, and 3, respectively. The amplitude and phase of corrective trunk movements were practically the same in all cycles of a trial including the first and the last ones (Fig. 2B), suggesting that the postural system equally well compensates for unpredictable (as in the first and last cycles) and predictable (as during regular tilting) postural disturbances.

In order to evaluate the lateral body movements in respect to a fixed coordinate system (Earth), Visualeyer and video recordings of all cats were performed from above. Figure 1D shows (for cat # 1) the body outline and the position of four midline markers at 0° (no tilt), as well as the position of these markers at the maximal tilts to the right (15°R) and to the left (15°L). Arrows indicate positions of a reference marker that was rigidly attached to the platform above its axis, at approximately the height of the top of the cat spine (26 cm). Excursions of this marker show the expected lateral deviations of the dorsal midline, which would occur at 15°R or 15°L tilt provided that the cat would not perform postural corrections ("uncorrected deviations"). The peak-to-peak value of uncorrected deviations was 14.3 cm (cat # 1). Due to postural corrections, the peak-to-peak deviations at the posterior and middle point of the trunk constituted about 5 cm, or 30% of the uncorrected value. In the anterior trunk, the peak-to-peak deviations constituted only about 3 cm, or 20% of the uncorrected value. The lateral deviations were practically absent at the mouth region. This good stabilization of the head in the Earth-related coordinate system allowed the animal to continuously lick food from the feeder despite the tilts of the platform. The presence of
almost continuous contact of the mouth with the feeder was demonstrated by recording electrical resistance between them (Lick in Fig. 3A). Similar results were obtained in all three cats. One can thus conclude that stabilization of the trunk position is rather efficient but it is not sufficient to maintain the mouth stable against the feeder. To reach this goal, the head stabilizing mechanisms must supplement those stabilizing the trunk position.

Corrections of trunk orientation were caused by a specific pattern of limb movements. The principal feature of these movements, observed in all three animals, was an extension at all main limb joints on the side moving down and flexion on the opposite side, as demonstrated by Visualeyer and video recordings of the cats from the side (Fig. 1A). Figure 1E shows the joint angles for two extreme positions, i.e., for 15° ipsilateral and contralateral tilts, measured in cat # 1. One can see that the flexion-extension movements in the joints were relatively small (10° peak-to-peak or less). Because of these movements, the effective length of the limbs on the side tilted down was larger than on the opposite side. Due to the difference in length, the limbs caused a lateral displacement of the trunk and thus maintained the trunk orientation close to the dorsal side-up one.

In contrast to small changes in the joint angles, tilts of the platform caused large changes in the contact forces. As shown in Fig. 2A, the forces under the left and right foot were modulated during the cycle of sinusoidal tilts in anti-phase to each other. Figure 2C,D shows the normal and tangential (lateral) components of the contact forces produced by the right fore and hind limbs, as a function of the phase of the tilt cycle. In both limbs, the normal and tangential forces changed approximately in-phase with tilt, and had their maximum and minimum, respectively, at the maximal tilt to the right (when the limbs were maximally extended, Fig. 1E), and to the left (when the limbs were maximally flexed). The ratio between the maximal and minimal values of the normal force was about 2. The tangential
force for both fore and hind limb was considerably smaller than the normal force. The
tangential force for the right limb changed its sign during a cycle – it was directed laterally
with right tilts and with small left tilts, and medially with larger left tilts.

The EMG responses to sinusoidal tilts in the limb extensor muscles led in phase the
force responses. Figure 2E,F shows the averaged EMG responses in the right *m. triceps*
(elbow extensor) and *m. gastrocnemius* (ankle extensor). The EMGs in both extensors had a
peak approximately 0.2 cycle before the maximal ipsilateral tilt, and a minimum
approximately 0.1 cycle before the maximal contralateral tilt. A similar pattern was observed
when recording the EMG of another ankle extensor, *m. soleus*. This pattern of extensor
activity was consistent across repeated tests and all subjects. The ratio between the maximal
and minimal EMG activity in the tilt cycle was 1.5-2.0. No tilt-related modulation was
observed in the EMG activity of *m. brachialis* (elbow flexor) in two cats, and a weak
modulation – in one cat. This was not because of bad recording conditions since a distinct
step-related EMG activity was recorded from *m. brachialis* in these cats during locomotion.

Effects of lateral turns of the head

In the cat standing on the horizontal, not tilting platform, a change of the feeder
position evoked an almost identical change of the head position, which allowed the animal to
keep eating from the feeder. Similar responses to feeder movement were observed when the
platform was periodically tilted (*test 2*). An almost continuous contact with the feeder, both in
the stationary lateral positions of the feeder and during its movements, can be seen in the *Lick*
trace in Fig. 3A. Figure 1F,G shows that lateral head deviations (induced by changes in the
feeder position) were not caused by lateral steps of the fore limbs - the feet remained on the
same spots of the platform both with the left and the right turns of the head. From Fig. 1F one
can see that lateral deviations of the head were primarily due to lateral bending of the anterior part of vertebral column.

A turn of the head, due to an ipsilateral displacement of the center of mass of the body, caused an additional loading of the ipsilateral fore limb, and unloading of the contralateral one. On the tilting platform (test 2), the force trajectory was correspondingly translated upward when the head was turned ipsilaterally, and downward when the head was turned contralaterally (Fig. 3B). Similar influences of the head position were found in the m. triceps EMG (Fig. 3D). In contrast to the fore limbs, both forces and extensor EMGs in the hind limbs depended rather weakly on the head position (Fig. 3C,E).

As one can see in Fig. 3A, the peak-to-peak compensatory trunk movements (Bd) in test 2 were practically identical for the two head positions. Also, they did not differ from those in test 1 (Fig. 2A). For cat # 2, the three values were 11.8 ± 0.2 cm, 11.9 ± 0.2 cm, and 11.3 ± 0.2 cm, respectively. Similar results were obtained in the two other cats. This finding indicates that the reaction to a given postural disturbance is the same at different body configurations assumed by the animal, suggesting that the gain in postural reactions to tilt does not change with voluntary changes of body configuration.

Responses of cortical neurons

Data were collected from a total of 23 tracks through the fore limb (n=12) and hind limb (n=11) areas in the left motor cortex of three cats. The microelectrode entry points into the cortex (cortical plate openings through which penetrations were made) are combined from all cats and shown in Fig. 4A. Matching between individual maps was accomplished by normalising the length of the cruciate sulcus (Cru) and the distance from it to the post-cruciate dimple (Pcd). Drawings of representative frontal sections through fore (a1) and hind (a2) limb
representations are shown in Fig. 4B; positions of reference lesions made in the areas of recording are indicated by black dots. Histological examination showed that all recordings have been made from area 4, including the activity of 90 identified pyramidal tract neurons (PTNs), 55 of which were recorded from the fore limb and 35 from the hind limb representation. The neuronal recordings were normally stable for the period of testing. There was no change in the amplitude of spikes that could be associated with tilts of the platform.

**Responses to tilts of the platform with symmetrical body configuration**

Figure 4C shows a representative example of PTN responses to sinusoidal platform tilts in the cat standing with its head directed forward (test 1). This neuron was recorded from the fore limb representation of the motor cortex (area 1 in Fig. 4A). The neuron exhibited pronounced modulation of its discharge frequency. The pattern of modulation was similar in all successive tilt cycles, with the peak activity occurring near the mid-cycle. This is well seen in the sequence of five cycles (Fig. 4C) and in the raster representing all sixty cycles of the test (Fig. 4D). Figure 4E shows the histogram of the discharge frequency of the neuron in different phases of the cycle (averaged over sixty cycles), the burst position in the cycle, and the preferred phase of discharge (arrow).

We considered a neuron as responding to tilts (modulated) if its mean frequency within the burst differed statistically from that in between the bursts (t-test). In the overwhelming majority of PTNs with deeper modulation (M > 20 %), the difference was highly significant (p < 0.01). Among the neurons with M < 20 %, however, the significance level was much lower (p = 0.05 or more). In the present study, only the neurons with M > 20 % were considered as responding to tilts (modulated).

Responses to tilts were observed in the overwhelming majority (78/90) of the recorded neurons, including 49/55 (89 %) of PTNs from the fore limb representation, and
29/35 (83%) of PTNs from the hind limb representation. These 78 modulated neurons will be considered below.

Figure 5 shows some characteristics of the populations of the fore and hind limb PTNs. Most PTNs fired at rest, i.e., when the animal was standing on the horizontal platform before the onset of tilting. The firing frequency at rest, averaged separately over the fore and hind limb populations, was 18.8 ± 1.5 imp/s (mean ± SEM) and 15.1 ± 1.5 imp/s, respectively. The mean frequency in the burst, averaged over the fore and hind limb populations, was 23.3 ± 2.2 imp/s and 22.8 ± 2.6 imp/s, respectively. The mean frequency in between the bursts for the two populations was 11.1 ± 1.4 and 8.9 ± 1.4 imp/s, respectively. The coefficient of frequency modulation (M) was 51 ± 3 % and 63 ± 4 %, respectively. For the two populations, the discharge frequencies, averaged over the tilt cycle, were 18.9 ± 1.8 imp/s and 17.3 ± 2.1 imp/s. These values were very close to those of resting discharge. This finding indicates that the tilt-related modulation was caused by an approximately equal increase of the activity in one part of the tilt cycle and a decrease in the other. From Fig. 5 one can see that the population characteristics of the fore and hind limb PTNs were similar.

Figures 6A and 6D show distribution of the phases of activity (burst positions) over the tilt cycle for the PTNs from the fore and hind limb representations, respectively. For each neuron, the preferred phase of its activity is indicated (diamonds). The preferred phases in individual PTNs were rather stable. The standard deviation of the preferred phase in successive tilt cycles, averaged over a population of PTNs, was 0.10 of the cycle; the SEM values in individual PTNs ranged from 0.005 to 0.02 of the cycle.

Most neurons fired one burst per cycle. Phases of activity of different neurons were distributed over the cycle. For the fore limb PTNs this distribution was almost even: 25 out of 49 PTNs (51%) had their preferred phase in the first half of the cycle (phases 0 to 0.5),
and 24 PTNs (49%) - in the second half (phases 0.5 to 1.0) (Fig. 6B). In individual animals (#1-3) the number of PTNs with preferred phases in the first and second halves of the cycle were 3/3, 11/9, and 11/12, respectively. A constancy of the population activity over the cycle was also reflected in the mean frequency histogram (Fig. 6C). The phase distribution of the hind limb PTNs was significantly different from that of fore limb PTNs (p < 0.05, χ²-test) in that it was uneven: 8 out of 29 PTNs (28%) had their preferred phase in the first half of the cycle, and 21 PTNs (72%) - in the second half (Fig. 6E). In individual animals (#1-3) the number of PTNs in the first and second halves of the cycle was 2/2, 1/5, and 5/14, respectively. Correspondingly, the population activity of the hind limb PTNs in the first half of the cycle was lower than in the second half (Fig. 6F).

Relation between neuronal responses to tilts and to receptive field stimulation

The somatosensory receptive fields were tested in a total of 44 PTNs (23 from the fore limb area, and 21 from the hind limb area). Thirty-seven PTNs out of 44 (84%) had excitatory receptive fields in the right fore or hind limb, 6 (14%) cells did not have any receptive fields, and one cell was inhibited by passive manipulation of the forelimb. Most of the excitatory receptive fields were “deep”: the cells responded to palpation of muscles or movements of joints, or both, but not to stimulation of fur alone (there was only one such cell). A summary of a number of PTNs with receptive fields on different segments of the fore and hind limb are given in Table 1. In 17 responding neurons (39% of the total number), responses had a directional preference: 8 neurons (18%) preferred flexion to extension, 6 neurons (14%) preferred extension to flexion. One neuron (2%) was activated not by flexion-extension but by large abduction movement of the limb, and 2 neurons (4%) - by large adduction movement.
We did not find any simple correlation between neuronal responses to somatosensory stimulation in resting position and their postural responses. Out of seven neurons responding to passive flexion in elbow, or hip, or whole limb, 3 neurons had their preferred phases in the first half of the tilt cycle (i.e., during flexion of the limb), and 4 neurons had the preferred phase in the second half (i.e., during limb extension). Out of six neurons responding to passive extension in elbow, or hip, or ankle, or toe joint, 1 neuron had the preferred phase in the first half of the tilt cycle (i.e., during flexion of the limb), and 5 neurons had the preferred phase in the second half (i.e., during limb extension). Similarly, all 3 neurons that were activated by large abduction-adduction movements of the limb were well modulated in postural tests despite such movements were not large. Moreover, 2 neurons, that were activated by abduction, had a preferred phase in the second half of the tilt cycle (when an adduction of the limb did occur), and 1 neuron responding to passive adduction had a preferred phase in the first half of the tilt cycle (when an abduction did occur). Finally, no peripheral receptive fields were found in 6 neurons (including 4 neurons from the fore limb and 2 neurons from the hind limb area); nevertheless, all these neurons were profoundly modulated in postural tests. Also, one neuron from the fore limb area was inhibited by somatosensory stimulation but responded well to tilts.

Thus, one can conclude that, in a considerable part of PTNs, the somatosensory signals that are received by these neurons in a quiescent animal cannot be responsible for modulation of their activity during active stabilization of posture.

Effects of lateral turns of the head

Lateral displacements of the head evoked a considerable loading of the ipsilateral fore limb and unloading of the contralateral one, whereas the hind limbs were almost unaffected
We examined responses to sinusoidal tilts of the platform in 41 fore limb PTNs and in 25 hind limb PTNs under two conditions – right and left positions of the head (test 2). Figure 7A shows a representative example of the forelimb PTN responses to tilts averaged separately for the right and left head positions. In this neuron, the maximal frequency of discharge during tilts was approximately 30% higher at the ipsilateral (left) head position than at the contralateral (right) one, whereas the phase of the maximum was the same at both head positions. A histogram in Fig. 7B shows a distribution of differences between the burst frequencies at the right and the left head positions for all tested fore limb PTNs. (Grey bars indicate the neurons with statistically significant difference in firing frequency.) An absolute value of the change in burst frequency in this group of PTNs was 6.5 ± 0.8 Hz (mean ± SEM), that is 28% of the mean burst frequency in the population of fore limb PTNs (23.3 Hz). The distribution was nearly symmetrical, that is approximately the same number of neurons from the left motor cortex (the right fore limb representation) increased and decreased their tilt-related activity with a turn of the head to the right or to the left.

The histogram in Fig. 7C shows a distribution of differences between the preferred phases of the tilt-related discharges at the right and left head positions for all tested fore limb PTNs. In most neurons (30/41, or 73%), the difference constituted less than 10% of the cycle. For this group of PTNs, an absolute value of the change in phase was 0.10 ± 0.02 (mean ± SEM).

For the hind limb PTNs, the corresponding histograms are presented in Figs. 7D and 7E. In this group of PTNs, an absolute value of the change in burst frequency between the two head positions was 4.5 ± 0.7 Hz, that is slightly less than in the fore limb PTNs (6.5 ± 0.8 Hz); the difference was not statistically significant, however. An absolute value of the change in phase for this group of PTNs was 0.06 ± 0.01. Thus, head turns were well reflected in the
burst frequency of the hind limb PTNs despite these turns caused only small changes of the hind limb motor pattern (Fig. 3C,E).

How do the above changes of the responses to tilt in the fore limb PTNs correlate with the changes in loading the limb due to the asymmetrical body configuration? To address this issue, we divided all tested fore limb PTNs into two groups, activated during loading or during unloading of the right fore limb in the tilt cycle. In group 1, we have included the neurons whose preferred phase was in the range from 0.75 to 1 and from 0 to 0.25, when the platform was tilted to the right and the contact forces produced by the right fore limb were larger (Fig. 2B). In group 2, we have included the neurons with the preferred phase ranging from 0.25 to 0.75, when the platform was tilted to the left and the contact forces were smaller (Fig. 2B). Histograms in Fig. 8A,B show distributions of differences between the burst frequencies with the right and the left head positions, for the two groups of PTNs. (Grey bars indicate the neurons with statistically significant difference in firing frequency.) For each of the two groups, the distribution was nearly symmetrical. Among 16 group 1 PTNs, 9 cells increased and 7 cells decreased their activity with the change of the head position from the right to the left; and among 25 group 2 PTNs these numbers were 12 and 13, respectively. Thus, in about a half of the neurons in each group, the activity was similarly related to loading (unloading) of the limb under both conditions, i.e., when loading was caused by the platform tilt or by the head turn. In another half of the neurons in each group, the activity increased with limb loading under one condition, and with unloading under the other condition.

A similar result was obtained when we divided the same population of fore limb PTNs in accordance with their relation to extensor EMG. In group 3 we included the PTNs with their preferred phase ranging from 0.5 to 1, when EMG was larger; in group 4 PTNs the
preferred phase ranged from 0 to 0.5, when EMG was smaller (Fig. 3E). From the histograms (Fig. 8C,D) one can see that in about a half of the neurons in each group, the activity was similarly related to the EMG level under both conditions, i.e., when an increase of EMG was caused by the platform tilt or by the head turn. In another half of the neurons in each group, the activity increased with an EMG increase under one condition, and with an EMG decrease under the other condition.

DISCUSSION

Maintenance of balance on the tilting platform

The basic body posture in standing quadrupeds, with their dorsal side up, is maintained by a closed-loop control system. When sensory inputs are signaling that the posture is deviated from the desired one, corrective motor responses are generated; they are aimed at restoration of the initial posture (for review see Horak and Macpherson 1995; Massion 1998). Our recent experiments on rabbits suggest that the dorsal side-up orientation of the fore- and hindquarters are maintained by relatively autonomous nervous mechanisms (Beloozerova et al. 2003c).

In order to elicit postural corrections, in the present study we employed the method of tilting the supporting platform (Deliagina et al. 2000; Beloozerova et al. 2003b,c). The postural task was complicated due to a requirement to stabilize the head against a target (feeder). To solve this task, cats first tended to stabilize their trunk position by extending the limbs on the side tilting down and flexing the limbs on the opposite side (Fig. 1C,E). This stabilization was rather efficient, but not sufficient to maintain the mouth against the feeder. To reach this goal, the head stabilizing mechanisms supplemented those stabilizing the trunk position (Fig. 1D).
Postural motor responses to platform tilts included an increase of the contact forces and of the activity of limb extensor muscles on the side moving down, and a decrease of these values on the opposite side. During the tilt cycle, both normal forces and extensor EMGs changed considerably but did not fall to zero (Fig. 2). Thus, maintenance of balance on the tilting platform is primarily based on a re-distribution of activity between the anti-gravity (extensor) muscles of the left and right limbs. An increase of extensor activity on the side moving down leads to the limb extension, and a decrease of extensor activity on the opposite side leads to the limb flexion under the effect of the body weight. The overall muscular activity pattern in each limb, therefore, can be roughly approximated as alternating periods of high and low levels of extensor activity. In the present study, no tilt-related modulation (or a weak modulation) was observed in the EMG activity of *m. brachialis* (elbow flexor). However, in a similar study on rabbits it was shown that some limb flexors could well respond to tilts (Deliagina et al. 2000; Beloozerova et al. 2003c).

Cats standing on the tilting platform usually adopt a posture with the distance between the hind limb feet 1.5-2 times larger than between the fore limb feet (Fig. 1B,C). One can suggest that, due to a wider base of support, the hind limbs have a larger contribution to the maintenance of equilibrium in the frontal (roll) plane.

Experiments on rats, rabbits and cats presented evidences that the closed-loop system, responsible for maintenance of the basic (dorsal side-up) body posture, is driven primarily by signals from limb mechanoreceptors (Beloozerova et al. 2003c; Deliagina et al. 2000; Inglis and Macpherson 1995; Stapley et al. 2002). An EMG phase lead in relation to the force (Fig. 2) suggests that the higher order components (e.g. velocity) of sensory signals can take part in driving the motor output.
In periodical postural tasks, the control system can, in principle, anticipate forthcoming postural disturbances and operate as a feed-forward system. In the present study, however, it was shown that the amplitude and phase of corrective trunk movements were practically the same in all cycles of a trial including the first and the last ones (Fig. 2B). This finding means that the system equally well compensated for unpredictable (as in the first and last cycles) and predictable (as during regular tilting) postural disturbances. Also, postural responses were equally well pronounced with regular (sinusoidal), with less regular (trapezoid), or irregular (combination of sinusoidal and trapezoid) postural stimuli, as shown in our recent experiments on rabbits (Beloozerova et al. 2003c).

By changing the feeder position, we motivated cats to maintain equilibrium at different body configurations – with the head directed forward, or turned voluntary to the right or to the left (Fig. 1F,G). A turn of the head caused an ipsilateral displacement of the center of mass, an additional loading of the ipsilateral fore limb, and unloading of the contralateral one, as well as the corresponding asymmetry in extensor activity (Fig. 3). The system for trunk stabilization produced postural corrections of the same magnitude at any head position (Figs. 2A and 3A). However, the motor patterns under these three conditions were different, especially when comparing the right and left head positions (Fig. 3B,D). One can suggest that the command for a voluntary turn of the head is accompanied by the commands addressed to the postural system (Horak and Macpherson 1997; Massion 1994; Massion and Dufosse 1988). One of these commands elicits anticipatory postural adjustments to compensate for destabilizing effects of the lateral displacement of the center of mass during head movements. This issue was not addressed in the present study. Another command affects the set-point of the closed-loop postural mechanisms and thus modifies the pattern of responses to externally applied postural disturbances.
Posture-related activity of pyramidal tract neurons

The main finding of this study is that the activity of PTNs from the fore and hind limb representations of the motor cortex strongly correlates with the tilts of the platform and with the corrective postural responses caused by these tilts. Since motor functions of the motor cortex are well established (see e.g. Canedo 1997), one can suggest that, by sending tilt-related commands to the medulla and to the spinal cord via PTNs, the motor cortex can phasically affect the corresponding motor centers and, therefore, can contribute to the control of posture. Under similar experimental conditions but in a different species (rabbit), a tilt-related modulation was observed in the layer V corticofugal neurons (presumably including PTNs) from the limb representation of the motor cortex (Beloozerova et al. 2003b). Thus, in both species, the activity of motor cortex strongly correlates with a highly automatic, involuntary motor activity – the maintenance of posture. The magnitude of modulation of PTNs activity in the postural task was comparable to that observed during locomotion (Beloozerova and Sirota 1988, 1993; Drew 1988, 1993; Beloozerova et al. 2003a).

A difference was found between the patterns of modulation of the fore limb and the hind limb populations of PTNs. In the fore limb population, the preferred phases of activity of individual PTNs were almost evenly distributed over the tilt cycle (Fig. 6A,B), and a modulation of extensor activity (with a peak in the second half of the cycle, Fig. 2) was not reflected in the PTN population activity. By contrast, the majority of hind limb PTNs had their preferred phases in the second half of the cycle, during the period of increased extensor activity (Fig. 6D,E). This difference could be attributed to a different role of the fore and hind limbs in the maintenance of lateral stability. One could suggest that the hind limbs, with their wide base of support (Fig. 1B,C), perform the main, robust contribution to the compensation
for lateral tilts, whereas the role of fore limbs would be the fine adjustments of posture, that requires cortical control in all phases of the tilt cycle.

The other major finding of this study is that voluntary modifications of the stabilized body posture are well reflected in the activity of PTNs. Deviation of the head to the right and to the left caused substantial changes in the fore limb contact forces and extensor EMGs (Fig. 3), as well as a 28% change in the mean burst frequency of the population of the fore limb PTNs. This finding supports the hypothesis advanced by Ioffe et al. (1986) about involvement of the motor cortex in voluntary modifications of the basic body posture in quadrupeds.

There are a number of evidences that corrective postural responses underlying trunk stabilization are driven primarily by the signals from limb mechanoreceptors (Beloozerova et al. 2003c; Deliagina et al. 2000; Inglis and Macpherson 1995; Stapley et al. 2002). One can suggest that the tilt-related cortical activity is also driven by this input. The broad range of phase relationships between the PTNs activity and the tilt suggests that the motor cortex is responding to sensory inputs from various mechanoreceptors that are activated when the limbs flex and extend, as well as when the limbs are loaded and unloaded. Our attempt to estimate the source of tilt-related modulation of PTNs by studying their receptive fields has shown, however, that somatosensory signals, which are received by cortical neurons in a quiescent animal, could be responsible for modulation of PTNs activity during posture stabilization only in a part of the neurons, whereas in other PTNs the modulation cannot be explained by a direct action of this input. A similar result was obtained earlier in our experiments on rabbits (Beloozerova et al. 2003b). Presumably, signals from limb mechanoreceptors are processed in the spinal and brain stem postural networks before they reach the motor cortex. “Efference copy” signals can also play a role in the modulation of
descending postural commands, as was earlier demonstrated for the descending locomotor commands (see e.g. Orlovsky et al. 1999).

There is a longstanding controversy about what movement variables are encoded in the activity of motor cortex neurons. Some studies suggest that intrinsic parameters (forces, muscle activities) are represented (see e.g. Evarts 1968; Smith et al. 1975; Kalaska and Crammond 1992), whereas other studies suggest that extrinsic parameters (position, movement direction) are encoded (see e.g. Georgopoulos et al. 1982). Finally, still other data suggest that the activity of cortical neurons can represent a combination of the two groups of variables (e.g. Thach 1978; Sergio and Kalaska 2003; Kakei et al. 2003).

The postural task employed in the present study was mainly a "force task" in the sense that tilts of the platform caused considerable changes in the extensor activity and in the force produced by the limb, but only slight changes in the joint angles and limb position. One could therefore expect a close (positive or negative) correlation between the PTN activity and the forces and/or the extensor EMGs. This hypothesis was only partly supported in the experiments with additional loading/unloading of the fore limbs caused by turns of the head (Fig. 3). We have found that a half of the fore limb PTNs were similarly related to loading (unloading) of the limb under the two conditions, i.e., when loading was caused by tilt and by turn of the head (Fig. 8A,B). This sub-population of fore limb PTNs can be assigned a function of force control. Another half of the fore limb PTNs increased their activity with loading under one condition, and with unloading under the other condition (Fig. 8A,B). This sub-population seems to perform functions other than force control. A similar heterogeneity of the fore limb PTNs was observed in their relation to the extensor EMG (Fig. 8C,D): about a half of PTNs correlated with the EMG, and the other half did not. The hind limb PTNs also
well responded to head turns (Fig. 7D,E) despite these turns caused only small changes of the hind limb motor pattern (Fig. 3C,E).

The absence of any simple correlation between the activity of many cortical neurons on one hand, and the variables characterizing the motor pattern on the other hand, is a common finding in many studies on the motor cortex (see e.g. Drew 1993; Kakei 2003). It seems likely that these neurons do not directly participate in the production of motor output. In the postural system, their possible function may be to contribute to the activation and reconfiguration of the brain stem-spinal postural networks. Such a function seems to be necessary when one considers the enormous variety of posture modifications accessible for the animals and humans (Horak and Macpherson 1995). In the present study we have found that most PTNs substantially changed their activity with voluntary modifications of the body configuration (Fig. 7).

Among other possible functions, not related directly to the production of motor output, the PTNs could participate in the modulation of afferent signals transmission to different motor centers. Finally, the tilt-related modulation of PTNs could be important for coordination of posture and voluntary limb movement. In this respect, there could be a parallel between the postural task and locomotion. The step-related modulation of PTNs during regular locomotion largely determines the phase of their response during voluntary gate modifications (Drew 1988, 1993; Beloozerova and Sirota, 1988, 1993); similarly, the tilt-related modulation of PTNs may determine the phase of their response during voluntary limb movement.

In conclusion, the present study has demonstrated that (1) cortical output mediated by PTNs is closely related to a highly automatic motor activity, the maintenance of the body posture, and (2) voluntary modifications of posture are also well reflected in the PTNs
activity. It was also found that the activity of individual PTNs correlates with different variables of motor output, suggesting their different functional role.

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LEGENDS TO FIGURES

Figure 1. Experimental design. A-D: experimental design for testing postural and neuronal responses to tilts. A cat with implanted electrodes was standing on a platform (P) that could be tilted in the frontal plane. Cat was continuously licking food from the feeder (feeder position is indicated by black bars in A,D,F and by black circles in B,C,G). In A, the body outline (view from the left side) is shown for the horizontal position of the platform, together with the stick diagrams for the fore and hind limbs. (Abbreviations: S – shoulder, E – elbow, H – hip, K – knee, A – ankle). In B,C, the body outline (view from the front) is shown for two positions of the platform, horizontal and 15°L, respectively. Postural corrections were characterized by measuring a lateral displacement of the upper point of the anterior part of the trunk in relation to the platform (body displacement, Bd in A-C). Contact forces produced by the limbs were measured by means of two force plates positioned either under the fore limbs or under the hind limbs (not shown). Each force plate measured separately the normal and tangential (lateral) components of the force (F_N and F_T in C). D: postural responses at 3 points along the body midline and at the mouth. The body outline (view from above) is shown for zero tilt (0°). The position of the body longitudinal midline is shown for 0°, 15°L, and 15°R tilts (solid lines). A reference marker was rigidly attached to the platform above its axis at the height of the top of the spine. Excursions of this marker (shown by arrows and interrupted lines) indicate the deviations of the body back midline that would occur without postural corrections. E: angles in different joints of the left limbs at the maximal (15°L and 15°R) platform tilts, measured in one representative experiment. F,G: experimental design for induction of different body configurations. The feeder was sequentially positioned at the points 7 cm to the right and 7 cm to the left from the sagittal plane (Fd, feeder displacement).
When the feeder moved, the cat followed the feeder with its mouth and then maintained one of the two different, highly asymmetrical postures. The body outline (view from above in $F$ and from the front in $G$) is shown for these two body configurations, together (in $F$) with the position of the body midline (the same markers as in $D$). Shaded circles in $D$ and $F$ indicate the feet positions to emphasize that these positions did not change during tilts and during changes of the body configuration.

**Figure 2.** Postural motor responses to tilts with symmetrical body configuration. $A$: periodic tilts of the platform (Tilt) caused modulation of the normal ($F_N$) and tangential ($F_T$) contact forces produced by the fore limbs, as well as corrective lateral body displacements (Bd) in anti-phase to tilts. Shaded column highlights one of the tilt cycles to facilitate comparison between curves. $B$: corrective lateral body displacements caused by a series of sinusoidal tilts. $C,D$: representative averaged forces, produced by the right fore and hind limbs, as a function of the phase of the tilt cycle (filled circles – normal force, $F_N$; open circles – tangential force, $F_T$). $E,F$: representative averaged EMG responses in the extensor muscles of the right fore limb (Tric R) and hind limb (Gast R) as a function of the phase of the tilt cycle. The EMGs are normalized to their peak values. In $C-F$, the peak right tilt was taken as the cycle onset.

**Figure 3.** Effect of the head position on the postural motor responses to tilts. $A$: a cat was licking food from the feeder whose position alternated between $\pm 7$ cm from the sagittal plane (Fd). These stationary positions are indicated by arrows on the Fd trace. The cat followed the feeder with its mouth, as shown by the mouth contact sensor (Lick, contact - up). Periodic tilts of the platform caused modulation of the EMGs in extensor muscles of the left and right
fore limbs (Tric L and Tric R), as well as corrective lateral body displacements (Bd) in anti-phase to tilts. B,C: representative averaged forces, produced by the right fore and hind limbs in one cat, as a function of the phase of the tilt cycle. Averaging was performed separately for the right (filled circles) and left (open circles) head positions. D,E: representative averaged EMG responses in the extensor muscles of the right fore limb (Tric R) and hind limb (Gast R) as a function of the phase of the tilt cycle. Averaging over 20-60 tilt cycles was performed separately for the right and left head positions. The EMGs are normalized to the peak values of the responses at the right feeder position. Designations as in Fig. 2.

**Figure 4.** Areas of recordings (A,B) and a representative example of PTN responses to tilts with symmetrical body configuration (C-E). A, Areas of recording within representations of the fore and hind limb in the left motor cortex (1 and 2, respectively; Cru – cruciate sulcus, Pcd – post-cruciate dimple). The microelectrode entry points into the cortex (cortical plate openings through which penetrations were made) are combined from all cats and shown by black circles. In A, a1 and a2 indicate approximate positions at which sections (shown in B) were taken. B: drawings of representative frontal sections through the fore limb (a1) and hind limb (a2) representations. Reference lesions in the areas of recordings are shown by black dots. C: a PTN from the fore limb area of the motor cortex was recorded along with platform tilts (Tilt), body postural corrections (Bd), EMGs of right and left m. triceps (Tric R, Tric L), and signals from the mouth-feeder contact sensor (Lick). D,E: activity of the same neuron is presented as a raster of 60 successive tilt cycles (D), and as a histogram (E). In E, the preferred phase of discharge (arrow) and the burst position are indicated.
**Figure 5.** Population characteristics of fore limb and hind limb PTNs responses to sinusoidal tilts with symmetrical body configuration. There are presented: Rest – mean discharge frequency when standing without postural disturbances, Tilt – mean frequency in the tilt cycle, Burst – mean frequency in the burst, Interburst – mean frequency between the bursts, Modul – coefficient of frequency modulation: \( M = 1 \frac{F_{\text{INTER}}}{F_{\text{BURST}}} \).

**Figure 6.** Phase characteristics of PTNs from the fore limb (A-C) and the hind limb (D-F) representations. A,D: phase distribution of bursts of individual neurons in the tilt cycle, with the preferred phase indicated (diamonds). The burst of activity of each neuron is presented in black only one time in the cycle. The neurons are rank ordered according to their preferred phase. B,E: percent of neurons with the preferred phase in the first or the second half of the cycle. C,F: a histogram of the mean frequency of neurons in different phases of the tilt cycle.

**Figure 7.** Effect of head position upon PTNs responses to tilts. A: a representative example of responses to tilts in a fore limb PTN; the responses were averaged separately for the right and left head positions. B: a histogram of the algebraic differences between the burst frequencies at the right and left head positions (right minus left) for all tested fore limb PTNs. C: a histogram of the algebraic differences between the preferred phases at the right and left head positions (right minus left) for all tested fore limb PTNs. D: a histogram of the algebraic differences between the burst frequencies at the right and left head positions (right minus left) for all tested hind limb PTNs. E: a histogram of the algebraic differences between the preferred phases at the right and left head positions (right minus left) for all tested hind limb PTNs. In B-E, gray bars indicate the neurons with statistically significant difference in firing frequency; empty bars indicate the neurons in which the difference was not significant.
Figure 8. Correlation between PTN responses to tilts and to head turns. A-D: histograms of the algebraic differences between the burst frequencies at the right and left head positions (right minus left) for 4 groups of PTNs differing in their preferred phase. Numbers of neurons that increased or decreased their frequency are indicated in rectangles. (See legend to Fig. 7.)
Fig. 2
Fig. 3
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Fig. 6
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Fig. 8