

Interlimb postural coordination in the standing cat

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The dorsal-side-up body posture in standing quadrupeds is maintained by coordinated activity of four limbs. We studied this coordination in the cat standing on the platform periodically tilted in the frontal plane. By suspending different body parts, we unloaded one, two, or three limbs. The activity of selected extensor muscles and the contact forces under the limbs were recorded. With all four limbs on the platform, extensors of the fore- and hindlimbs increased their activity in parallel during ipsilateral downward tilt. With two forelimbs on the platform, this muscular pattern persisted in the forelimbs and in the suspended hindlimbs. With two hindlimbs on the platform, the muscular pattern persisted only in the hindlimbs, but not in the suspended forelimbs. These results suggest that coordination between the two girdles is based primarily on the influences of the forelimbs upon the hindlimbs. However, these influences do not necessarily determine the responses to tilt in the hindlimbs. This was demonstrated by antiphase tilting of the fore- and hindquarters. Under these conditions, the extensors of the fore- and hindlimbs appeared uncoupled and modulated in antiphase, suggesting an independent control of posture in the fore- and hindquarters. With only one limb supporting the shoulder or hip girdle, a muscular pattern with normal phasing was observed in both limbs of that girdle. This finding suggests that reflex mechanisms of an individual limb generate only a part of postural corrections; another part is produced on the basis of crossed influences.

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The basic, dorsal-side-up body posture in standing quadrupeds is maintained by the postural system. This closed-loop control system performs a highly automatic, non-voluntary motor function (Magnus, 1924; Bard & Macht, 1958). The system operates on the basis of sensory feedback signals and generates a corrective motor response with any perturbation of posture (for review, see Horak & Macpherson, 1996; Macpherson *et al.* 1997*b*; Massion, 1998; Deliagina & Orlovsky, 2002). The information on the current body posture and its perturbations is delivered primarily by limb mechanoreceptors (Inglis & Macpherson, 1995; Deliagina *et al.* 2000; Stapley *et al.* 2002; Beloozerova *et al.* 2003*b*), and to a small extent by the vestibular and visual systems (Maioli & Poppele, 1991).

In standing quadrupeds, each of the four limbs participates in supporting the body weight. When the animal's posture is perturbed, each of the limbs contributes to the generation of a corrective motor response (Lacquaniti *et al.* 1984; Macpherson, 1988*a,b*; Jacobs & Macpherson, 1996; Macpherson *et al.* 1997*a*; Beloozerova *et al.* 2003*b*). To join the efforts of individual limbs, they must be accurately coordinated. One possible means for coordination was proposed by the hypothesis of

a single regulated variable (see, e.g. Ghez, 1991; Massion, 1994; Massion *et al.* 1997). According to this idea, sensory information from individual limbs is processed and integrated to obtain a generalized characteristic of body posture, like a position of the centre of mass or a direction of the body axis. With a deviation of this regulated variable from its desired value, specific commands are sent to individual limbs to elicit their coordinated movements.

In contrast to the concept of one regulated variable, Beloozerova *et al.* (2003*b*) suggested that the postural system in quadrupeds consists of two subsystems, stabilizing the dorsal-side-up orientation of the fore- and hindquarters, respectively. Coordination of activities of the two subsystems is achieved due to the interactions of their control mechanisms. A similar functional organization was earlier suggested for the locomotor system (von Holst, 1938; Shik & Orlovsky, 1965; Orlovsky *et al.* 1999).

In the present study, we investigated interlimb coordination in the standing cat, and used the previously developed technique for perturbing the posture (Beloozerova *et al.* 2005). The cat was standing on the platform, and maintained equilibrium when the platform was periodically tilted in the frontal plane.

Responses to tilts included extension of the fore- and hindlimbs on the side tilting downward, and flexion of the limbs on the opposite side. By suspending a part of the body, we unloaded one, two, or three limbs and thus excluded them from the maintenance of body posture. By recording responses to tilt in such a 'reduced' postural system, we have characterized (i) the role of reflex mechanisms of individual limbs in the generation of postural corrections; (ii) postural capacities of the shoulder and hip girdles; and (iii) the role of mutual influences between different components of the system for interlimb coordination. Results of this study support the hypothesis of independent control of posture of the anterior and posterior parts of the trunk.

Methods

Experiments were performed on three adult cats. Most of the methods have been described (Beloozerova *et al.* 2003a, 2005) and will be reported briefly here. All experiments were conducted with the approval of the Barrow Neurological Institute Animal Care and Use Committee.

Implantation of EMG electrodes was performed under isoflurane anaesthesia using aseptic procedures. Bipolar electrodes (flexible Teflon-insulated stainless-steel wires) were implanted bilaterally into the elbow extensor triceps muscle (Tric), and into the knee extensor vastus muscle (Vast). The wires were positioned under the skin and soldered to the connector fixed on the skull.

A description of the basic arrangement for postural tests has been provided previously (Beloozerova *et al.* 2003a, 2005). The cats were trained to quietly stand on a split platform that consisted of two parts – the F-platform under the forelimbs and the H-platform under the hindlimbs (Fig. 1A and B). The cat was rewarded by a paste-like food ejected from the 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 and B). To examine the motor responses to externally applied perturbations of posture, the platforms under the cat were periodically tilted in the frontal (roll) plane of the animal. A sine-like tilt trajectory was used, with a period of 1 s and amplitude of ± 15 deg; the effectiveness of such stimulation was shown earlier (Beloozerova *et al.* 2005). The F- and H-platforms were tilted either in-phase (Fig. 1A and C), or in antiphase (Fig. 1D and E). All cats were easily engaged in this postural task and maintained equilibrium during tilts. They tended to compensate for the platform tilts by performing lateral displacements of the body in relation to the supporting platform, which allowed them to hold the mouth against the feeder and to keep licking food despite the platform tilts.

The following tests were carried out. Tests 1–3 and 5–8 were performed with coupled (tilted in-phase) F-platform

and H-platform, which thus constituted a single platform. These tests differed in the composition of the group of limbs supporting the body. Test 4 was performed on the two platforms tilted in antiphase.

Test 1 (control)

The cat was standing on the non-split platform with all four limbs, and compensated for the platform tilts producing corrective movements by all of the limbs (Fig. 1A–C).

In tests 2–4, we examined postural functions of a single (shoulder or hip) girdle, as well as interactions between the girdles.

Test 2

The posterior part of the trunk was suspended in a hammock and slightly lifted, so that the hindlimbs were hanging freely and did not touch the platform. In this test, postural function, i.e. compensation for the platform tilts was performed by only the forelimbs (Fig. 1F).

Test 3

The anterior part of the trunk was suspended in a hammock and slightly lifted, so that the forelimbs were hanging freely and did not touch the platform. In this test, postural function was performed by only the hindlimbs (Fig. 1G).

Test 4

In this test, the two platforms were uncoupled, and the cat was standing with its forelimbs on the F-platform, and with its hindlimbs on the H-platform. The platforms were tilted in antiphase (Fig. 1D and E).

In tests 5–8, we examined postural functions of a single (fore or hind) limb, as well as interactions of the limbs within a girdle. For this purpose, one of the limbs of the shoulder or hip girdle was lifted, while the other limb remained on the platform. Two methods for lifting the limb were used, passive and active. With passive lifting, the experimenter took the limb by hand (in the elbow or ankle region), lifted it for a few centimetres, and kept at this position during the test (about 10 s). With this method one could not exclude, however, that the lifted limb was still loaded by a small part of the body weight, and thus slightly 'assisted' the supporting limb. This problem was absent when using the method of active lifting. When standing on four limbs, the cats easily lifted one of them in response to tactile stimulation of its foot.

Test 5

One of the forelimbs was lifted (Fig. 1H), and postural corrective movements were performed by one forelimb and two hindlimbs.

Test 6

One of the hind limbs was lifted (Fig. 1I), and postural corrective movements were performed by two forelimbs and one hindlimb.

Test 7

Test 7 was a combination of tests 2 and 5 (Fig. 1F and H). The hindquarters of the cat were suspended in the

hammock. In addition, one of the forelimbs was lifted. In this test, postural corrective movements were performed by only one limb.

Test 8

Test 8 was a combination of tests 3 and 6 (Fig. 1G and I). The forequarters of the cat were suspended in the hammock. In addition, one of the hindlimbs was lifted. In this test, postural corrective movements were performed by only one limb.

The following values were recorded during postural tests: (i) two mechanical sensors measured the tilt angles of the F-platform and H-platform (Tilt F and Tilt H in Fig. 1A); (ii) in the previous study (Beloozerova *et al.* 2005)

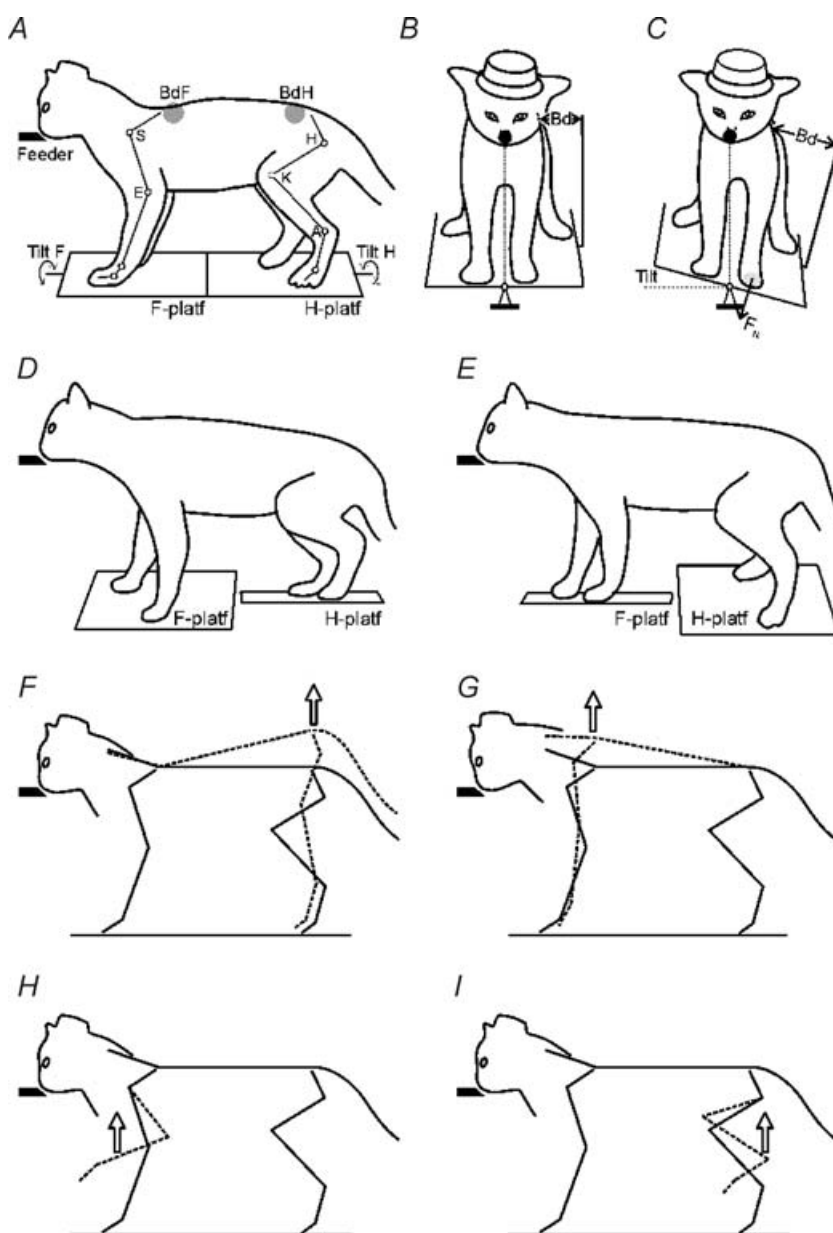


Figure 1. Experimental design

A–E, a cat was standing on two platforms, one under the forelimbs (F-platf) and the other under the hindlimbs (H-platf). The platforms were tilted in the frontal plane. The cat was continuously licking food from the feeder (feeder position is indicated by black bars in the side view and by black circles in the front view). A–C, in-phase tilts of the two platforms. In A, the body outline (view from the left side) is shown for the horizontal position of the platforms, together with the stick diagrams for the fore- and hindlimbs (abbreviations: S, shoulder; E, elbow; H, hip; K, knee; A, ankle). In B and C, the body outline (view from the front) is shown for two positions of the platform, horizontal and 15 deg left, respectively. Postural corrections were characterized by measuring a lateral displacement of the upper point of the fore and hind parts of the trunk in relation to the corresponding platform (body displacements, BdF and BdH, in A–C). The normal component of the contact force produced by each limb was measured by means of the force plate (shown for only the left forelimb, F_N in C). D and E, antiphase tilts of the two platforms. The body outline is shown for two extreme positions of the platforms. F–I, experimental design for reducing the number of limbs standing on the platform. F, lifting the hindquarters; G, lifting the forequarters; H, lifting one forelimb; I, lifting one hindlimb.

it was shown that lateral displacements of the upper point of the trunk in relation to the platform well characterized the efficacy of stabilization of the trunk position. In the present study, the lateral displacements were measured separately for the fore and hind parts of the trunk by means of mechanical sensors (BdF and BdH in Fig. 1A–C); (iii) contact forces produced by each of the feet (normal component, F_N) were measured by means of the four force plates positioned under the limbs (shown for only the left forelimb in Fig. 1C). A disappearance of the contact force under a limb during lifting (in Tests 2–3 and 5–8) indicated that this particular limb did not support the body; (iv) to be sure that the position of the head against the feeder was stabilized, a contact of the tongue and lips with the feeder was continuously monitored by measuring an electrical conductance between the feeder and the animal; (v) the EMG signals were rectified and smoothed (time constant, 50 ms).

A representative example of the data recording (tests 1 and 2) is shown in Fig. 2. In every experimental session, each of the tests with body lifting (tests 2–3 and 5–8) and antiphase tilting (test 4) alternated several times with test 1 (control). In each cat, the experimental sessions (trials) were performed repeatedly (up to 36 times) during the period of 1–2 months.

About 30 tilt cycles were performed to collect data on the motor responses in every postural trial. Each of the tilt cycles was divided into 20 equal bins, the peak of the right tilt being taken as the cycle onset. The body position, EMG and force signals were averaged for each bin, and then over all consecutive cycles of a given test (as in Fig. 3).

The limb configuration (side view) induced by platform tilts was recorded by a video camera (30 frames s^{-1}). The fur on the lateral aspect of legs was shaved,

and light-reflecting markers were attached to the skin projections of the main limb joints (Fig. 1A).

A depth of the tilt-related modulation of EMG was calculated in the following way:

$$M = (1 - E_{\min}/E_{\max}) \times 100\%$$

where E_{\min} and E_{\max} are the minimal and the maximal values of EMG in the tilt cycle, respectively. In Results, averages are presented (if otherwise not indicated) as mean \pm s.d. Statistical comparisons were made using *t* test, with the significance level $P = 0.05$.

Results

The results obtained in different cats (nos 1–3) were in essence similar. Below we will illustrate these results using the experimental data for cat 1. If there were differences between the trials in one subject and between the subjects, this will be specifically indicated. Among numerous values measured in different tests, we selected six major ones (the amplitude of postural corrections, phase of the peak EMG, and depth of EMG modulation in the fore- and hindquarters), and characterized them quantitatively for individual cats and for all cats together (Tables 1–3). Conclusions of the present study are based on these major results.

Postural performance in control

In test 1 (control) we examined postural performance in the cat standing with all its limbs on the tilting, non-split platform (Fig. 1A–C). Normally during tilting the cat positioned its limbs so that the distance between the feet

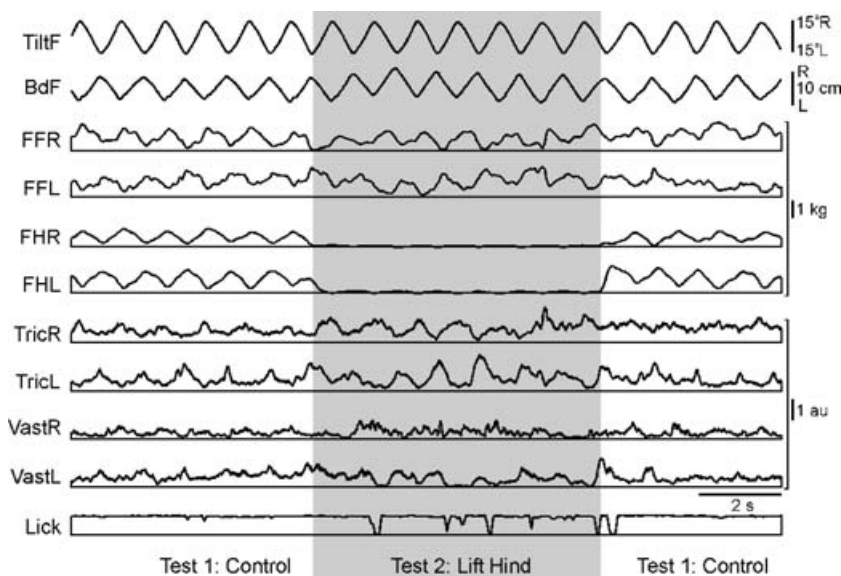


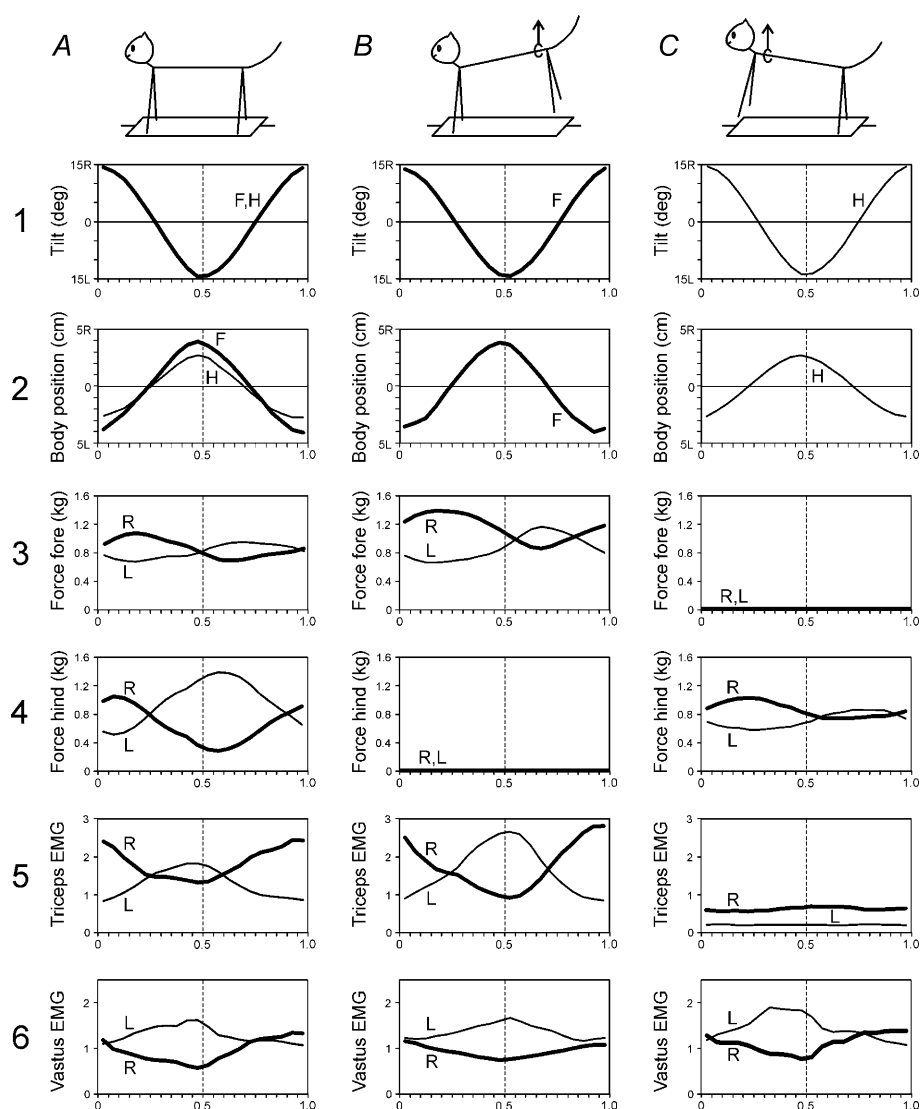
Figure 2. Representative example of postural responses in test 1 (control) and in test 2 (hindquarters lifted)

The following traces are shown: TiltF, tilt of the F-platform (tilt of the H-platform was identical); BdF, lateral position of the fore part of the body; FFR, contact force under the right forelimb; FFL, contact force under the left forelimb; FHR, contact force under the right hindlimb; FHL, contact force under the left hindlimb; TricR, EMG of the right triceps; TricL, EMG of the left triceps; VastR, EMG of the right vastus; VastL, EMG of the left vastus; Lick, contact (up) between the mouth and the feeder.

Table 1. Major results of test 1 (control)

Cat no.	A ₁ Fore	A ₁ Hind	M ₁ Tric	M ₁ Vast	φ_{TRI}	φ_{VAST}
1	7.1 ± 2.2	5.2 ± 1.7	54 ± 10	64 ± 14	0.09 ± 0.04	0.10 ± 0.07
2	8.0 ± 0.4	6.2 ± 0.4	54 ± 22	91 ± 5	0.09 ± 0.05	0.06 ± 0.01
3	7.5 ± 0.8	5.3 ± 0.7	60 ± 18	51 ± 22	0.11 ± 0.07	0.08 ± 0.06
All	7.5 ± 0.5	5.6 ± 0.5	56 ± 4	69 ± 21	0.10 ± 0.01	0.08 ± 0.02

Designations: A₁ Fore, amplitude of corrective forelimb movements; A₁ Hind, amplitude of corrective hindlimb movements; M₁ Tric, depth of modulation of Tric EMG (%); M₁ Vast, depth of modulation of Vast EMG; φ_{TRI} , phase lead of peak Tric EMG in relation to peak ipsilateral tilt. φ_{VAST} , phase lead of peak Vast EMG in relation to peak ipsilateral tilt. All values are given for individual cats and for all three cats together (mean ± s.d.). Number of trials (*n*) for cats 1/2/3 are *n* = 8/6/5.

**Figure 3. Effects of lifting of the hind or forequarters**

A, control; B, hindquarters lifted; C, forequarters lifted. The scheme of experiment is shown above each column. The kinematical, force, and EMG data were averaged over 30 tilt cycles; the peak right tilt was taken as the cycle onset. The data are presented for the forequarters (F), hindquarters (H), right limbs (R), and left limbs (L). EMG scale (arbitrary units) is the same in all columns. Abscissa: phase of the cycle.

Table 2. Major results of tests 2–4

Cat no.	Test 2 (<i>n</i> = 16/8/4)			Test 3 (<i>n</i> = 15/9/3)		Test 4 (<i>n</i> = 10/8/5)		
	<i>A</i> ₂ / <i>A</i> ₁ Fore	<i>M</i> ₂ Vast	$\varphi_1 - \varphi_2$ Vast	<i>A</i> ₃ / <i>A</i> ₁ Hind	<i>A</i> ₄ / <i>A</i> ₁ Fore	<i>A</i> ₄ / <i>A</i> ₁ Hind	φ_{TRI}	φ_{VAST}
1	1.09 ± 0.13	29 ± 9	−0.06 ± 0.07	1.09 ± 0.27	1.15 ± 0.17	1.12 ± 0.21	0.06 ± 0.08	0.09 ± 0.03
2	0.95 ± 0.04	37 ± 11	−0.05 ± 0.11	0.81 ± 0.09	0.98 ± 0.11	0.94 ± 0.11	0.13 ± 0.05	0.03 ± 0.11
3	0.98 ± 0.09	40 ± 15	0.06 ± 0.08	0.88 ± 0.14	0.88 ± 0.14	0.92 ± 0.13	0.08 ± 0.10	0.05 ± 0.04
All	1.01 ± 0.07	35 ± 6	−0.02 ± 0.07	0.93 ± 0.15	1.00 ± 0.14	0.99 ± 0.11	0.09 ± 0.04	0.06 ± 0.03

Designations: *A*₂/*A*₁ Fore, ratio of amplitudes of corrective forelimb movements in tests 2 and 1; *M*₂ Vast, depth of modulation of Vast EMG (%); $\varphi_1 - \varphi_2$ Vast, phase difference of peak Vast EMG between tests 1 and 2; *A*₃/*A*₁ Hind, ratio of amplitudes of corrective hindlimb movements in tests 3 and 1; *A*₄/*A*₁ Fore, ratio of amplitudes of corrective forelimb movements in tests 4 and 1; *A*₄/*A*₁ Hind, ratio of amplitudes of corrective hindlimb movements in tests 4 and 1; φ_{TRI} and φ_{VAST} , phase lead of peak Tric or Vast EMG in relation to peak ipsilateral tilt of the corresponding platform. All values are given for individual cats and for all three cats together (mean ± s.d.). Number of trials (*n*) for cats 1/2/3 are indicated in the upper row.

Table 3. Major results of tests 5–8

Cat no.	Tests 5 and 7 (<i>n</i> = 21/17/4)				Tests 6 and 8 (<i>n</i> = 36/9/4)			
	φ_{TRI} Supp	φ_{TRI} Lift	<i>M</i> _{TRI} Supp	<i>M</i> _{TRI} Lift	φ_{VAST} Supp	φ_{VAST} Lift	<i>M</i> _{VAST} Supp	<i>M</i> _{VAST} Lift
1	0.08 ± 0.06	0.07 ± 0.08	36 ± 8	32 ± 11	0.07 ± 0.11	0.07 ± 0.12	45 ± 15	51 ± 22
2	0.12 ± 0.08	0.05 ± 0.04	38 ± 14	43 ± 24	0.09 ± 0.10	0.12 ± 0.06	54 ± 33	47 ± 17
3	0.10 ± 0.07	0.04 ± 0.05	30 ± 16	47 ± 14	0.07 ± 0.09	0.13 ± 0.10	30 ± 15	26 ± 14
All	0.10 ± 0.02	0.05 ± 0.02	35 ± 4	41 ± 8	0.08 ± 0.02	0.11 ± 0.03	43 ± 12	41 ± 13

Designations: φ_{TRI} Supp, phase lead of peak Tric EMG (supporting limb) in relation to peak ipsilateral tilt; φ_{TRI} Lift, phase lead of peak Tric EMG (lifted limb) in relation to peak ipsilateral tilt; *M*_{TRI} Supp, depth of modulation of Tric EMG (supporting limb); *M*_{TRI} Lift, depth of modulation of Tric EMG (lifted limb); φ_{VAST} Supp, phase lead of peak Vast EMG (supporting limb) in relation to peak ipsilateral tilt; φ_{VAST} Lift, phase lead of peak Vast EMG (lifted limb) in relation to peak ipsilateral tilt; *M*_{VAST} Supp, depth of modulation of Vast EMG (supporting limb); *M*_{VAST} Lift, depth of modulation of Vast EMG (lifted limb). All values are given for individual cats and for all three cats together (mean ± s.d.). Number of trials (*n*) for cats 1/2/3 are indicated in the upper row.

was about 8 cm for the forelimbs and about 15 cm for the hindlimbs. A tilt of the platform elicited a stereotypic postural response—an extension of the fore- and hindlimbs on the side moving down, and a flexion on the opposite side, as shown schematically in Figs 1C and 5A and D (see also Beloozerova *et al.* 2005). The limb movements made the trunk and head displace laterally in relation to the platform, in the direction opposite to the tilt. These lateral body movements reduced deviations of the trunk and head from the dorsal-side-up position. By means of sensors BdF and BdH (Fig. 1A–C), we recorded lateral displacements of the upper points of the fore and hind parts of the trunk, respectively, in relation to the platform. These corrective trunk movements occurred in antiphase with the platform tilts (compare TiltF and BdF trajectories in Fig. 2, test 1). The antiphase relationships between the platform tilts and the corrective movements of the fore- and hindquarters are well seen in Figs 3A1 and 2 (average over 30 cycles). The peak-to-peak value of corrective movements was about 8 cm for the forequarters and about 6 cm for the hindquarters. Due to postural corrections, the cat stabilized its mouth position against the feeder, and continued licking food despite tilts of the platform.

An almost continuous contact between the mouth and the feeder was demonstrated by measuring the electrical conductance between them (Lick trace in Fig. 2).

Contact forces under the feet were modulated in the rhythm of tilts (Fig. 2). There was a phase delay (0.1–0.2 cycle) of the force trajectories in relation to the tilt trajectory (Fig. 3A1, 3 and 4).

The extension of limbs on the side tilting down and flexion of limbs on the opposite side was caused by a specific modulation of the activity of their extensor muscles (Beloozerova *et al.* 2005), including Tric and Vast (Fig. 2). Figure 3A5 and 6 show the average EMG responses in Tric and Vast on the two sides. The EMGs slightly led in phase the tilt movements, with a peak about 0.1 cycle before the maximal downward tilt on the ipsilateral side. The depth of modulation *M* (see Methods) was 50–70%.

Major characteristics of postural responses in test 1 are summarized in Table 1. One can see that the amplitudes of postural corrections, depth of modulation of muscular activity, and phases of activity of muscles in the tilt cycle were consistent across repeated trials and similar in all three subjects.

It should be noted that, in all cats, the force trajectories in the two symmetrical limbs (fore or hind) in most trials were not quite symmetrical as, e.g. in Fig 3A4, where the peak forces under the left and right hindlimbs were 1.4 and 1.1 kg, respectively, suggesting an uneven distribution of the body weight between the limbs. This asymmetry could vary in sequential trials, but the ratio between the forces on the two sides did not exceed 1.4 in all subjects.

Postural functions of the shoulder and hip girdles

Postural functions of the shoulder girdle were examined in test 2, with only forelimbs on the platform (Fig. 1F). When the hindquarters were lifted, postural corrections in the forequarters persisted. Figure 2 shows the recording of postural responses under two conditions, i.e. when the cat was standing on all four limbs (test 1), and when the hindquarters were lifted (test 2). Lifting the hindquarters was monitored by a disappearance of the contact forces under the hindlimbs. The activity of the remaining part of the postural system occurred sufficient to stabilize the mouth position against the feeder, and to continue licking food (see Lick trace in Fig. 2). Video recording of the cat at the lifted position has shown that, when the posterior part of the trunk was suspended in a hammock, the hindlimbs were strongly extended (this is shown schematically in Fig. 1F), and did not perform any tilt-related movements in the sagittal plane. Small (<1 cm) tilt-related lateral oscillations of the suspended hindlimbs (probably caused by trunk muscles) were sometimes observed.

The representative average characteristics of postural performance in test 2 (cat 1) are shown in Fig. 3B. We will compare them to control (Fig. 3A). At the lifted position, the efficacy of postural corrections in the forequarters was similar to that in control – the peak-to-peak value of corrective movements (about 8 cm) was the same (compare Fig. 3A2 and B2). The temporal patterns of the forelimb forces and the Tric EMGs were also close to normal ones (compare Fig. 3A3 and B3 as well as Fig. 3A5 and B5), but their amplitudes were higher at the lifted position, suggesting an increase of the part of the body weight supported by the forelimbs. In other test 2 trials in cat 1, as well as in other cats, the force and EMG amplitudes in the forelimbs could slightly increase, decrease, or remain unchanged.

Periodic responses to tilts were also observed in the suspended hindlimbs. Both the left and the right Vast were active, and their EMGs were modulated with the peak activity timed to approximately the maximal ipsilateral tilt (Fig. 3B6). This EMG pattern did not differ qualitatively from that observed in control (Fig. 3A6).

The major results of test 2 were as follows (Table 2, test 2): (1) responses to tilts in the forelimbs were similar to those in control. The ratio between the peak-to-peak values of corrective movements in test 2 and test 1 was

close to unity; (2) the temporal pattern of tilt-related modulation of Vast EMG in the suspended hindlimbs was similar to that in control. The depth of modulation M in test 2 was considerable. The difference between the phases of maximal Vast EMG in test 1 and test 2 was very small; this difference was less than the precision of phase measurements. In only 4/28 (14%) of trials, the tilt-related modulation of the Vast EMG in the suspended limbs was not observed, probably because of a lower level of EMG activity in these trials. These findings suggest that (i) the postural mechanism of the forelimbs by itself well compensates for tilts of the anterior part of the body; and (ii) the hindlimbs receive rhythmical tilt-related influences from the forelimbs.

Postural functions of the hip girdle were examined in test 3, with only hindlimbs on the platform (Fig. 1G). We lifted the forequarters so that the animal was still able to lick food from the feeder, as shown schematically in Fig. 1G. Video recording of the cat at the lifted position has shown that the forelimbs were extended (this is shown schematically in Fig. 1G), and did not perform any tilt-related movements in the sagittal plane. When the forequarters were lifted, the hindlimbs continued to perform postural corrections.

The representative average characteristics of postural performance in test 3 (cat 1) are shown in Fig. 3C. We will compare them to control (Fig. 3A). At the lifted position, the efficacy of postural corrections in the hindquarters was similar to that in control (compare Fig. 3A2 and C2) – the peak-to-peak value of corrective movements (about 5 cm) was practically the same. The temporal patterns of the hindlimb forces and the Vast EMGs were also close to normal ones (compare Fig. 3A4 and C4 as well as Fig. 3A6 and C6), but the force amplitudes were smaller at the lifted position, suggesting a decrease of the part of the body weight supported by the hindlimbs. No periodic responses to tilts were observed in the suspended forelimbs: both left and right Tric EMGs were much smaller than in control, and were practically not modulated (Fig. 3C5).

The major results of test 3 were as follows (Table 2, test 3): (1) responses to tilts in the hind limbs were similar to those in control. The ratio between the peak-to-peak values of corrective movements in test 3 and test 1 was close to unity; (2) no tilt-related modulation of Tric EMG was observed in the suspended forequarters (27 trials). These findings suggest that (i) the postural mechanism of the hindlimbs by itself well compensates for tilts of the posterior part of the body, and (ii) the forelimbs receive very weak (if any) rhythmical tilt-related influences from the hindlimbs.

A degree of independence of the shoulder and hip girdles was examined in test 4, with antiphase tilts of the fore- and hindquarters. When the F-platform and H-platform were tilted in antiphase, the cats were easily engaged in this complex postural task. They compensated for tilts

of a platform by extending the limb on the side moving downward, and flexing the limb on the side moving upward (Fig. 1*D* and *E*). Since the platforms were tilted in antiphase, the ipsilateral fore- and hindlimbs performed flexion–extension movements in antiphase to each other, whereas the diagonal limbs were moving in-phase.

The average characteristics of postural performance in test 4 are shown in Fig. 4*B*. All characteristics are presented in relation to the tilt cycle of the F-platform. One can compare them to control (Fig. 4*A*). The lateral

displacements of the fore and hind parts of the trunk were in antiphase to the tilts of the corresponding platform (compare Fig. 4*B1* and 2). The efficacy of postural corrections was similar to that in control – the peak-to-peak value of corrective movements in the forequarters was 7 cm in test 4 against 8 cm in control; in the hindquarters it was 4 cm against 5 cm in control (compare Fig. 4*A2* and *B2*).

Contact forces under the fore- and hindlimbs were strongly modulated in the rhythm of tilts, with their

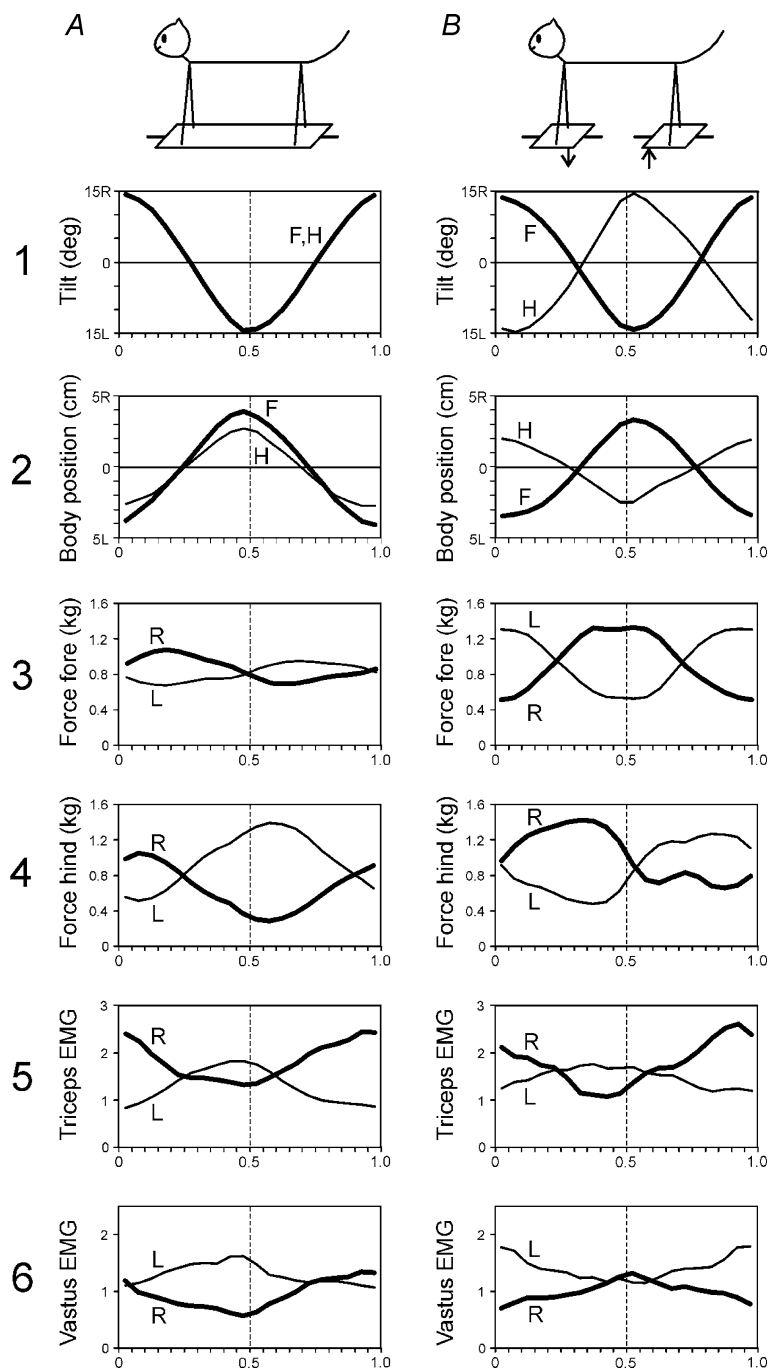


Figure 4. Effects of antiphase tilts of the fore and hind platforms

A, control. *B*, antiphase tilts of the two platforms. The peak right tilt of the F-platform was taken as the cycle onset in all graphs. Designations as in Fig. 3.

peaks delayed by 0.3–0.4 cycle in relation to the maximal ipsilateral downward tilt of the corresponding platform (Fig. 4B3 and 4). These delays were larger than in control (Fig. 4A3 and 4).

The temporal pattern of the Tric activity was close to the normal one (compare Fig. 4A5 and B5). The Tric EMGs led in phase the tilt movements of the F-platform, with the peak about 0.1 cycle before the downward tilt on the ipsilateral side (the range of phase lead was 0.0–0.2 cycle).

The temporal pattern of the Vast activity in test 4 was also close to that in control, but in relation to the H-platform (Fig. 4B6). The Vast EMGs changed approximately in-phase with the tilt movements of the H-platform, with the peak at the maximal downward tilt on the ipsilateral side (the range of phase lead was 0–0.2 cycle). In relation to the F-platform, however, the Vast EMGs occurred in antiphase to the tilt movements.

The major results of test 4 were as follows (Table 2, test 4): (1) responses to tilts in the forelimbs were similar to those in control. The ratio between the peak-to-peak values of corrective movements in test 4 and test 1 was close to unity; (2) responses to tilts in the hindlimbs were similar to those in control. The ratio between the peak-to-peak values of corrective movements in test 4 and test 1 was close to unity; (3) the Tric and Vast activity switched from the in-phase pattern in control to the antiphase pattern in test 4. The peak EMG slightly led in phase the maximal ipsilateral tilt of the corresponding platform. These findings suggest that postural corrections in the fore- and hindquarters are generated by two different mechanisms; each of them is driven by tilts of the corresponding platform.

Postural functions of single limbs

Postural functions of a single limb were examined in the experiments with a single-limb support of a girdle whereas the contralateral limb was lifted (tests 5–8). No substantial difference was found between the effects of passive and active lifting; these results will be described together. Also, the activity of the supporting limb was similar when the other girdle was not suspended (tests 5 and 6) or was suspended (tests 7 and 8).

Compensatory changes of the effective length of the supporting limb

Figure 5A–C shows representative stick diagrams (based on video recordings) of the left forelimb (cat 1) for the two extreme (up and down) platform positions in control (A), in test 5 (the right forelimb was lifted, B), and in test 7 (all limbs except for the left forelimb were lifted, C). In all three tests, the limb joints were flexing when the platform under the limb was moving upward, and extending when

it was moving downward. As a result, the effective length of the limb (the distance from the shoulder joint to the foot) was changing in antiphase with the support height, with its maximal value at the maximal tilt downward, and its minimal value at the maximal tilt upward. Due to these changes in length, the vertical excursions of the platform under the forelimb (2.3 cm peak-to-peak) were only partly transmitted to the trunk: the shoulder joint exhibited excursions of 0.7 cm peak-to-peak in control (A), 1.3 cm in test 5 (B), and 1.6 cm in test 7 (C). Thus, when the shoulder girdle was supported by only one forelimb, compensation for movements of the platform was present, but it was much less efficient than in control. The residual tilt-caused trunk displacements did not prevent the cat from licking food from the feeder, however. Similar

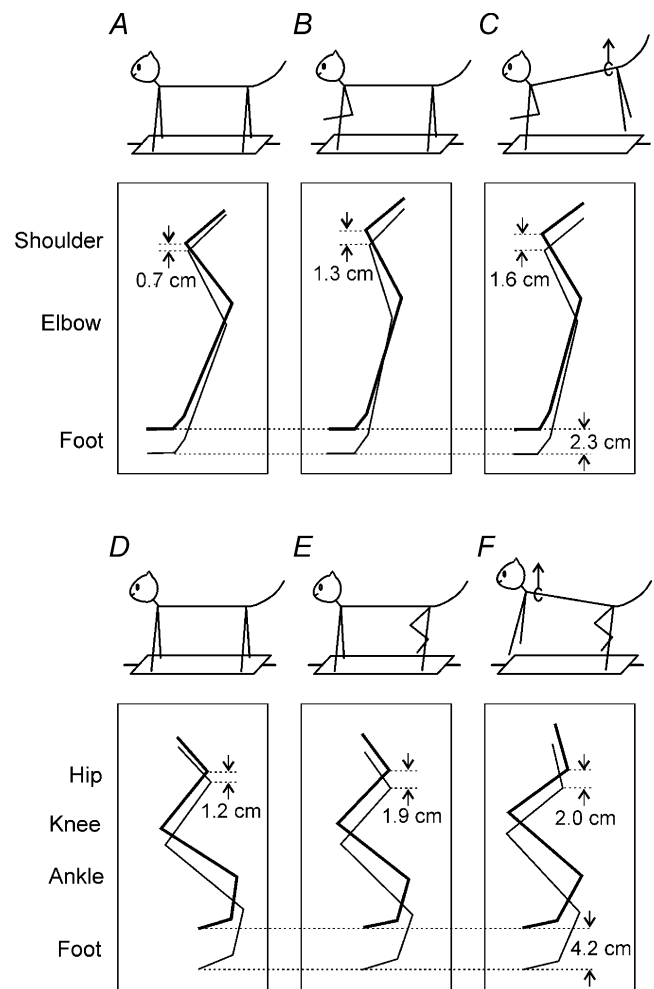


Figure 5. Effects of tilts on the limb configuration

A–C, stick diagrams of the forelimb for two extreme (up and down) platform positions in control (A), when the contralateral forelimb was lifted (B), and when the contralateral forelimb and the hindquarters were lifted (C). D–F, stick diagrams of the hindlimb for the two extreme (up and down) platform positions in control (D), when the contralateral hindlimb was lifted (E), and when the contralateral hindlimb and the forequarters were lifted (F).

results (i.e. smaller changes in length with a single-limb support than in control) were obtained in all three cats. On the average over 12 trials in all subjects, relative changes in the effective length of the forelimb (at the up and down platform positions) were $10 \pm 3\%$ (mean \pm s.e.m.) in control (test 1) against $5 \pm 2\%$ with one-limb support of the shoulder girdle (tests 5 and 7 taken together). The difference was statistically significant ($P < 0.05$, t test).

Similar results were obtained for the hindlimb. Figure 5D–F shows stick diagrams for control (D), test 6 (the right hindlimb was actively lifted, E), and test 8 (all limbs except for the left hindlimb were suspended, F). The vertical excursions of the platform under the hindlimb (4.2 cm peak-to-peak) were larger than under the forelimb (2.3 cm, see Fig. 5A–C) because of a wider base of support (Fig. 1B). Due to compensatory changes of the effective length of the limb (the distance from the hip joint to the foot), the platform movements were only partly transmitted to the trunk, and the hip joint exhibited excursions of 1.2 cm peak-to-peak in control (D), 1.9 cm in test 6 (E), and 2.0 cm in test 8 (F). Thus, compensation for platform movements with a single supporting hindlimb was much less efficient than in control. Similar results (i.e. smaller changes in length with a single-limb support) were obtained in all three cats. On the average over 12 trials in all subjects, relative changes in the effective length of the hindlimb were $18 \pm 2\%$ in control against $8 \pm 1\%$ with a

single-limb support of the hip girdle (tests 6 and 8 taken together). The difference was statistically significant.

Force and EMG responses with a single-limb support of a girdle

We examined the force and EMG responses to tilt in the supporting forelimb and in the lifted forelimb in tests 5 and 7. Because of a similarity of the results obtained in these tests, here we illustrate only the results of test 7. Figure 6B shows representative average responses in the forelimbs in test 7, when only the right forelimb was on the platform, whereas all other limbs were suspended (cat 1). One can compare these responses to control (Fig. 6A). The contact force under the supporting (right) limb increased considerably in test 7 as compared to control (see Fig. 6A2 and B2). The temporal pattern of modulation was similar to control, but the depth of modulation was smaller. The activity of Tric in the supporting limb was higher than in control. The temporal pattern of Tric EMG modulation was similar to that in control: the EMG changed approximately in-phase with the tilt movements, with its peak at the maximal downward tilt on the ipsilateral side (compare Fig. 6A3 and B3). In the suspended (left) forelimb, the Tric EMG was considerably reduced, but remained modulated. The temporal pattern

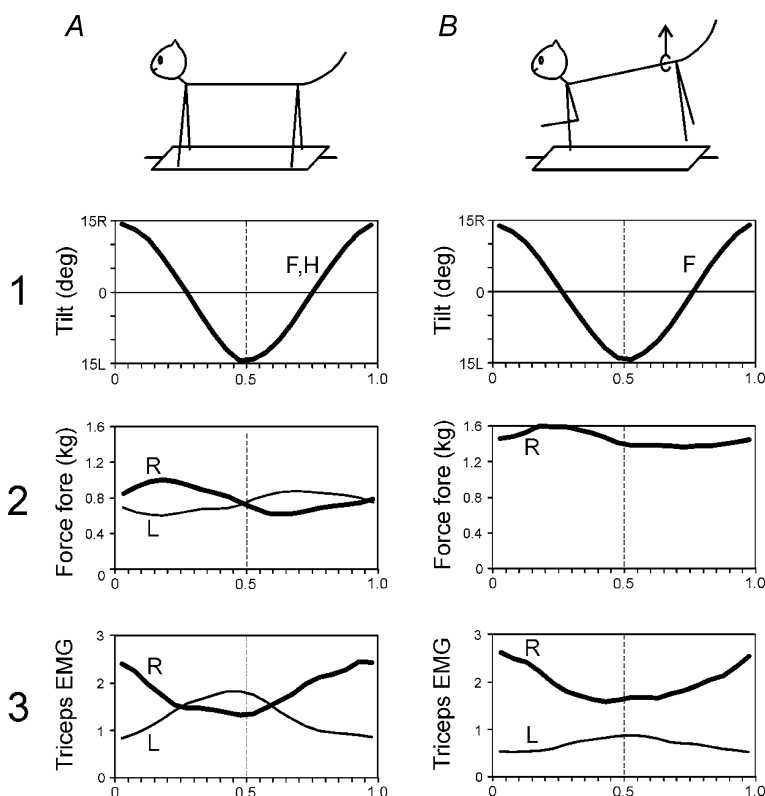


Figure 6. Operation of postural mechanisms of the shoulder girdle

A, control; B, the hindquarters and the left forelimb were lifted. Designations as in Fig. 3.

of modulation was similar to control, and the left Tric was active in antiphase to the right Tric.

We examined the force and EMG responses to tilt in the supporting hindlimb and in the lifted hindlimb in tests 6 and 8. Because of a similarity of the results obtained in these tests, here we illustrate only the results of test 8. Figure 7B shows representative average force and EMG responses to tilt in test 8, when the left hindlimb was on the platform, whereas all other limbs were suspended. One can compare these responses to control (Fig. 7A). The contact force under the supporting (left) hindlimb increased considerably in test 8 as compared to control (compare Fig. 7A2 and B2). The temporal pattern of force modulation was similar to control, but the depth of modulation was smaller. The activity of Vast in the left limb was higher than in control. The pattern of Vast EMG modulation was similar to that in control: the EMG changed approximately in antiphase with the tilt movements, with its peak slightly before the maximal downward tilt on the ipsilateral side (compare Fig. 7A3 and B3). In the lifted (right) hindlimb, the Vast EMG decreased but remained modulated. The temporal pattern of modulation was similar to control, and the left Vast was active in antiphase to the right Vast.

The major results of the experiments with only one limb supporting the shoulder or the hip girdle (tests 5–8) were as follows. (1) the compensatory changes of the effective length of the supporting limb persisted, but their values were significantly reduced as compared to control (Fig. 5). Two other major results are reflected in Table 3: (2) the extensor (Tric or Vast) activity in the supporting limb exhibited a significant tilt-related modulation ($M = 30\text{--}40\%$) with the temporal pattern similar to control: the maximal EMG slightly led in phase the peak ipsilateral tilt. In only 4% of trials, the tilt-related modulation in the supporting limb was not observed; (3) the extensor activity in the lifted limb also exhibited a significant tilt-related modulation ($M = 30\text{--}40\%$) with the temporal pattern similar to control. As in control, the maximal EMG slightly led in phase the peak ipsilateral tilt. In only 12% of trials, the tilt-related modulation in the lifted limb was not observed. These findings suggest that (i) the tilt-related responses in the supporting limb were caused by sensory signals coming from this limb; and (ii) the suspended contralateral limb received rhythmical influences from the supporting limb.

Discussion

The postural task used in the present study was very demanding for the subjects. To be able to continuously lick food from the feeder, the cat had to compensate for tilts of the platform and to stabilize the mouth position against the feeder with a high precision. As estimated

in our previous study (Beloozerova *et al.* 2005), without postural stabilization the ± 15 deg tilts of the platform would cause the lateral head excursions of 15 cm peak-to-peak. Due to an efficient trunk and head stabilization, the head excursions were reduced to less than 1 cm. The goal of the present study was to characterize functional organization of the trunk-stabilizing system.

Independent control of posture of the anterior and posterior parts of the body

Our experiments with suspension of the anterior or the posterior part of the body have shown that postural responses to tilts in a given girdle (shoulder or hip) persist when the other girdle does not participate in the maintenance of posture (Fig. 3). When the hindquarters were suspended, the forelimbs compensated for the platform tilts as efficiently as in control, and the cat continued licking food from the feeder. These experiments clearly showed that postural activity in one of the girdles is not necessary for the normal postural functioning of the other girdle.

When the hindquarters were suspended and the hindlimbs did not support the body, these limbs were strongly extended in the knee and ankle joints due to a high level of activity of the corresponding muscles, as documented by recording the Vast EMG (Fig. 3B). A tilt-related modulation of the Vast EMG was also observed. As in control (Fig. 3A), Vast was coactivated with ipsilateral Tric.

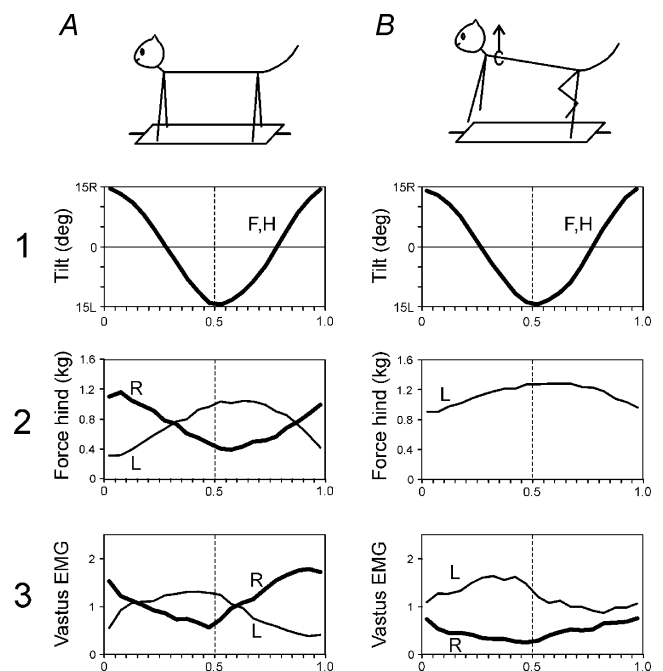


Figure 7. Operation of postural mechanisms of the hip girdle
A, control; B, the forequarters and the right hindlimb were lifted. Designations as in Fig. 3.

These experiments have shown that postural mechanisms of the shoulder girdle exert influences on the mechanisms of the hip girdle; these influences elicit modulation of the Vast activity with a normal temporal pattern in relation to the platform tilts. Thus, the motor responses in the suspended hindlimbs were based on the information about tilts obtained by the forelimbs' somatosensory system.

When the forequarters were suspended and the forelimbs did not support the body, these limbs were extended. Practically, no tilt-related modulation of the Tric EMG was observed (Fig. 3C). These experiments taken together suggest that the influences of postural mechanisms of the shoulder girdle upon those of the hip girdle are stronger than the influences in the opposite direction.

The experimental design with antiphase tilts of the two platforms allowed us to change the phase relationships between the postural responses in the forelimbs and in the hindlimbs, and to cause a mismatch between the local somatosensory input to the hindlimb mechanisms on one hand, and the influences they receive from the forelimbs on the other hand. In control (in-phase tilts of the two platforms), the motor responses in the ipsilateral limbs, as well as the ipsilateral Tric and Vast EMGs were in-phase with each other (Fig. 4A). By contrast, with antiphase tilts they appeared in antiphase (Fig. 4B), despite the forelimb influences that tended to cause the in-phase activity in the hindlimbs (Fig. 3B).

These results were obtained for a complex postural task – independent tilts of the two platforms. For this particular situation, they make unlikely the hypothesis of the united

control of posture of the fore- and hindquarters in quadrupeds (see, e.g. Ghez, 1991; Massion, 1994; Massion *et al.* 1997). The more likely explanation for our 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 even when the surfaces under the fore- and hindlimbs are tilted differently (Fig. 8). A model with united control of the fore and hindquarters (one regulated variable) seems to be applicable to simpler postural tasks, however.

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 maintain the interlimb coordination (von Holst, 1938; Shik & Orlovsky, 1965; Orlovsky *et al.* 1999). Interestingly, the asymmetry, that is stronger influences of the forelimb mechanisms on the hindlimb mechanisms, was also found in the locomotor system (Shik & Orlovsky, 1965). This reflects a leading role of the forelimbs in many motor behaviours (e.g. in overstepping obstacles, Drew, 1991). In some behaviours, however, like bipedal standing in rabbits (Lyalka *et al.* 2005), the hindlimbs seem to play a leading role. It is likely that the system of interactions between the fore- and hindlimb controllers is under supra-spinal control. Based on theoretical considerations, it

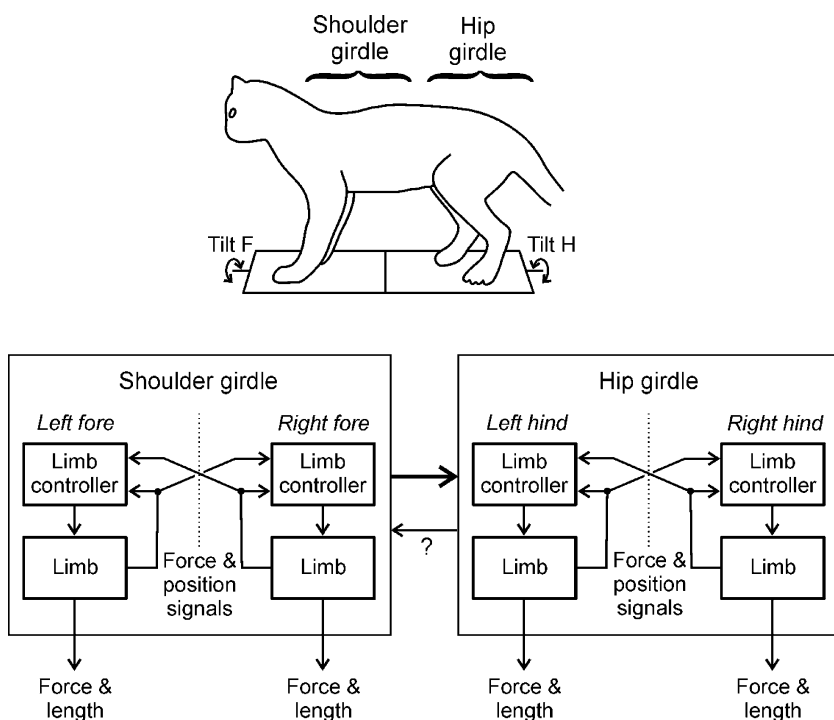


Figure 8. Proposed scheme for sensorimotor processing in the postural system stabilizing the back-up trunk orientation

The system consists of two subsystems, one for the shoulder girdle and the other for the hip girdle. They compensate for tilts of the anterior and posterior parts of the body, respectively (Tilt F and Tilt H). Each subsystem includes two controllers, one for the left limb and one for the right limb. Each limb controller contains a reflex mechanism driven by somatosensory input from its own limb. These local reflexes partly compensate for tilts. The limb controllers also receive somatosensory input (direct or subjected to processing) from the contralateral limbs. The motor responses to these crossed influences are added to the local reflexes. The forelimb controllers exert influences on the hindlimb controllers promoting their coordination. Reversed influences are questionable. See text for explanation.

was suggested that a control system consisting of semi-autonomous subsystems could better adapt to complicated environmental conditions as compared to a centralized system (Gelfand & Zetlin, 1971).

A number of studies have shown that, under certain conditions, the system controlling the head position can operate independently from that controlling the trunk posture (Berthoz & Pozzo, 1988; Barberini & Macpherson, 1998; Deliagina *et al.* 2000; Boyle, 2001). Given that the trunk posture in quadrupeds is maintained by two mechanisms, one can conclude that the whole body is stabilized due to a simultaneous activity of the three principal mechanisms.

Postural mechanisms of a single girdle

In the first part of the present study we have found that each pair of limbs (fore or hind) well compensates for the lateral tilts of the corresponding platform, with a response pattern similar to control (Fig. 3). What is the functional organization of postural mechanisms of each girdle? One extreme would be that the mechanisms of two limbs strongly interact when generating postural corrections, and each girdle thus represents a functional unit. The other extreme would be that postural responses in an individual limb are primarily driven by sensory input from that particular limb, and each limb thus represents a functional unit.

To address this issue, we compared the limb movements in control with those when only one limb was supporting the anterior or the posterior part of the body. In control, tilting the platform evokes an increase of the 'effective length' of the forelimb and the hindlimb on the side tilting downward, and shortening of the limbs on the opposite side (Fig. 5A and D). This leads to a reduction of the trunk tilt, that is, to stabilization of the dorsal-side-up trunk position (as shown schematically in Fig. 1B and C). Lengthening of the limb is due to the extension at joints, whereas shortening is due to the flexion at joints. These movements at joints are primarily caused by modulation of the activity of extensor muscles – the extensor activity increases on the side moving down, and decreases on the opposite side (Fig. 3A). Thus, the extensor muscles increase their activity when they are shortening, and decrease their activity when they are lengthening (see also Beloozerova *et al.* 2005). Similar results were obtained for the rabbit keeping balance on the tilting platform (Deliagina *et al.* 2000; Beloozerova *et al.* 2003b).

When examining the one-limb support of a girdle, we found a qualitatively similar motor pattern. A single limb (fore or hind) was able to support the corresponding part of the body, and to partly compensate for the platform tilts by changing its effective length (Fig. 5). The compensatory changes in length, however, were considerably smaller than in control and therefore the residual vertical excursions

of the trunk were much larger. The extensor EMG in the supporting limb (fore or hind) was considerably larger than in control, which was necessary to counteract the additional load (Figs 6 and 7). The pattern of EMG modulation was qualitatively similar to control: an extensor activity increased when the platform under the limb was moving downward and the limb was extending, and decreased when the platform was moving upward and the limb was flexing (Figs 6 and 7). These findings suggest that the control mechanisms of an individual limb contribute to the generation of postural responses to tilt, but the contribution is rather limited. A detailed analysis of these mechanisms requires special studies; for discussion of possible sensory origin of postural reflexes in a limb, see Gossard *et al.* (1994), Pearson (1995), Pratt (1995), and Duysens *et al.* (2000).

In the contralateral limb, which did not contact the platform, the extensor activity was usually present and modulated in relation to the tilt cycle. The temporal pattern of modulation was similar to control, with the peak at the maximal ipsilateral tilt, that is, in antiphase to the extensor EMG in the supporting limb (Figs 6 and 7). The presence of responses to tilt in the lifted limb suggests that this limb receives tilt-related influences from the supporting limb. Under normal conditions, these crossed influences would produce the motor effects that are added to the postural responses elicited in the limb by its local somatosensory input (Fig. 8). The lack (or decrease) of crossed influences from the contralateral limb, when this limb is lifted, seems to be the main cause for the reduction of compensatory responses when a girdle is supported by a single limb. One can thus conclude that both local reflexes of an individual limb and crossed influences between symmetrical limbs are important for normal functioning of the postural mechanisms of the shoulder girdle and of the hip girdle.

References

- Barberini CL & Macpherson JM (1998). Effect of head position on postural orientation and equilibrium. *Exp Brain Res* **122**, 175–184.
- Bard P & Macht MB (1958). The behavior of chronically decerebrated cat. In *Neurological Basis of Behaviour*, ed. Wolstenholme GEW, O'Connor CM, pp. 55–71. Churchill, London.
- Beloozerova IN, Sirota MG, Orlovsky GN & Deliagina TG (2005). Activity of pyramidal tract neurons in the cat during postural corrections. *J Neurophysiol* **93**, 1831–1844.
- Beloozerova IN, Sirota MG, Swadlow HA, Orlovsky GN, Popova LB & Deliagina TG (2003a). Activity of different classes of neurons of the motor cortex during postural corrections. *J Neurosci* **23**, 7844–7853.
- Beloozerova IN, Zelenin PV, Popova LB, Orlovsky GN, Grillner S & Deliagina TG (2003b). Postural control in the rabbit maintaining balance on the tilting platform. *J Neurophysiol* **90**, 3783–3793.

- Berthoz A & Pozzo T (1988). Intermittent head stabilization during postural and locomotory tasks in humans. In *Posture and Gait: Development, Adaptation and Modulation*, ed. Amblard B, Berthoz A & Clarac F, pp. 189–198. Excerpta Medica, Amsterdam.
- Boyle R (2001). Vestibular control of reflex and voluntary head movement. *Ann NY Acad Sci* **942**, 364–380.
- Deliagina TG, Beloozerova IN, Popova LB, Sirota MG, Swadlow H, Grant G & Orlovsky GN (2000). Role of different sensory inputs for maintenance of body posture in sitting rat and rabbit. *Motor Control* **4**, 439–452.
- Deliagina TG & Orlovsky GN (2002). Comparative neurobiology of postural control. *Curr Opin Neurobiol* **12**, 652–657.
- Drew T (1991). Visuomotor coordination in locomotion. *Curr Opin Neurobiol* **1**, 652–657.
- Duysens J, Clarac F & Cruse H (2000). Load-regulating mechanisms in gait and posture: comparative aspects. *Physiol Rev* **80**, 83–133.
- Gelfand IM & Zetlin ML (1971). On the mathematical modeling of mechanisms of the central nervous system. In *Models of Structural-Functional Organization of Certain Biological Systems*, ed. Gelfand IM, Fomin SV, Zetlin ML, pp. 2–23. MIT Press, Massachusetts.
- Ghez C (1991). Posture. In *Principles in Neural Science*, ed. Kandel ER, Schwartz JH, Jessell TM, pp. 567–607. Elsevier, New York.
- Gossard JP, Brownstone RM, Barajon I & Hultborn H (1994). Transmission in a locomotor-related group 1b pathway from hind limb extensor muscles in the cat. *Exp Brain Res* **98**, 213–228.
- von Holst E (1938). Über relative Koordination bei Säugern und beim Menschen. *Pflügers Arch* **240**, 44–59.
- Horak F & Macpherson J (1996). Postural orientation and equilibrium. In *Handbook of Physiology. Exercise: Regulation and Integration of Multiple Systems*, ed. Shepard J, Rowell L, pp. 255–292. Oxford University Press, New York.
- Inglis JT & Macpherson JM (1995). Bilateral labyrinthectomy in the cat: effects on the postural response to translation. *J Neurophysiol* **73**, 1181–1191.
- Jacobs R & Macpherson JM (1996). Two functional muscle groupings during postural equilibrium in standing cats. *J Neurophysiol* **76**, 2402–2411.
- Lacquaniti F, Maioli C & Fava E (1984). Cat posture on the tilted platform. *Exp Brain Res* **57**, 82–88.
- Lyalka FV, Zelenin PV, Karayannidou A, Orlovsky GN, Grillner S & Deliagina TG (2005). Impairment and recovery of postural control in rabbits with spinal cord lesions. *J Neurophysiol* **94**, 3677–3690.
- Macpherson JM (1988a). Strategies that simplify the control of quadrupedal stance. I. Forces at the ground. *J Neurophysiol* **60**, 204–217.
- Macpherson JM (1988b). Strategies that simplify the control of quadrupedal stance. II. Electromyographic activity. *J Neurophysiol* **60**, 218–231.
- Macpherson JM, Deliagina TG & Orlovsky GN (1997b). Control of body orientation and equilibrium in vertebrates. In *Neurons, Networks, and Motor Behavior*, ed. Stein PSG, Grillner S, Selverston AI, Stuart DG, pp. 257–267. MIT Press, Cambridge.
- Macpherson JM, Fung J & Lacobs R (1997a). Postural orientation, equilibrium, and the spinal cord. In *Advances in Neurology*, Vol. 72 *Neuronal Regeneration, Reorganization, and Repair* ed. Seil FJ, pp. 227–232. Lippincott-Raven Publishers, Philadelphia.
- Magnus R (1924). *Körperstellung*. Springer, Berlin.
- Maioli C & Poppele RE (1991). Parallel processing of multisensory information concerning self-motion. *Exp Brain Res* **87**, 119–125.
- Massion J (1994). Postural control system. *Curr Opin Neurobiol* **4**, 877–888.
- Massion J (1998). Postural control systems in developmental perspective. *Neurosci Biobehav Rev* **22**, 465–472.
- Massion J, Popov K, Fabre J, Rage P & Gurfinkel V (1997). Is the erect posture in microgravity based on the control of trunk orientation or center of mass position? *Exp Brain Res* **114**, 384–389.
- Orlovsky GN, Deliagina TG & Grillner S (1999). *Neuronal Control of Locomotion. From Mollusc to Man*. Oxford University Press, Oxford.
- Pearson KG (1995). Reflex reversal in the walking systems of mammals and arthropods. In *Neural Control of Movements*, ed. Ferrell WR, Proske U, pp. 135–141. Plenum Press, London.
- Pratt CA (1995). Evidence of positive force feedback among hind limb extensors in the intact cat. *J Neurophysiol* **73**, 2578–2583.
- Shik ML & Orlovsky GN (1965). Co-ordination of the limbs during running of the dog. *Biophysics* **10**, 1148–1159.
- Stapley PJ, Ting LH, Hulliger M & Macpherson JM (2002). Automatic postural responses are delayed by pyridoxine-induced somatosensory loss. *J Neurosci* **22**, 5803–5807.

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