THE CONTROL OF LIMB GEOMETRY IN CAT POSTURE

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SUMMARY

1. The aim of this study is to address the problem of the controlled variable in quadrupedal stance. In particular, we considered whether the projection of the centre of mass of the body on the support surface or the joint torques or the geometrical configuration of the limbs are primarily controlled.

2. Cats were trained to stand freely on a platform which could be tilted in the sagittal plane by up to ±20 deg. The normal and tangential components of the contact forces at each paw were measured by means of load cells. The position of limb joints was recorded by means of the ELITE system.

3. The projection of the centre of body mass on the platform, as well as the orientation and length of limb axes, varied to only a limited extent with tilt angle. In particular, the limb axes were closely lined up with the vertical, as were the vectors of the contact forces at the paws. As a result, the torques at the proximal joints (scapula and hip) were close to zero and the torques at the other joints varied little with table tilt.

4. In order to test the different hypotheses on postural control, an external load (10–20% of the animal weight) was applied to the cat forequarters. The projected centre of mass consistently shifted forwards, contrary to the hypothesis that this parameter is controlled in stance. Instead, the geometry of limb posture remained unmodified after load application, even though the torques at forelimb joints were much greater than in the control.

5. This postural behaviour showed no sign of adaptation over a period of 24 h of continuous load application.

6. It is concluded that limb geometry is primarily controlled in stance. The results are discussed in the context of current notions on hierarchical control and body scheme.

INTRODUCTION

The maintenance of balance represents a major goal of postural control. Although balance has often been equated to the outcome of the neural control processes which oppose the perturbing action of external forces (including gravity) (Schuster &

Talbott, 1980; Nashner & McCollum, 1985), the specific nature of the controlled variable (or variables) has yet to be determined.

According to one hypothesis, the orientation of the trunk of the body in space would be stabilized by means of vestibular and neck reflexes (Mittelstaedt, 1964; Roberts, 1973). Signals from neck receptors encoding the orientation of the head relative to the trunk would be subtracted from otolith signals encoding head orientation relative to the gravity vector, thus providing an error signal proportional to the deviation of the trunk from the vertical. However, it has previously been demonstrated (Lacquaniti, Maioli & Fava, 1984) that the orientation of the trunk is not effectively stabilized in intact cats. In fact, when cats stand on a surface which is statically tilted in the sagittal plane by to ± 30 deg from the horizontal, the orientation of the trunk changes in parallel with the tilt of the support surface. It has subsequently been demonstrated that the gain of vestibulospinal reflexes in the direction of pitch is quite low even in decerebrate cats (Wilson, Schor, Suzuki & Park, 1986).

A different hypothesis is that the projection of the centre of mass of the body on the support surface (CMP) is a regulated variable in stance (cf. Brookhart, Parmeggiani, Petersen & Stone, 1965; Massion & Gahéry, 1979; Crenna, Frigo, Massion & Pedotti, 1987). An estimate of current CMP (which reflects the weight distribution between fore- and hindlimbs) could be available by monitoring the contact forces at the paws. A reference value of CMP would be centrally pre-set and any deviation of the current CMP from this reference would be corrected by means of appropriate muscle responses (Rushmer, Russel, Macpherson, Phillips & Dunbar, 1983; Nashner & McCollum, 1985).

Indeed, it has been demonstrated experimentally that CMP is approximately constant under a variety of conditions and it is promptly restored after it has been suddenly displaced by an external perturbation (Brookhart *et al.* 1965; Brookhart & Talbott, 1974; Coulmance, Gahéry, Massion & Swett, 1979; Macpherson, 1988). However, it has been shown that not only CMP but also variables pertaining to postural geometry, namely the length and orientation of the main axes of the limbs, vary little in the cat irrespective of platform inclination (Lacquaniti *et al.* 1984). Thus, under normal conditions, one cannot determine whether the CMP or the geometrical configuration of the body are directly controlled in stance.

In order to distinguish between these two possibilities, we have here applied an external load to the cat forequarters. In this manner, a change of the weight distribution between fore- and hindlimbs was experimentally induced, namely CMP was shifted forwards. The hypothesis that CMP is the controlled variable predicts that the system compensates for the applied perturbation by modifying postural geometry in such a way as to restore the reference CMP. In contrast, if the geometrical variables are primarily controlled, no change in the configuration of the limbs is to be expected in spite of the extra load carried by the forelimbs.

The experiments to be described in this paper were also designed to address the question of the functional significance of the postural behaviour in stance. It has previously been suggested that the posture normally adopted by cats at all platform inclinations, involving limited changes in the length and vertical orientation of the limb axes, might be advantageous from a mechanical standpoint (Lacquaniti *et al.*

1984). In fact, the animal can minimize the torques at the proximal joints by keeping the vectors of the contact forces at the paws approximately lined up with the limb axes. This strategy has the additional benefit that the net torques needed to stabilize the posture at each limb joint undergo limited changes with platform inclination (Gray, 1944). This hypothesis was here tested by measuring the contact force vectors at the paws and computing the joint torques. Furthermore, by decoupling the changes in postural geometry from those in statics in the load perturbation experiments, we could also address the question of whether the maintenance of a preferred distribution of torques among limb joints has priority over the maintenance of preferred postural geometry, or vice versa. Some of the preliminary observations of this study have been published as short communications (Maioli, Lopiano & Lacquaniti, 1986; Maioli & Lacquaniti, 1988).

METHODS

The general experimental procedures have been previously described (Lacquaniti *et al.* 1984). Here we summarize the main aspects of the methodology, as well as those which depart from the previous approach.

Four female adult cats (1·9–2·4 kg weight) were trained to stand, unrestrained, on four force plates (6 × 6 cm), mounted on a movable platform which could be tilted in the sagittal plane by means of a servo-controlled torque motor. The force plates (coated with rough rubber) were instrumented with strain gauges to measure both normal and tangential (sagittal) components of the contact forces at each paw. The mean cross-talk was 4·1 and 1·7 % for the normal and tangential components, respectively. The calibration of the force plates and the compensation of the cross-talk were performed by means of a computerized calibration procedure prior to each experiment. In order to estimate the accuracy of the measured contact forces, the regression line between the measured and the expected values of force was computed. On average, the standard errors of the regression line were 1·5 and 3·3 g for the normal and the tangential forces, respectively. The distance between the anterior and the posterior force plates was adjusted to the animal's size, while the distance between the left and right plates was 9 mm. The position of limb joints in the sagittal plane was recorded by means of the ELITE system (Ferrigno & Pedotti, 1985; Lacquaniti, Ferrigno, Pedotti, Soechting & Terzuolo, 1987). To this end, a 50 Hz TV camera was placed orthogonal to the sagittal plane of the animal and monitored small reflective markers (ϕ 6 mm) attached to the skin overlying wrist, shoulder, upper end-point of the scapular spine, hip, ankle and the proximal interphalangeal joints of the Vth digit at fore- and hindpaws. Data were calibrated in a 40 × 50 cm area using a two-dimensional quadratic fitting. With this procedure the spatial accuracy of the ELITE system was better than 0·2 mm. Due to skin slippage (Miller, Van Der Burg & Van Der Meché, 1975), the co-ordinates of knee and elbow joints could not be measured directly in a reliable way and were computed trigonometrically from the co-ordinates of the adjacent joints. The co-ordinates of the feet contact points were computed as the projection of the paw markers on the support surface.

During training, cats were rewarded with food after they stood still for 5 s with a difference in left–right weight distribution not exceeding 10 % of the body weight.

Experimental protocol

Experimental sessions replicated the conditions of the training sessions. In most experiments, however, a load was suspended on the mid-line under the pectoral girdle of the animal. The load, consisting of a cylindrical bag (3 × 9 cm) filled with lead pellets, was fixed between the chest and a cloth vest which was tailored to the forequarters of the cat. The load was located about 9 cm in front of the estimated centre of body mass. Preliminary experiments were carried out in order to verify that standing posture was not significantly altered by wearing the vest without the load. Two series of experiments were then carried out. In the first series, loads with a different weight were applied to the animal in several experimental sessions. Three conditions were studied: no load,

and loads of 10 and 20 % of the animal weight. Two to four sessions for each condition were carried out for each cat over a period of up to 2 years. During each experiment, the inclination of the platform was randomly changed by up to ±20 deg from the horizontal (10 deg steps). The duration of each session ranged typically from 30 to 60 min. Measurements were started immediately after load application. For each trial, contact forces and joint positions were sampled by the computer for 1 s.
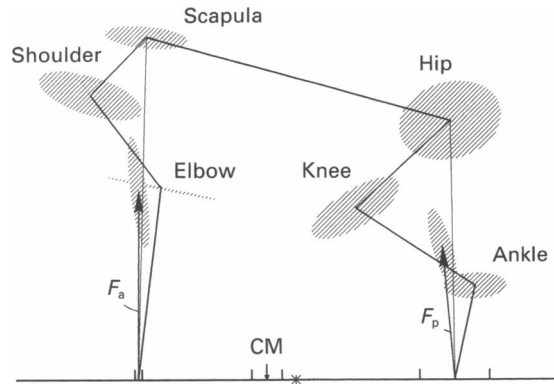

Fig. 1. Stick diagram of the average posture (fifteen trials) of one cat on the horizontal platform. F_a and F_p are the contact force vectors at the fore- and hindpaws, respectively. The shaded ellipses indicate the 95 % confidence limits of joint positions and contact forces. The tick marks indicate the 95 % confidence limits of paws contact points and the standard deviation of the projection of the centre of body mass (CM) on the support surface. The thin lines indicate the main axes of the limbs.

The second series of experiments was carried out to study the time course of the postural changes induced by the load application on a horizontal platform. To this end, standing posture was intermittently monitored in two cats before (control) and 0, 2, 6 and 24 h after the continuous application of a load 10 % of the animal weight. Finally, postural variables were recorded immediately after load removal. In a third cat the experimental series was discontinued 2 h after the load was applied. Each session lasted less than 30 min. In the intervals between experimental sessions, the animals were let free in a large, well-illuminated room. Care was taken that, even when the load was applied, the cats carried out their normal activities (e.g. walking, climbing, eating, etc.).

Data analysis

Cat posture was described using stick diagrams (Fig. 1). Ensemble averages (ten to thirty trials) were constructed from each experimental condition, after verification for each single trial of the following conditions: (1) maintenance of lateral symmetry in weight distribution, measured as the difference between the weight carried by left and right limbs; (2) maintenance of non-diagonal stance, evaluated as the difference between the weight carried by the crossed pairs of limbs; (3) stability of stance, measured as the largest standard deviation of the normal contact forces. Trials in which any of these criteria exceeded the value of 10 % of the animal weight were not included in the average and were separately analysed. Intertrial variability of average joint positions and contact forces was quantified by their 95 % confidence limits. A main axis of the limb was defined as the segment joining the most proximal joint to the paw contact point. The top of the scapular spine was defined as the proximal point of the forelimb, since it corresponds to the insertion area of the serratus ventralis muscle, which carries most of forequarters weight (Roberts, 1978). Furthermore it has been shown that, in locomotion, the forelimbs swing around that point, much in the same way as do the hindlimbs around the hip joint (Miller *et al.* 1975). Length and orientation of the main limb axes were computed. The orientation angle was defined with respect to the horizontal (positive in counter-clockwise direction). In addition, the following parameters were computed for each ensemble average: (1) the distance (*d*) between the CMP and the mid-point between fore- and hindpaws (CM in Fig. 1); (2) the net torques at the joints were computed using the contact forces measured at each paw and the biomechanical parameters of the limb segments,

derived as from Hoy & Zernicke (1985). Torques are positive in the counter-clockwise direction. (The wrist was not included in the analysis since it was fully extended under all experimental conditions.)

Normal posture: limb geometry

Figure 1 shows an ensemble average representative of cat posture on the horizontal platform. Note, in particular, that the main axes of the limbs are approximately
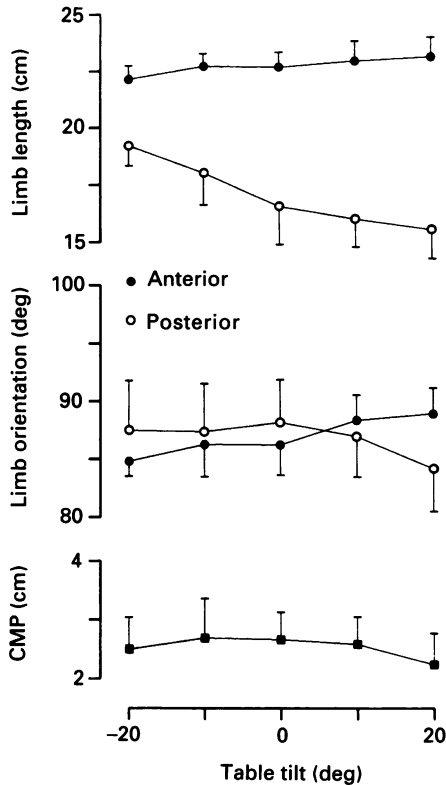

Fig. 2. Relationship between postural parameters and table angle (positive angles for nose-down tilts). Means and standard deviations of limb length, limb orientation and CMP were computed from two experiments of cat 2. Limb orientation is defined with respect to the horizontal (counter-clockwise is positive). ●, mean values for the forelimbs; ○, mean values for the hindlimbs. ■, mean CMP.

vertical. In agreement with the previous results (Lacquaniti *et al.* 1984), large tilts of the platform resulted in limited changes of the postural geometry which was observed on the horizontal platform. Thus, both orientation and length of the limb axes varied little. Though limited, such changes were significantly correlated with the tilt angle: nose-down (nose-up) tilts consistently involved flexion (extension) of the hindlimbs and forward (backward) inclination of the forelimbs.

Typical results are shown in Fig. 2: the data from all experiments in one cat have been pooled and the mean values and standard deviations of the geometrical
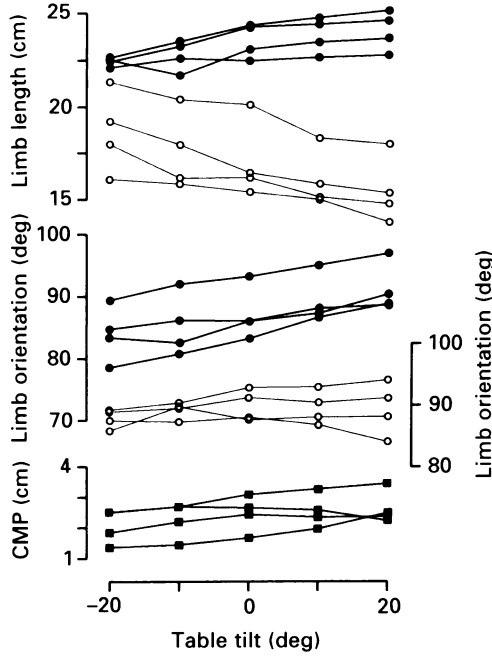
Fig. 3. Relationship between postural parameters and table tilt for all cats. The mean values for each cat were computed by pooling the results of all experiments. ●, mean values for the forelimbs; ○, mean values for the hindlimbs. ■, mean CMP.

TABLE 1. Linear regression analysis of the relationships between geometrical parameters and table tilt for normal posture

| Cat | Variable | Length (cm) | | Orientation (deg) | | CMP (cm) |
		Forelimb	Hindlimb	Forelimb	Hindlimb	
1	a	23·78	19·62	93·36	90·22	3·00
	b	0·056	−0·087	0·183	0·053	0·024
	r	0·938*	−0·971*	0·995*	0·835	0·980*
2	a	22·54	16·98	86·80	86·72	2·54
	b	0·015	−0·096	0·098	−0·075	−0·007
	r	0·878	−0·976*	0·960*	−0·750	−0·534
3	a	24·10	15·22	83·68	91·90	1·80
	b	0·065	−0·054	0·266	0·124	0·028
	r	0·980*	−0·953*	0·997*	0·968*	0·955*
4	a	22·90	16·06	86·00	87·88	2·22
	b	0·042	−0·075	0·190	0·032	0·013
	r	0·817	−0·944*	0·944*	0·361	0·826

a, intercept; *b*, slope; *r*, correlation coefficient (labelled with an asterisk if $P < 0.05$).
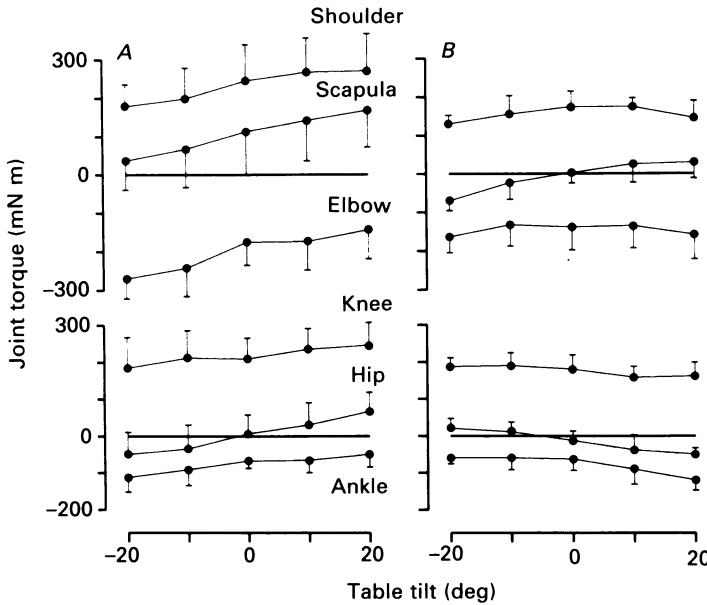
Fig. 4. Relationship between joint torques and table tilt. Means and standard deviations were computed from cat 1 (*A*) and cat 2 (*B*). Torques are positive in the counter-clockwise direction.
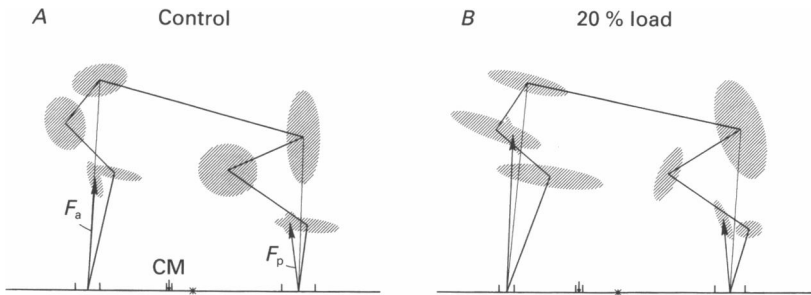

Fig. 5. Comparison of body posture on the horizontal platform with and without load. The stick diagrams (same format as in Fig. 1) depict the average posture (twelve trials) of cat 2 before (*A*) and immediately after (*B*) the application of an external load (20% of the animal's weight) under the pectoral girdle. Note that, after the load application, the forepaw contact forces increased markedly and the projected centre of body mass shifted forwards, but limb geometry did not change significantly with respect to the control.

parameters are plotted as a function of tilt angle (positive angles are for nose-down tilts). The average data obtained in all cats are superimposed in Fig. 3. Finally, the results of a linear regression analysis performed on the postural parameters of all cats are given in Table 1.

In all cats, the hindlimbs flexed slightly (by 4·6% of the limb length on the
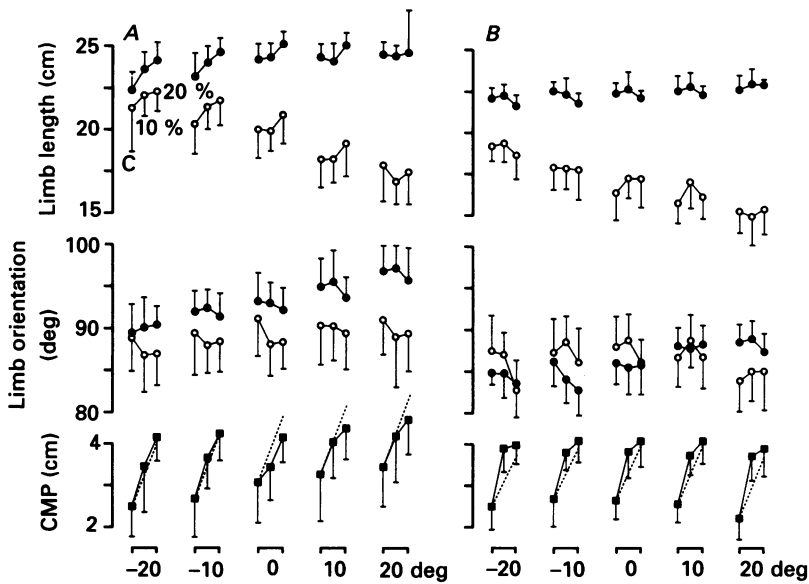
Fig. 6. Relationship between postural parameters and table tilt with and without load. Means and standard deviations of limb length, limb orientation and CMP have been computed in the control (labelled C) and after the application of a load 10 or 20 % of the animal's weight. Results from cat 1 are shown in *A* and from cat 2 in *B*. Note that limb length and orientation varied little with or without load. Instead, the projected centre of mass shifted forwards at all tilt angles in a roughly proportional manner to the load. The dashed lines indicate the theoretical displacement in CMP that would occur if the cat maintained after load application exactly the same postural geometry as in the control. ●, mean values for the forelimbs; ○, mean values for the hindlimbs. ■, mean CMP.

TABLE 2. Differences between the values of the limb geometrical parameters computed in the load experiments and in the control

Cat	Load (% body wt)	Length (cm)		Orientation (deg)	
		Forelimb	Hindlimb	Forelimb	Hindlimb
1	10	0·4 (1·7)	0·2 (1·0)	0·3	−1·7
	20	1·0 (4·2)	0·8 (4·1)	−0·6	−1·6
2	10	0·2 (0·9)	0·4 (2·3)	−0·5	1·0
	20	−0·2 (−0·9)	0·2 (1·2)	−1·2	−1·0
3	10	−0·2 (−0·8)	−0·5 (−3·3)	−0·9	−0·8
	20	−0·4 (−1·7)	−0·7 (−4·6)	−1·5	−3·7
4	10	—	—	—	—
	20	0·2 (0·9)	1·5 (9·3)	1·3	−4·9
Mean	10	0·1 (0·6)	0·0 (0·0)	−0·4	−0·5
	20	0·6 (0·6)	0·4 (2·5)	−0·5	−2·8

The length variations as percentage of the control values are indicated in parentheses.

horizontal platform per 10 deg tilt, on average) and the forelimb axis rotated forwards (by 1·8 deg per 10 deg tilt) nose-down tilts. (Opposite changes occurred with nose-up tilts.) The changes in the other postural parameters were even smaller and less consistent than those just described. Thus, in two cats the forelimbs extended
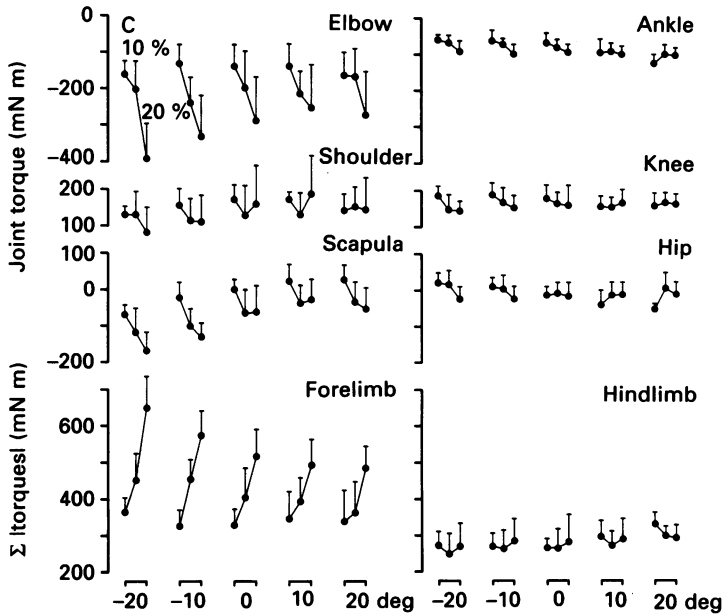

Fig. 7. Relationship between joint torques and table tilt with and without load in cat 2. The means and standard deviations of the torques are plotted in the upper three rows, the values for the sums of the absolute torques at all limb joints are plotted in the bottom row. This sum increased proportionally to the load at the forelimbs, while hindlimb joint torques did not change.

(by about 2·5 % of the limb length on the horizontal platform per 10 deg tilt) and in one cat hindlimbs rotated forwards (1·2 deg per 10 deg tilt) with nose-down tilts. Note that the direction of change in forelimb length was always reciprocal to that of hindlimb length. Because of the limited changes in postural geometry, the changes of CMP were also very small, a statistically significant correlation between this parameter and table tilt being observed only in two cats (a forward shift of about 2·6 mm per 10 deg of nose-down tilt).

Normal posture: joint torques

In the following section, it will be shown that the postural geometry normally adopted by cats is advantageous from a functional viewpoint. In fact, balance is maintained at all platform tilts with limited changes in the torques exerted at each joint. Furthermore the torques at the proximal joints are quite small, implying that little leverage is required by the proximal muscles to stabilize posture. Thus, the limbs become equivalent to mechanical struts, the contact force vectors being closely lined up with the limb's main axis.

Figure 4 shows the relationship between mean joint torques and table tilt in two

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cats. On the horizontal platform, proximal torques did not differ significantly from zero (with the exception of the torque at the scapula in Fig. 4A). The average values were 112·3, 2·4, −9·0 and 65·0 mN m for the scapula, and 7·2, −12·2, −1·0 and −7·2 mN m for the hip (cats 1–4 of Table 1, respectively). Note that the smallest absolute torques were observed at the top of the scapular spine and at the hip for the forelimbs and hindlimbs, respectively, as expected from the similarity of function of these two joint (Roberts, 1978).
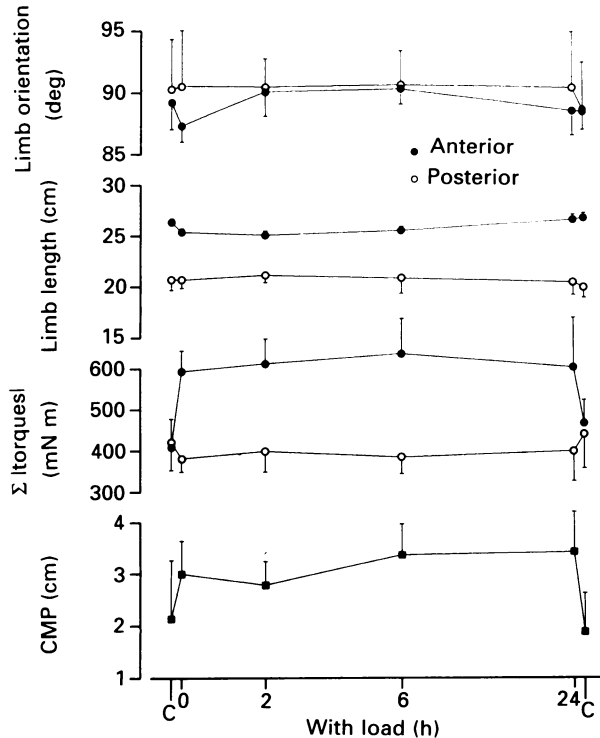

Fig. 8. Time course of postural changes after load application in cat 1. Means and standard deviations of the indicated variables have been computed before (labelled C), and immediately (time 0) and 2, 6 and 24 h after the continuous application of a load (10 % of the animal's weight). Note the lack of adaptation over the 24 h period. The values measured immediately after load removal are also plotted (C).

The data also show that the changes in mean torque at all joints are indeed limited, but are sometimes significantly correlated with table tilt. In fact, since neither magnitude nor direction of the average contact force vectors varied significantly with platform tilt, the changes in joint torques are expected to covary with those in the geometrical parameters. Thus, in the cat of Fig. 4A (cat 1 in Table 1), which exhibited among the largest changes in limb geometry, the changes in torque are significantly correlated with table tilt. By contrast, in the cat of Fig. 4B (cat 2 in Table 1), which showed smaller changes in limb orientation, torques are basically independent of table tilt. On this point, note the parallel change in joint torques in Fig. 4A, indicating that they are mostly produced by a change in the orientation of the limb axis since the direction of the contact force vector is, on average, roughly constant.

Posture with load application : limb geometry

The hypothesis that CMP is regulated in stance predicts that a static load perturbation applied under the pectoral girdle of the animal be compensated by rotating fore- and hindlimbs backwards so as to keep CMP constant. On the contrary, we consistently found that the geometry of limb posture was maintained unmodified after the load application, even though the weight carried by the forelimbs was much greater than before. This is demonstrated in Fig. 5: the average posture of one cat on the horizontal platform is shown before (A) and immediately after the application of a load corresponding to 20 % of the animal's weight (B). After the load application, the vertical component of the forepaw contact forces increased markedly, while that at the hindpaw did not change significantly. Accordingly, CMP shifted forwards with respect to the control (from 2·5 to 4·1 cm in front of the mid-point of the interfeet distance). By contrast, neither length nor orientation of the limbs' axes changed significantly (the average changes were −3 and 7 mm in length and −2·3 and −1·8 deg in orientation for the fore- and hindlimbs, respectively), indicating that postural geometry is primarily controlled in stance.

In general, the interfeet distance with 10 or 20 % load did not differ significantly from that without load, except in two cases: in one cat with 20 % load this distance was significantly greater than in the control, whereas in another cat with the same load it was significantly smaller. Thus, no consistent relationship existed between these two variables.

The contention that geometry is controlled in stance is corroborated by the additional observation that the normal pattern of variation of postural geometry, previously described by tilting the platform, was also present after load application. In Fig. 6, the mean values of the indicated variables obtained at different tilt angles are compared in the control (C) and after the application of load 10 or 20 % of the animal's weight (data from two cats are shown in Fig. 6A and Fig. 6B, respectively). It can be seen that nose-down (nose-up) tilts induced hindlimb flexion (extension) and forward (backward) rotation of the forelimbs not only in the control, as previously described, but also under both loading conditions. By contrast, CMP shifted forwards with respect to the control at all tilt angles, in a manner roughly proportional to the magnitude of the applied load. This can be appreciated by comparing the experimental data points with the dashed lines. The latter indicate the displacement in CMP that would be theoretically observed if the cat maintained, after the load application, exactly the same postural geometry measured in the control. A summary of the results obtained in all cats is provided in Table 2, which reports the difference (averaged across table tilts) between the values of the indicated parameters computed in the load experiments and the control values. (Variations as percentage of the control values are also provided in parentheses for the values of limb length.) In general, the differences between the postural geometry observed in the load experiments and the control were quite small and no consistent trends were found across animals. Note that the same results were also found in the trials involving left–right asymmetries in weight distribution (see Methods).

In cat 3 the shift in CMP induced by the external load was partially compensated under some circumstances. In fact, the shift in CMP with 20 % load was the same as that with 10 % load, but only during nose-down tilts. This partial compensation resulted from a slight backward inclination of the limbs.

Posture with load application : joint torques

The application of the load resulted in a substantial modification of the distribution of torque among forelimb joints. This was due to the fact that, while limb geometry did not change substantially with the load, both the magnitude and the direction of the contact force vector at the forepaws did change considerably. As it can be seen in Fig. 5, the forepaw force vector increased in magnitude and rotated forwards (the horizontal component of the vector did not change significantly, whereas the vertical component, which reflects weight distribution between fore- and hindlimbs, increased.)

Figure 7 shows a representative example of the changes in joint torques resulting from the application of a load 10 or 20 % of the animal's weight. The loads induced a marked (roughly proportional) increase of the absolute torque at the elbow and at the scapula, but not at the shoulder. The changes in elbow and scapula torques are due to the fact that the magnitude and the lever arm of the contact force at the forepaw (the lever arm corresponds to the distance between the joint and the line of action of the force) become greater than in the control. By contrast, as far as shoulder torque is concerned, the increment in the contact force and the decrement in the force lever arm tend to counteract each other. This pattern of torque modification was observed after load application in three cats. In the fourth animal, the increments of torque were more evenly distributed among forelimb joints.

Apart from the specific modality of torque distribution, the global effort exerted at the forelimbs after load application was much greater than in the control. Global effort can be estimated as the sum of the absolute torques at all limb joints (lower panels in Fig. 7). This sum increased considerably and proportionally to load magnitude at the forelimbs. By contrast, the hindlimb joint torques did not change, as expected.

Time course of postural changes after load application

We have described so far the changes in postural behaviour occurring immediately after the application of the load. Under such circumstances, postural geometry appears to be remarkably controlled, with the consequence that: (1) the normal weight distribution between fore- and hindlimbs is modified, and (2) the torques at the forelimb joints become much higher than in the control. The question then arises as to whether a prolonged application of the load results in an adaptation of postural behaviour tending to reduce the effort required by forelimb muscles.

To address this question, we monitored cat posture over a period of 24 h of continuous application of a load equal to 10 % of the animal weight. Figure 8 shows a representative example of the results obtained on the horizontal platform. In agreement with the previous observations, immediately after the application of the load (time 0), CMP shifted forwards and the sum of absolute joint torques at the forelimbs increased markedly, while no consistent changes occurred in limb geometry. This behaviour remained essentially unaltered throughout the 24 h period of observation. Note that, immediately after the removal of the load, the values of the summed torques at the forelimbs and of the CMP returned promptly to the respective control values obtained before the load application.

Control hierarchy

It is acknowledged that posture depends on a highly integrated, multisensory control system that is hierarchically organized (Bernstein, 1967; Roberts, 1978). This system comprises a number of inner control loops which utilize visual, vestibular and somatosensory inputs, and include several elementary reflexes (e.g. optokinetic, vestibular, neck and stretch reflexes). Although each individual loop may control its own set of variables, the co-ordinated action of the overall system must generally comply with the global requirement of the maintenance of balance. This can be achieved, however, in a variety of different ways. Here we have considered three different hypotheses, namely that the overall postural system primarily controls either the projected centre of mass or the joint torques or the geometrical configuration of the limbs. We showed that, under normal conditions, all of the above postural variables undergo limited changes in cats statically tilted at different inclinations. By contrast, when cat posture is perturbed by the application of an external load to the forequarters, only the geometrical configuration of the limbs is preserved and exhibits the same correlation with table tilt as under normal conditions. This occurs at the expense of marked changes in the projected centre of mass and joint torques, since the forelimbs carry all the extra load. The abnormal distribution of effort between fore- and hindlimbs shows no sign of adaptation over a period of 24 h of continuous application of the load. Thus, the inescapable conclusion is that limb geometry is primarily controlled during stance, at least under the present experimental conditions.

Of course, this does not imply that the postural system has no access to sensory information on the contact forces at the paws, nor that it cannot control such forces under certain circumstances. In fact, there is growing evidence in favour of such control in posture (Macpherson, 1988). For instance, Gahéry & Legallet (1981) found that a load, which was applied to one limb of intact cats standing on a horizontal platform, could be distributed between the crossed pairs of limbs. Also, it has been shown that the active tangential components of the paw contact forces, which are required to stabilize cat posture on a tilted platform, are finely partitioned between fore- and hindpaws (Maioli *et al.* 1986). However, the crucial point to be noted about both sets of observations is that the redistribution of such contact forces does not require any change of postural geometry (Gray, 1944). When the redistribution of forces would instead involve a departure of body posture from its reference geometry, as in the present loading experiments, then the hierarchy of controlled variables is such that the maintenance of geometry takes precedence over the maintenance of force distribution. The primacy of postural geometry is robust inasmuch as it is preserved even when the support surface is made slippery, or when cat posture is dynamically perturbed (Maioli & Poppele, 1989). It remains to be seen, however, whether the control hierarchy is fixed or can be adapted to particular environmental conditions (cf. Horak & Nashner, 1986).

Body scheme

In the following section we shall address the question of the significance of the geometrical parameters that are controlled in stance. Although *a priori* there are three degrees of freedom at either fore- or hindlimbs in the sagittal plane (see Fig. 1), it has previously been demonstrated that the geometrical configuration of each limb is completely specified by only two independent variables (Maioli & Lacquaniti, 1988). This is due to the existence of a strong neural constraint taking the form of a planar covariation of the joint angles.

Here we showed that two global variables pertaining to the geometry of the main axis of the limbs, namely the angle of orientation with respect to the vertical and the length of the axis, are appropriate to depict the observed changes in postural geometry. These two co-ordinates correspond to an extrinsic polar reference frame. The hypothesis that the postural control system utilizes a polar reference frame is novel (see, however, Gray, 1944). The implications *vis-à-vis* the problem of the central representations of arbitrary postures are considered elsewhere (Maioli & Lacquaniti, 1988). Here we note that similar organizational principles may apply to both posture and movement, in so far as the same co-ordinate system appears to be involved in their central representations. In fact, a polar reference frame has also been implicated for the sensorimotor transformations involved in reaching movements of the upper limb in primates (Georgopoulos, Schwartz & Kettner, 1986; Soechting & Flanders, 1989).

Although there is strong evidence in favour of a polar reference frame for the control of limb geometry in cats, a number of other two-dimensional sets of variables could capture the observed changes in body geometry equally well, provided that the position of the limb is defined in absolute (extrinsic) space. The need for an absolute reference frame is implied by the tendency, exhibited by all cats under both normal and loaded conditions, to maintain the limb axis closely lined up with the vertical. In this context, the weak but consistent rotation of forelimb axis with table tilt could be explained either as the steady-state error of a feedback mechanism tending to correct deviations in limb orientation or as due to a systematic error in the estimate of the vertical. It should be noted, however, that the orientation of the limbs must change somewhat if limb length has to change. In fact, small reciprocal changes in limb length were here observed as a function of table tilt (see Fig. 3). Such changes are compatible with those expected from the action of the vestibular and neck reflexes described in limb muscles in decerebrate cats (Lindsay, Roberts & Rosenberg, 1976; Wilson *et al.* 1986).

Psychophysical studies have demonstrated that the estimate of the vertical in man depends on a weighed combination of labyrinthine gravitoinertial cues, as well as visual and somatosensory cues (Mittelstaedt, 1983; Young, 1984; Jeannerod & Biguer, 1987). Conflicting information coming from different sensors can result in substantial tilts of the perceived vertical and in corresponding changes of body posture. For instance, tilting the visual surround can induce a compensatory body tilt in a standing observer, even with loss of balance. Thus, the idea has been put forward that spatial orientation processes, such as those involved in posture, may require the computation of the state vector of linear and angular positions of the

body trunk based on the estimated vertical (Young, 1984). Note that this problem has also been addressed in optimal stochastic control theory: a hyperstate is computed that includes both the system outputs and a vector of state variables estimated on the basis of an internal reference model (cf. Åström, 1983). The analogy has been drawn between the notion of state and the neurological notion of body scheme intended as an internal model of the geometrical relations between body parts and external environment (Gurfinkel & Levik, 1979; Boylls, 1985).

On the basis of the present results, we would like to propose that the body scheme for cat posture comprises the geometrical configuration of the limbs. The problem of the maintenance of balance would then be equated to that of maintaining a preferred silhouette of the limbs. In other words, small changes of the projected centre of mass and thus stability of the body are predicted outputs of the postural control system endowed with the described body scheme. This prediction is normally realized but can fail under altered conditions, as when a load is applied or the visual surround is tilted. No correction of the output can occur unless the model of the body scheme is adapted to the new conditions (Clément, Gurfinkel, Lestienne, Lipshits & Popov, 1984). The lack of adaptation to the extra load over the 24 h of observation indicates that the body scheme can be surprisingly rigid. A reason for this intrinsic rigidity can be found in the mechanical advantages normally inherent in the standard posture. In fact, the limbs act as struts with small torques at the proximal joints and approximately constant torques at the other joints independent of table tilt (Fig. 4).

REFERENCES

ÅSTRÖM, K. J. (1983). Theory and applications of adaptive control. A survey. *Automatica* **19**, 471–486.

BERNSTEIN, N. (1967). *The Co-ordination and Regulation of Movements.* Pergamon Press, Oxford.

BOYLLS, C. C. (1985). Postural control analysis: adopting a stance. *Behavioral and Brain Sciences* **8**, 150–151.

BROOKHART, J. M., PARMEGGIANI, P. L., PETERSEN, W. A. & STONE, S. A. (1965). Postural stability in the dog. *American Journal of Physiology* **208**, 1047–1057.

BROOKHART, J. M. & TALBOTT, R. E. (1974). The postural response of normal dogs to sinusoidal displacement. *Journal of Physiology* **243**, 287–307.

CLÉMENT, G., GURFINKEL, V. S., LESTIENNE, F., LIPSHITS, M. I. & POPOV, K. E. (1984). Adaptation of postural control to weightlessness. *Experimental Brain Research* **57**, 61–72.

COULMANCE, M., GAHÉRY, Y., MASSION, J. & SWETT, J. E. (1979). The placing reaction in the standing cat: a model for the study of posture and movement. *Experimental Brain Research* **37**, 265–281.

CRENNA, P., FRIGO, C., MASSION, J. & PEDOTTI, A. (1987). Forward and backward axial synergies in man. *Experimental Brain Research* **65**, 538–548.

FERRIGNO, G. & PEDOTTI, A. (1985). ELITE: a digital dedicated hardware system for movement analysis via real-time TV signal processing. *IEEE Transactions in Biomedical Engineering* **BME-32**, 943–950.

GAHÉRY, Y. & LEGALLET, E. (1981). Influence of initial posturo-kinetic co-ordination in the cat. *Experimental Brain Research* **44**, 177–186.

GEORGOPOULOS, A. P., SCHWARTZ, A. B. & KETTNER, R. E. (1986). Neuronal population coding of movement direction. *Science* **233**, 1416–1419.

GRAY, J. (1944). Studies in the mechanics of the tetrapod skeleton. *Journal of Experimental Biology* **20**, 88–116.

GURFINKEL, V. S. & LEVIK, YU. (1979). Sensory complexes and sensorimotor integration. *Human Physiology* **5**, 269–281.

HORAK, F. B. & NASHNER, L. M. (1986). Central programming of postural movements: adaptation to altered support–surface configurations. *Journal of Neurophysiology* **55**, 1369–1381.

HOY, M. G. & ZERNICKE, R. F. (1985). Modulation of limb dynamics in the swing phase of locomotion. *Journal of Biomechanics* **18**, 49–60.

JEANNEROD, M. & BIGUER, B. (1987). The directional coding of reaching movements. A visuomotor conception of spatial neglect. In *Neurophysiological and Neuropsychological Aspects of Spatial Neglect*, ed. JEANNEROD, M., pp. 87–113. Elsevier, Amsterdam.

LACQUANITI, F., FERRIGNO, G., PEDOTTI, A., SOECHTING, J. F. & TERZUOLO, C. (1987). Changes in spatial scale in drawing and handwriting: Kinematic contributions by proximal and distal joints. *Journal of Neuroscience* **7**, 819–828.

LACQUANITI, F., MAIOLI, C. & FAVA, E. (1984). Cat posture on a tilted platform. *Experimental Brain Research* **57**, 82–88.

LINDSAY, K. W., ROBERT, T. D. M. & ROSENBERG, J. R. (1976). Asymmetric tonic labyrinth reflexes and their interaction with neck reflexes in the decerebrate cat. *Journal of Physiology* **261**, 583–601.

MACPHERSON, J. M. (1988). Strategies that simplify the control of quadrupedal stance. I. Forces at the ground. *Journal of Neurophysiology* **60**, 204–217.

MAIOLI, C. & LACQUANITI, F. (1988). Determinants of postural control in cats: a biomechanical study. In *Posture and Gait: Development, Adaptation and Modulation*, ed. AMBLARD, B., BERTHOZ, A. & CLARAC, F., pp. 371–379. Elsevier, Amsterdam.

MAIOLI, C., LOPIANO, L. & LACQUANITI, F. (1986). Further observations on biomechanics of cats standing on a tilted platform. *Neuroscience Letters Supplement* **26**, S272.

MAIOLI, C. & POPPELE, R. (1989). Dynamic postural responses in the cat involve independent control of limb length and orientation. *Society of Neuroscience Abstracts* **15**, 392.

MASSION, J. & GAHÉRY, Y. (1979). Diagonal stance in quadrupeds: a postural support for movement. In *Reflex Control of Posture and Movement, Progress in Brain Research*, vol. 50, ed. GRANIT, R. & POMPEIANO, O., pp. 219–226. Elsevier, Amsterdam.

MILLER, S., VAN DER BURG, J. & VAN DER MECHÉ, F. G. A. (1975). Coordination of movements of the hindlimbs and forelimbs in different forms of locomotion in normal and decerebrate cats. *Brain Research* **91**, 217–237.

MITTELSTAEDT, H. (1964). Basic control patterns of orientational homeostasis. *Symposium of the Society for Experimental Biology* **18**, 365–385.

MITTELSTAEDT, H. (1983). A new solution to the problem of the subjective vertical. *Naturwissenschaften* **70**, 272–281.

NASHNER, L. M. & MCCOLLUM, G. (1985). The organization of human postural movements: a formal basis and experimental synthesis. *Behavioral and Brain Sciences* **8**, 135–172.

ROBERTS, T. D. M. (1973). Reflex balance. *Nature* **244**, 156–158.

ROBERTS, T. D. M. (1978). *Neurophysiology of Postural Mechanisms*. Butterworths, London.

RUSHMER, D. S., RUSSEL, C. J., MACPHERSON, J., PHILLIPS, J. O. & DUNBAR, D. C. (1983). Automatic postural responses in the cat: responses to headward and tailward translation. *Experimental Brain Research* **50**, 45–61.

SCHUSTER, D. & TALBOTT, R. E. (1980). Optimal and adaptive control in canine postural regulation. *American Journal of Physiology* **239**, R93–114.

SOECHTING, J. F. & FLANDERS, M. (1989). Sensorimotor representations for pointing to targets in three-dimensional space. *Journal of Neurophysiology* **62**, 582–594.

WILSON, V. J., SCHOR, R. H., SUZUKI, I. & PARK, B. R. (1986). Spatial organization of neck and vestibular reflexes acting on the forelimbs of the decerebrate cat. *Journal of Neurophysiology* **55**, 514–526.

YOUNG, L. R. (1984). Perception of the body in space: mechanisms. In *Handbook of Physiology*, section 1, vol., 3, part 2, ed. BROOKHART, J. M. & MOUNTCASTLE, V. B., pp. 1023–1066. American Physiological Society, Bethesda, MD, USA.