

Ratio of Shear to Load Ground-Reaction Force May Underlie the Directional Tuning of the Automatic Postural Response to Rotation and Translation

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Ting, Lena H. and Jane M. Macpherson. Ratio of shear to load ground-reaction force may underlie the directional tuning of the automatic postural response to rotation and translation. *J Neurophysiol* 92: 808–823, 2004. First published April 14, 2004; 10.1152/jn.00773.2003. This study sought to identify the sensory signals that encode perturbation direction rapidly enough to shape the directional tuning of the automatic postural response. We compared reactions to 16 directions of pitch and roll rotation and 16 directions of linear translation in the horizontal plane in freely standing cats. Rotations and translations that displaced the center of mass in the same direction relative to the feet evoked similar patterns of muscle activity and active ground-reaction force, suggesting the presence of a *single*, robust postural strategy for stabilizing the center of mass in both rotation and translation. Therefore we postulated there should be a common sensory input that encodes the direction of the perturbation and leads to the directional tuning of the early electromyographic burst in the postural response. We compared the mechanical changes induced by rotations and translations prior to the active, postural response. The only consistent feature common to the full range of rotation and translation directions was the initial change in ground-reaction force angle. Other variables including joint angles, ground-reaction force magnitudes, center of pressure, and center of mass in space showed opposite or nonsignificant changes for rotation and translation. Change in force angle at the paw reflects the ratio of loading force to slip force, analogous to slips during finger grip tasks. We propose that cutaneous sensors in the foot soles detect change in ground-reaction force angle and provide the critical input underlying the directional tuning of the automatic postural response for balance.

INTRODUCTION

When standing balance is perturbed, an automatic postural response is evoked that counteracts the destabilizing effects of the perturbation and restores balance. The pattern of muscle activation in the postural response is tuned to the direction of the disturbance. Directional tuning is important for generating the appropriate direction of force against the support surface to arrest the motion of the center of mass and restore balance. It is not known which sensory inputs encode the directional features of this triggered response. We address this question using a novel approach of comparing two quite different postural perturbations of the support surface, rotation, and translation to tease out the significant sensory events that encode direction of the disturbance and give rise to the automatic postural response.

Directional tuning of the initial electromyographic (EMG) burst of the automatic postural response has been described for multidirectional translation in both cats (Macpherson 1988b) and humans (Carpenter et al. 1999; Henry et al. 1998) and in multidirectional

rotations in humans (Carpenter et al. 1999). The rapidity of these responses (40–60 ms in cats and 80–120 ms in humans) suggests that the nervous system must determine the direction of the perturbation and activate the appropriate muscles before the perturbation causes appreciable destabilization of the body. Although vestibular, visual, proprioceptive, and cutaneous inputs are all thought to play a role in postural equilibrium and orientation (Horak and Macpherson 1996), only proprioceptive or cutaneous channels are likely candidates for encoding the direction of disturbance and shaping the directional tuning of the automatic postural responses to support surface disturbances.

Muscle-stretch receptors cannot provide unambiguous directional information about support surface motion because there is no apparent relationship between those muscles that are stretched by a perturbation and those that participate in the initial postural response. An example is the response of human subjects to rotation and translation perturbations in the sagittal plane in various postures. During stance (Nashner 1976), ankle extensors are activated in the automatic postural response to backward translation and toes-down rotation (Fig. 1A) but stretched by the perturbation in the former case and shortened in the latter. Conversely, these same muscles are stretched during both backward translation and toes-up rotation, but the postural response is evoked in opposite muscles: ankle extensors for backward translation and flexors for toes-up rotation. Similarly, in a seated position (Forssberg and Hirschfeld 1994), rotation and translation of the support surface evoke opposite stretch responses in the hip musculature for directions that show similar postural responses. Therefore some sensory input other than the pattern of muscle stretch must provide the directional cue for the automatic postural response.

Neither is vestibular input a likely candidate for triggering the automatic postural response. Despite the postural instability associated with vestibular impairment, the timing and directional tuning of postural responses to translation in cats (Inglis and Macpherson 1995) and in the sagittal plane in humans (Horak et al. 1990; Runge et al. 1998) are not altered after vestibular loss. Similarly, normal directional tuning for rotation is maintained in vestibular-loss subjects (Carpenter et al. 2001). However, delayed postural responses are observed after large-fiber peripheral sensory neuropathy in cats (Stapley et al. 2002) and in humans with somatosensory loss (Bloem et al. 2000, 2002; Inglis et al. 1994). The cats with somatosensory loss and postural delays exhibited instability and difficulty maintaining balance after perturbations (Stapley et al. 2002); this suggests that somatosensory receptors of some kind are important for initiating postural responses. It has

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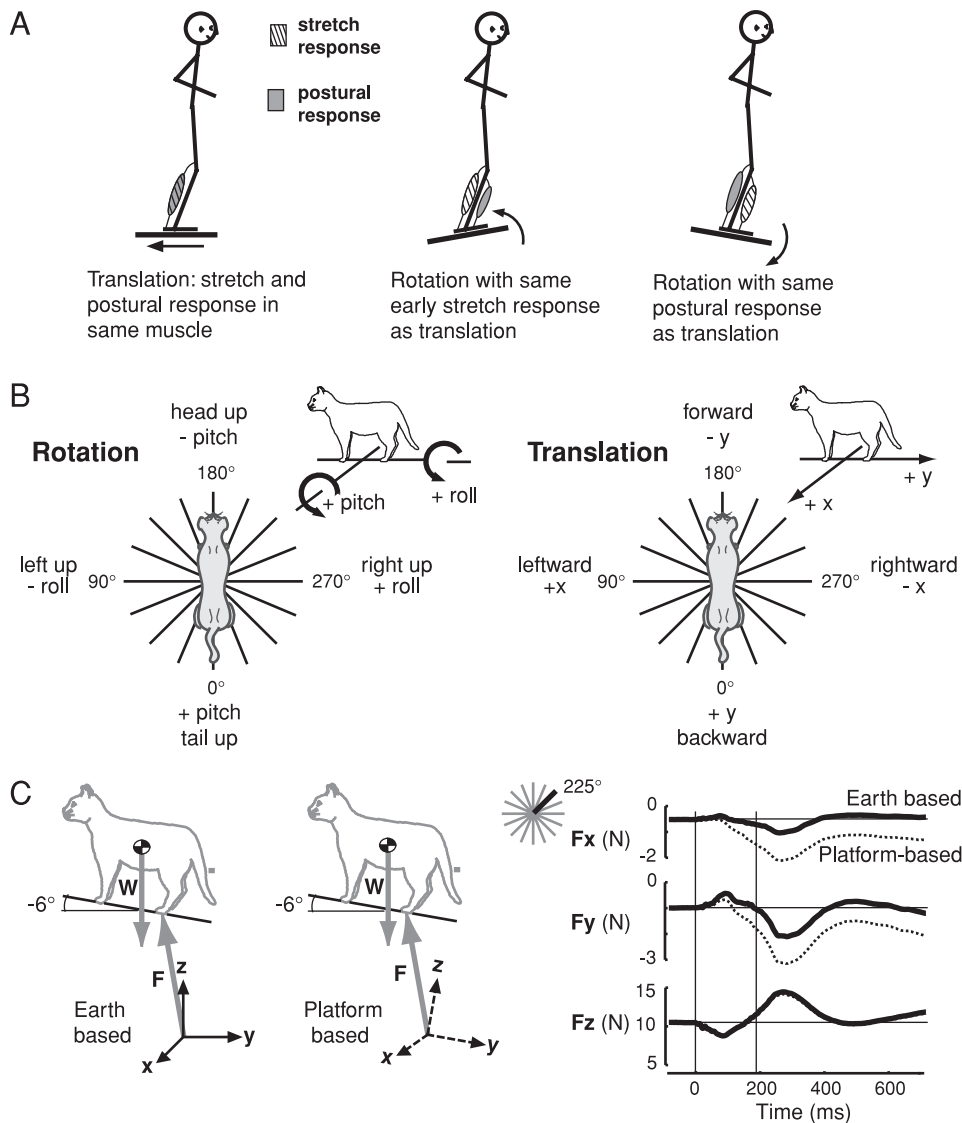


FIG. 1. *A*: schematic of opposite relationship between muscle stretch and postural responses in ankle muscles during rotation and translation perturbations. *B*: coordinate system for rotations and translations of the support surface in 16 evenly spaced directions around the horizontal plane. *C*: Earth- and platform-based coordinates for ground-reaction forces. In the Earth-based system, the z axis was aligned with Earth-vertical, and the y and x axes with the longitudinal and lateral axes of the platform, respectively. Actual ground-reaction force measures were in platform-based coordinates because the force plates rotated with the platform during rotational perturbations. *Right*: example force traces recorded during rotation and represented in the 2 coordinate systems, showing the effect of the gravity component on F_x and F_y in the platform-based system.

been suggested that trunk and proximal leg proprioceptors provide the adequate trigger for balance reactions (Bloem et al. 2002), but this has not been rigorously tested.

The question remains as to the source of the directional encoding in the automatic postural response. We propose that a full comparison of the effects of rotation and translation across many directions provides a means to determine the identity of sensory signals that underlie directional tuning of the rapid postural response. Examination of published data from human subjects reveals that the directional tuning of postural EMG activity is similar for rotation and translation when toes-up/toes-down and left-up/right-up rotations are compared with anterior/posterior and left/right translations, respectively (cf. Carpenter et al. 1999 Figs. 7–10; Henry et al. 1998 Fig. 3). The rotations and translations that evoked similar postural responses induced opposite changes in such variables as ankle angle, muscle length, and center of pressure excursion, suggesting that proprioceptive inputs from limb muscles and joints cannot yield a simple signal encoding the direction of the perturbation and therefore are not likely to shape the directional component of the postural response.

A study comparing the response to forward translation and legs-up rotation in subjects seated with their legs extended revealed similar muscle responses even though most kinematic changes were opposite for the two perturbation types, including motion of the head, which precluded a role for vestibular receptors (Forssberg and Hirschfeld 1994). Pelvis rotation was similar in both disturbances leading the authors to suggest that the trigger for the postural response could arise from either proprioceptors in the pelvis/lumbar region and/or cutaneous receptors in the buttocks and thighs. This study provides further corroboration that somatosensory inputs are the likely source for directional information but does not identify the type of input, proprioceptive versus cutaneous.

When varying amounts of translation and rotation were combined in the perturbing stimulus during stance in human subjects, the only variable that appeared to correspond to the evoked postural response was the direction of the center of mass (CoM) destabilization (Gollhofer et al. 1989). It is not likely that CoM displacement is sensed directly as its location depends on the configuration of the body. However, there are some sensory signals that may vary in conjunction with CoM

position. For example, it has been proposed that load receptors such as Golgi tendon organs may play a critical role in producing the proper muscle activity for weight support in bipedal stance (Dietz 1998; Dietz et al. 1992).

Using the model of standing balance in the cat, we address two key questions regarding the automatic postural response: how similar is the neural strategy for balance control in the same subject for two very different perturbations, rotation, and translation and what channels of sensory information might provide the directional information for shaping the rapid postural response? We addressed these questions by comparing postural responses within subjects for multidirectional perturbations of the support surface. Because postural responses are elicited in cats within 40–60 ms of perturbation onset, the directionally specific information that shapes the postural response must activate sensory receptors within the first 30–50 ms of postural destabilization. We compared the active postural response to rotations and translations within the same subjects as well as the initial, passive effects induced by each type of perturbation prior to the active response.

METHODS

Apparatus

Perturbations were delivered to standing cats using two different platforms, a translating one (Macpherson et al. 1987) and a rotating one, both instrumented with force plates (Fig. 1B). The latter platform could rotate in any combination of pitch and roll using hydraulic actuators. The force plates were centered on the platform, and rotations occurred about the midpoint of the platform at the level of the force plate surfaces. Three vertically oriented linear actuators at the front, back, and one side of the platform controlled pitch and roll angles. The three actuators were controlled from a PC using a real-time control system (AMLAB Technologies, Lewisham, Australia). Linear displacement transducers on each actuator, and rotary potentiometers measuring platform pitch and roll, allowed the position and orientation of the platform to be monitored and adjusted. The dynamic characteristics of pitch-and-roll constant-velocity ramps were matched such that all of the perturbations had similar rise time and maximum velocity.

Training procedures

Four adult cats (3 female, 1 male; 3.2–3.8 kg) were trained using food reinforcement to stand quietly with each paw on a separate force plate. The distance between the force plates was set to the “preferred” stance distance (26–28 cm length, 8 cm width, center-to-center) determined by the natural paw separation assumed by each cat on the floor. Each animal was required to distribute its weight equally between the legs of each girdle (within 10% of body weight for left and right sides) and to stand quietly for several seconds to receive a food reward. The training methods have been previously described in detail (Macpherson et al. 1987).

EMG recordings

After training was completed, each cat was implanted with indwelling EMG electrodes in 16 muscles under general anesthesia using aseptic technique (see Macpherson 1988b). Electrode wires were accessed through two connectors mounted on the head. A variety of muscles were recorded in hindlimb and forelimb. Cats were allowed to fully recover from the surgery before participating in experiments.

Data collection

Three sessions each of rotations and translations were collected with five trials at each of 16 evenly spaced directions per session (Fig.

1B). Rotation perturbations consisted of a ramp-and-hold tilt of 6° amplitude and 40°/s mean maximum velocity. Data in each trial were collected for 3 s—a 300-ms background period of quiet stance, a 200-ms constant-velocity tilt, and a 2,500-ms hold period in which the inclination of the platform was maintained. The platform was returned to its original, level position after each trial. The translation perturbations were linear ramp-and-hold displacements in the horizontal plane of 5-cm amplitude, 370-ms duration, and 15-cm/s mean maximum velocity (Macpherson 1988a). The perturbation amplitudes in rotation and translation were chosen to produce similar amplitude and rate of rotation about the toe joints—metacarpophalangeal (MCP) and metatarsophalangeal (MTP).

Ground-reaction forces at each paw, raw EMGs, and platform kinematics were collected at 1,200 samples/s using the AMLAB system. Kinematic data from body segments were collected at 120 samples/s using a Vicon (Oxford Metrics) system for three cats (*Kn*, *An*, *Wo*) and an Optotrak (Northern Digital, Waterloo, Ontario, Canada) system for one cat (*Ve*). For the Vicon system, 4-mm-diam reflective spheres were cut at 2/3 diam, and the flat surface of the marker was glued to the skin overlying bony landmarks of the fore- and hindlimb joints bilaterally (MCP, wrist, elbow, shoulder, scapular tip, MTP, ankle, knee, hip, and iliac crest). For the Optotrak system, infrared LED's were glued on the landmarks of one side of the cat using Stomahesive paste (Convatec, Princeton, NJ). Head position and orientation in space was recorded at 120 samples/s using either a Minibird (Ascension Technologies) or Fastrak (Polhemus) affixed to the EMG connector.

Data analysis

Data were filtered and processed off-line using a set of custom MATLAB (MathWorks, Natick, MA) routines: force data were low pass filtered at 100 Hz and kinematic data at 7 Hz, and EMG data were high-pass filtered at 35 Hz, demeaned, and rectified. For some analyses, EMG signals were then low-pass filtered at 30 Hz. The trials from each session were averaged by perturbation direction.

Forces from the rotating platform were analyzed in both platform- and Earth-based coordinate systems (Fig. 1C) and included vertical (F_z), longitudinal (F_y), and lateral (F_x) components. The force plates recorded normal and tangential (shear) force components with respect to the platform surface (platform-based coordinates). These data were rotated according to the measured pitch and roll angles of the platform to obtain forces in Earth-based coordinates. This allowed the force associated with weight bearing to be quantified by F_z alone. In a platform-based coordinate system (Lacquaniti and Maioli 1994), the antigravity support force has components in both tangential and normal directions when the platform tilts and forces required for weight support are confounded with those required for lateral and longitudinal stabilization. For the translating platform, the Earth- and platform-based coordinate systems were always aligned.

The horizontal CoM displacement was obtained by calculating the net horizontal plane forces (F_x and F_y in Earth-based coordinates), dividing by the body mass, and integrating twice (Macpherson 1994). The x and y coordinates of the center of pressure (CoP) were calculated by summing the vertical forces under the right paws and the forepaws, respectively, and dividing by the summed vertical forces under all of the paws, then scaling to left-right and fore-hind paw distance, respectively. During static conditions, the CoP and projection of the CoM in the horizontal plane are assumed to be equivalent.

The coordinate systems used to describe rotation and translation directions (Fig. 1B) were aligned such that the horizontal displacement of the CoM relative to the feet at the end of the perturbation was in the same direction for matching rotation and translation perturbations (Fig. 6A). For example, a 270° rotation that tilted the right side of the cat up and the left side down, induced a leftward movement of the CoM relative to the feet. In a 270° translation, the platform moved rightward, and therefore the CoM moved leftward with respect to the feet (Fig. 6C, bottom).

The locations of the fore- and hindlimb joint centers were estimated from marker positions by subtracting joint radii, skin widths, and marker widths. Joint positions were used to compute joint angles as well as trunk and limb axis angles in both Earth- and platform-based coordinate systems. The forelimb axis was defined as the segment connecting the MCP joint and the shoulder joint; the hindlimb axis, by the MTP and hip joints. The trunk axis was determined by ipsilateral shoulder and hip joints in the sagittal plane and left-right pelvis markers in the frontal plane.

Force, kinematic, and EMG responses were compared within each cat during the passive and active periods after onset of rotations and translations. Passive responses refer to changes induced immediately after onset of the perturbation, during the latent period prior to any active postural response; active responses refer to the automatic postural response evoked by the perturbation. The passive changes in kinetic and kinematic variables were quantified for the period 0–30 ms after platform onset (Fig. 2, gray bars), which represents approximately one-half the latency of the postural EMG response. In some cases, this period was extended to 45 ms because changes ≤ 30 ms were too small to establish a trend. Active responses in EMG and force were quantified for the periods of 60–135 and 120–195 ms, respectively, after the onset of platform movement. These time windows were similar to the ones used in a previous study (Jacobs and Macpherson 1996).

The early change from background levels of the kinematic and

kinetic variables were regressed against platform displacement for the sagittal and frontal planes independently. That is, platform displacement was resolved into two components along the cardinal planes for each direction of rotation and translation: pitch angle and anteroposterior (AP) displacement in the sagittal plane; roll angle and medial-lateral (ML) displacement in the frontal plane (Fig. 8A). We assumed that, for a variable to act as a directional trigger for the automatic postural response, it must evoke a sensory signal within the early time period, and the signal should show directional tuning in terms of a significant relationship to amplitude of platform displacement in *both* sagittal and frontal planes. We reasoned that if any stimulus effects showed similar directional tuning for the two perturbation types such variables could function as a directional cue for the automatic postural response.

RESULTS

Overview

Rotations and translations of the support surface that were paired according to the direction of CoM destabilization elicited similar automatic postural responses in terms of EMG directional tuning, and active force and kinematic responses. In contrast, the two perturbation types differed in the initial, passive kinematic

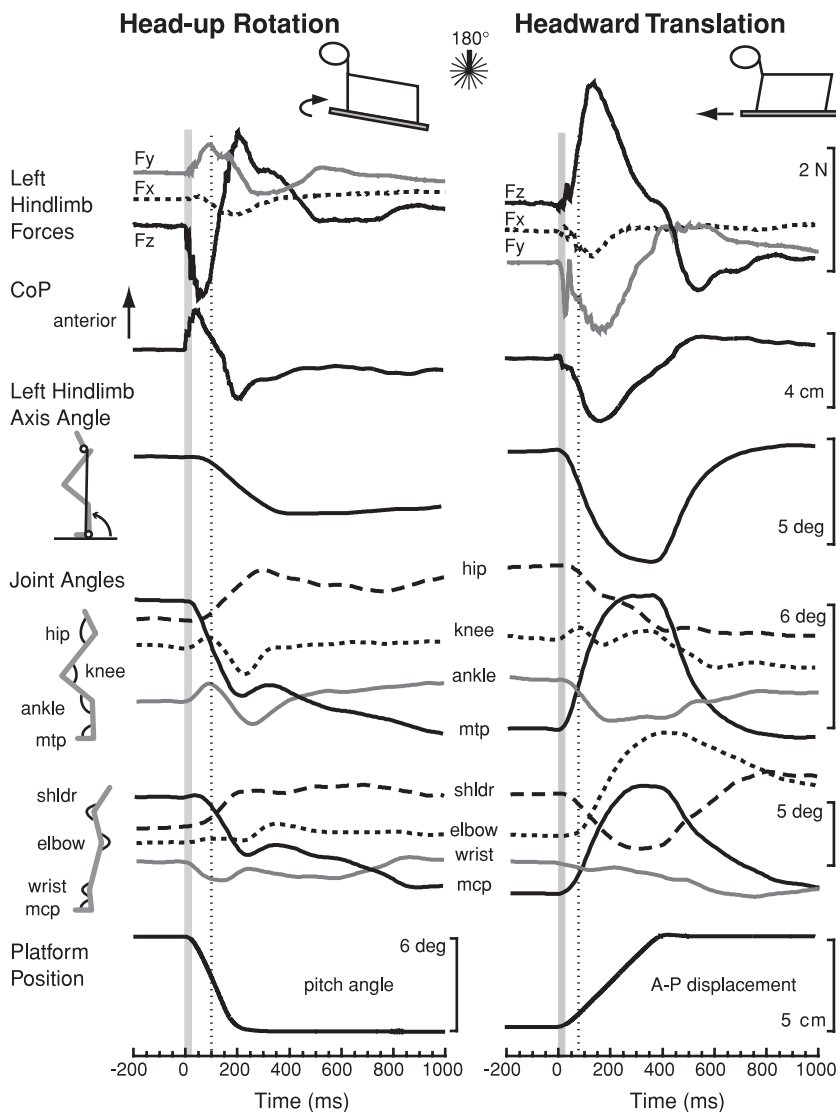


FIG. 2. Example of kinetic and kinematic variable changes during 180° rotations and translations, which evoke similar postural responses. Gray bar, the 1st 30 ms after perturbation onset, during which time the directionally tuned automatic postural response is generated. Note that the overall change in hindtoe [metatarsophalangeal (MTP)] and foretoe [metacarpophalangeal (MCP)] joint angles are of similar rate and magnitude but opposite direction for rotation and translation. Dotted vertical lines, the time at which active ground-reaction forces are generated by the postural response. Note that the passive changes in almost all of the variables are initially opposite.

and kinetic effects (Fig. 2). The only consistently similar feature in the initial effects caused by paired rotations and translations was the change in the angle of the ground-reaction force vector in the sagittal and frontal planes (Table 1). Rotation and translation evoked opposite initial effects in most other variables, including change in vertical forces, horizontal forces, CoP, limb axis angles, and joint angles. We shall first present the data demonstrating that the *active* postural responses are similar. Then, we will describe the initial *passive* changes in all variables that were induced by rotation and translation.

Automatic postural responses are similar in rotations and translations

Rotation and translation perturbations evoked similar patterns of EMG activity in the automatic postural response. For

example, maximal activity in the left hindlimb extensors occurred during both types of perturbation at 225° (head up/right up rotations, and forward/rightward translations), as shown for *cat Kn* (Fig. 3A). Postural responses occurred at ~60 ms after the onset of rotations and slightly earlier in translations, and the magnitude of the response was smaller in rotations than in translations. To compare directional tuning, the EMG amplitude values were normalized to the maximum mean change in activity within each perturbation type and plotted against perturbation direction (Fig. 4). Directional tuning was remarkably similar in all of the extensor muscles (Fig. 4). Some flexor muscles, such as tibialis anterior (TIBA) or posterior semi-membranosus (SEMP) were activated during translations ~45° but not during the corresponding rotations (Fig. 3B). However, the forelimb flexor, biceps brachii (BICB), was activated for both perturbation types (Fig. 3B). Decreased activity in toni-

TABLE 1. *Slope relationships between early variable changes and platform displacement*

Dependent Variable	Plane of Displacement	<i>An</i>		<i>Kn</i>		<i>Ve</i>		<i>Wo</i>	
		Rotation	Translation	Rotation	Translation	Rotation	Translation	Rotation	Translation
Sagittal force angle, forelimb	S	—	—	—	—	—	—	—	—
Frontal force angle, forelimb	F	—	—	—	—	—	—	—	—
Sagittal force angle, hindlimb	S	ns	—	—	—	—	—	ns	—
Frontal force angle, hindlimb	F	—	—	—	—	—	—	—	—
Sagittal force amplitude, forelimb	S	—	+	—	+	—	+	—	+
Frontal force amplitude, forelimb	F	+	—	ns	+	—	ns	+	—
Sagittal force amplitude, hindlimb	S	+	—	+	—	+	—	+	—
Frontal force amplitude, hindlimb	F	ns	ns	ns	+	—	+	+	—
<i>F_x</i> amplitude, forelimb	F	+	+	+	+	ns	+	ns	+
<i>F_y</i> amplitude, forelimb	S	—	+	—	+	—	+	—	+
<i>F_z</i> amplitude, forelimb	S	—	+	—	+	—	+	—	+
<i>F_z</i> amplitude, forelimb	F	+	ns	ns	+	—	ns	+	ns
<i>F_x</i> amplitude, hindlimb	F	+	+	+	+	ns	+	ns	+
<i>F_y</i> amplitude, hindlimb	S	—	+	—	+	—	ns	—	+
<i>F_z</i> amplitude, hindlimb	S	+	—	+	—	+	—	+	—
<i>F_z</i> amplitude, hindlimb	F	ns	+	ns	+	—	ns	+	—
Summed <i>F_x</i> amp	F	+	+	+	+	ns	+	+	+
Summed <i>F_y</i> amp	S	—	+	—	+	—	+	—	—
Summed <i>F_z</i> amp	S	—	+	—	+	—	+	—	ns
Summed <i>F_z</i> amp	F	ns	+	ns	ns	ns	ns	ns	ns
Sagittal CoP displ	S	—	+	—	+	—	—	—	+
Frontal CoP displ	F	—	+	—	+	—	—	—	+
Sagittal CoM displ	S	+	+	+	+	+	ns	—	+
Frontal CoM displ	F	ns	+	ns	+	—	+	—	+
Sagittal MCP angle	S	+	—	—	—	ns	—	ns	—
Sagittal wrist angle	S	+	+	+	+	+	ns	+	+
Sagittal wrist angle	F	ns	ns	+	—	+	—	+	—
Sagittal elbow angle	S	—	—	—	—	ns	—	—	ns
Sagittal elbow angle	F	ns	ns	ns	+	ns	ns	+	ns
Sagittal shoulder angle	S	—	+	—	+	—	+	—	+
Frontal shoulder angle	F	ns	ns	ns	+	ns	ns	—	ns
Sagittal MTP angle	S	+	—	+	—	+	—	—	+
Sagittal ankle angle	S	—	+	—	+	—	+	—	+
Sagittal knee angle	S	—	—	—	—	ns	—	—	—
Sagittal knee angle	F	ns	—	ns	ns	ns	ns	ns	ns
Sagittal hip angle	S	ns	+	ns	+	+	ns	+	—
Frontal hip angle	F	ns	ns	ns	+	ns	ns	ns	ns
Head x displ	F	+	—	ns	—	ns	ns	ns	ns
Head y displ	S	ns	—	ns	—	ns	ns	ns	ns
Head z displ	S	ns	—	ns	—	ns	ns	ns	ns
Head z displ	F	ns	—	ns	—	ns	ns	ns	ns
Head pitch	S	ns	—	ns	—	ns	ns	ns	ns
Head roll	F	ns	—	ns	—	ns	ns	ns	+

Bolded variables signify that the same slope relation was found in rotations and translations in at least 2 cats. S, sagittal plane platform displacement: pitch rotation/AP translation. F, frontal plane platform displacement: roll rotation/ML translation. +, positive slope relation, significant to $P < 0.05$; —, negative slope relation, significant to $P < 0.05$; ns, no significant relationship. CoP, center of pressure; CoM, center of mass; MCP and MTP, metacarpo- and metatarsophalangeal.

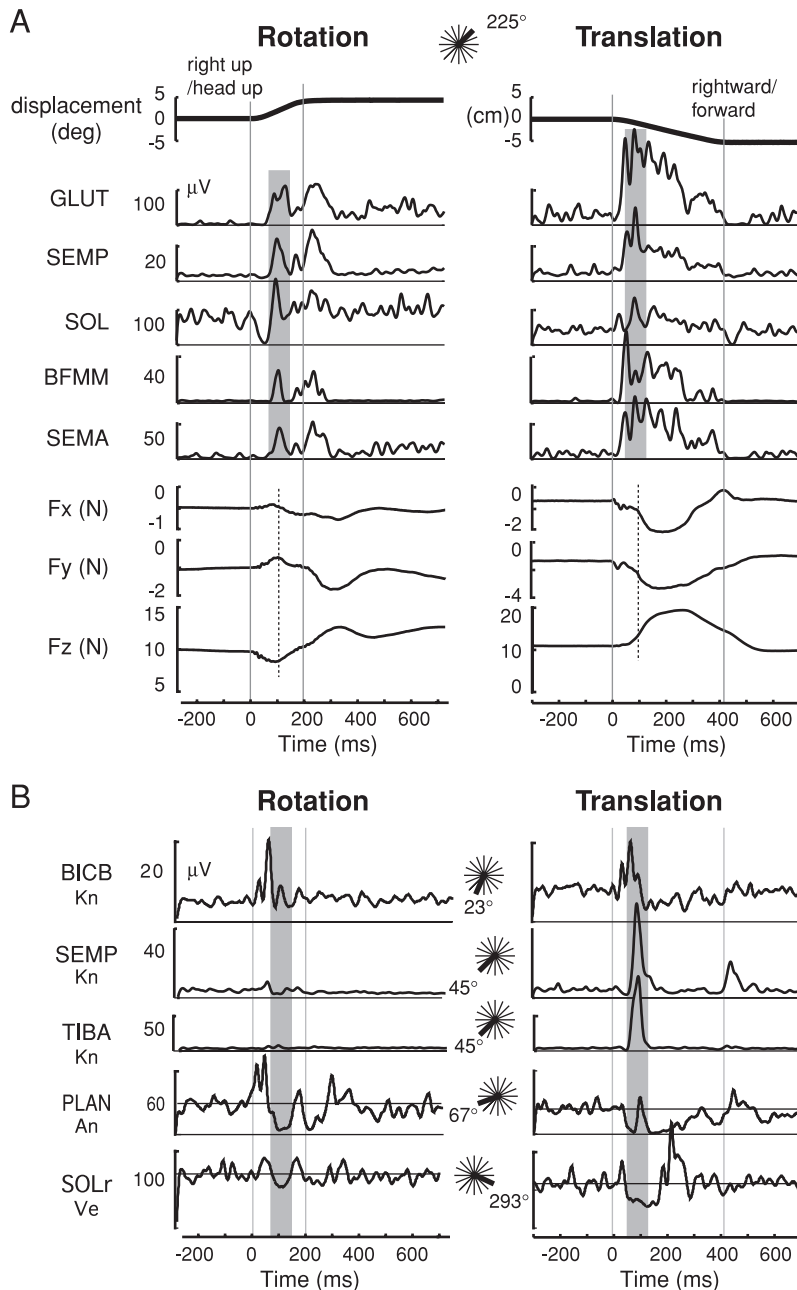


FIG. 3. *A*: left hindlimb extensor electromyographic (EMG) and force responses to rotation and translation at 225° in cat *Kn*. *Top*: platform displacement; vertical gray lines demark onset—at time 0—and offset of platform motion. The 3 components of the left hindlimb ground-reaction force are also shown. Note the overall smaller amplitude of response for rotation compared with translation. Vertical dotted lines in the force traces, the beginning of the active force response resulting from the evoked muscle activity. *B*: example EMG responses to various directions of perturbation in cats *Kn*, *An*, and *Ve*. Posterior semimembranosus (SEMP) and tibialis anterior (TIBA) showed robust flexor responses for translation but not for rotation, however the elbow flexor biceps brachii (BICB) responded to both rotation and translation. For directions in which the postural response unloaded the hindlimb, tonic activity in the extensors was reduced during both perturbation types: plantaris (PLAN) and soleus, right side (SOLr). Note also the short latency response evoked in the ankle plantarflexor, PLAN, during rotation. GLUT, gluteus medius; BFMM, middle biceps femoris; SEMA, anterior semimembranosus.

cally active extensors was often observed for similar directions of rotation and translation (Figs. 3*B* and 4) although occasionally absent for rotations (see SOLr in Fig. 4*D*).

Not only were the postural EMGs similar for rotation and translation, but the active force change resulting from the EMG response was also similar in the Earth-based coordinate system (Fig. 5*A*). During extensor responses of the left hindlimb, for example, the vertical forces began to increase and the horizontal forces to decrease ~ 50 ms after EMG onset (i.e., 100 ms after perturbation onset) in both translation and rotation (see Fig. 3*A*, vertical dotted lines). Similarly, the active vertical forces decreased and the horizontal forces increased after flexor responses in translation as well as for the same directions of rotation; although few flexor EMGs were evoked for rotation, the activity in tonic extensors decreased. For both pertur-

bation types, the horizontal plane forces also exhibited the force-constraint strategy previously identified during translations, whereby changes in the force vector tended to be aligned along the diagonal regardless of perturbation direction (Fig. 5*B*). Earlier periods of force changes that are assumed to be due to passive characteristics of the musculoskeletal system did not demonstrate this directional constraint for either perturbation type as the passive forces tend to oppose the direction of perturbation.

During both rotations and translations, the CoM was propelled toward the limbs that exhibited extensor postural responses. Thus displacement of the CoM with respect to the feet showed similar directional tuning for rotations and translations although the amplitude of displacement at the end of the perturbation was smaller for rotations (Fig. 6, *A* and *B*). After

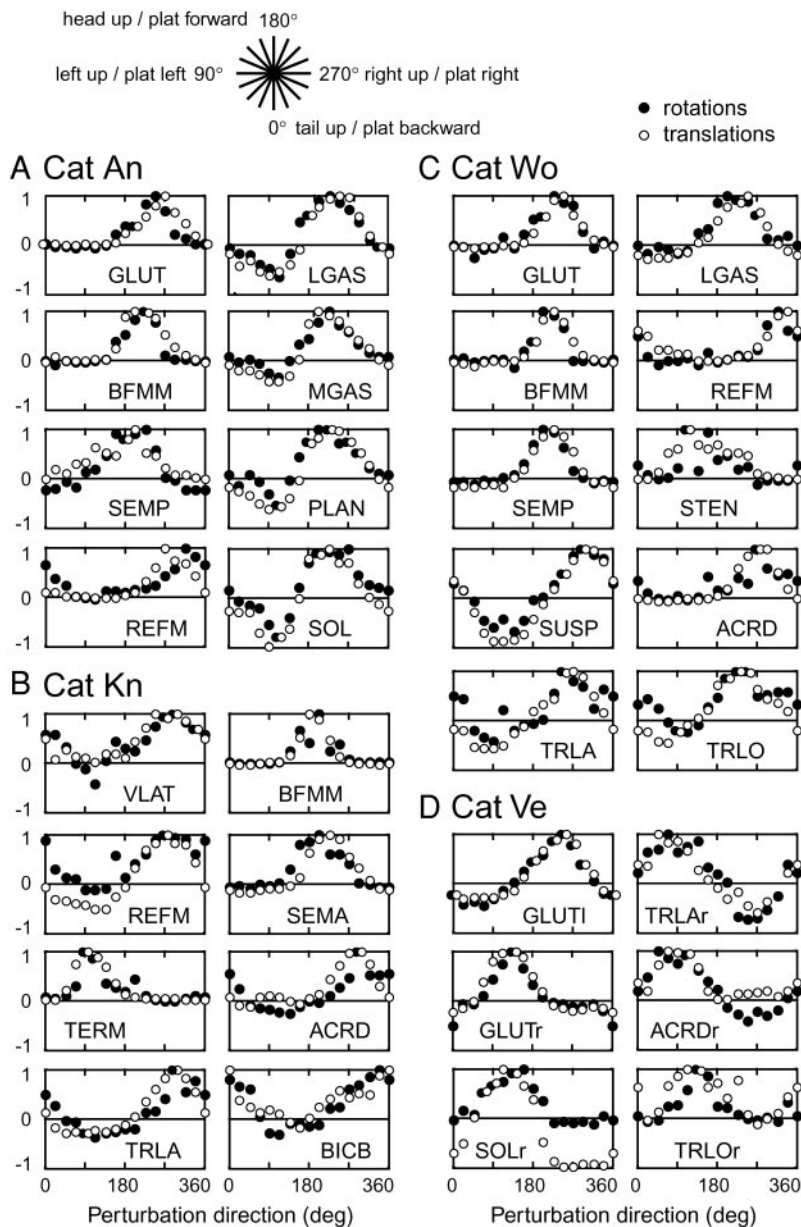


FIG. 4. EMG tuning curves of the automatic postural responses to rotations (●) and translations (○) in each of the 4 cats (A–D). The mean change in integrated EMG activity for the period 60–135 ms after onset of platform movement was normalized to the maximum response within each perturbation type and plotted against direction of perturbation (EMG tuning curve). Note the remarkable similarity in directional tuning for the two perturbation types. The coordinate system for rotations and translations is shown at the top. LGAS, lateral gastrocnemius; MGAS, medial gastrocnemius; REFM, rectus femoris; VLAT, vastus lateralis; TERM, teres major; ACRD, acromiodeltoid; TRLA, triceps brachii, lateral head; TRLO, triceps brachii, long head; STEN, semitendinosus; SUSP, supraspinatus. For *cat Ve* (D), l or r appended to the muscle name indicates recorded side (left or right); for all other cats, muscles were on the left side.

translations, the CoM returned to the origin with respect to the paws, whereas after rotations, it continued to be displaced toward the downhill limbs (Fig. 6B, gray lines). Therefore a reversal in CoM motion with respect to the feet that was observed during translations was absent in rotations (Fig. 6C). Nevertheless, balance was maintained in all conditions.

Given the similarities between rotation and translation in the characteristics of the automatic postural response (EMG and force tuning), we examined the initial effects of the two perturbation types to identify common features that may provide the directional component of the postural response. The regression of each variable onto platform motion was examined first for significance and then the sign of the slope was compared for rotation and translation (Table 1). Only those variables with similar sign for the two perturbation types (i.e., similar directional tuning) were considered as candidates for the directional signal (Table 1, variables in bold) and their

slopes and coefficients of determination (r^2) are reported in Table 2 for all four cats.

Initial, passive effects of rotations and translations

The ground-reaction force angle in the sagittal and frontal planes (platform-based coordinates) was the only variable that changed in the same direction for both sagittal and frontal plane rotation and translation perturbations during the initial, passive period (20 ms after platform onset in translations and 30 ms after platform onset in rotations). Ground-reaction forces in platform coordinates were filtered at 20 Hz, and the vertical and horizontal components were combined to compute force vector angle in each of the sagittal and frontal planes. After the onset of perturbation, the ground-reaction force angle rotated in the same direction under each of the four limbs during any given set of paired rotation and translation (Fig. 7A). The amplitude of force-angle change was smaller for

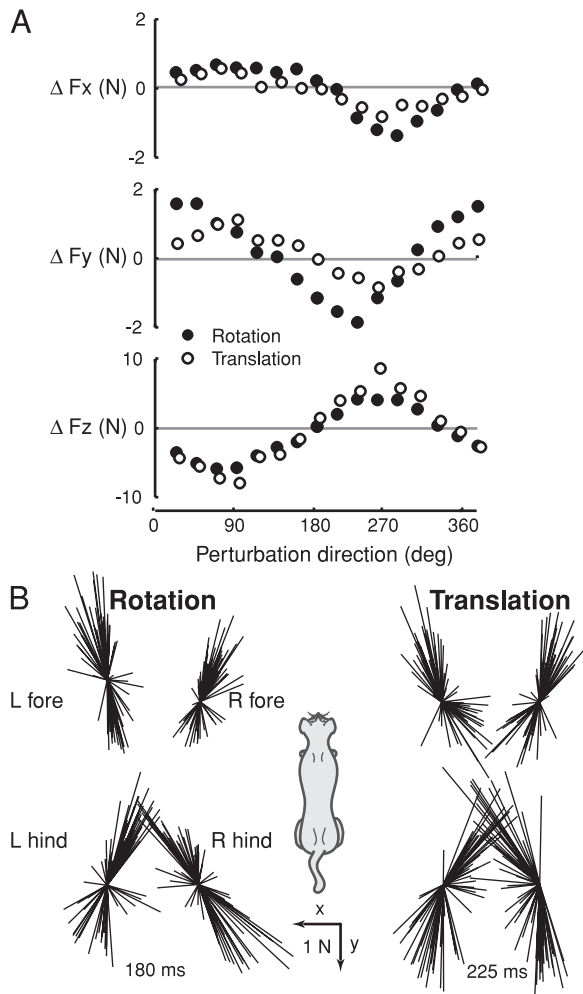


FIG. 5. Active force response. *A*: mean change in the 3 force components under the left hindlimb (*cat Ve*) for the period 120–195 ms after onset of platform movement, plotted against direction of perturbation. This period reflects forces generated as a result of the EMG postural response. Note the similar tuning profiles for rotations (●) and translations (○). *B*: peak active change in horizontal plane force under each of the 4 limbs, during rotations (*left*) and translations (*right*) for *cat Ve*. Each vector takes origin at the same point for a given limb and the responses to all 16 directions of perturbation are superimposed. Note the clustering of the vectors along the diagonals—termed the force constraint. The force changes reached a peak earlier in time for rotation versus translation because the perturbation duration was shorter, hence the time for which the plots were generated is earlier (180 ms for rotations, 225 ms for translations).

rotation than for translation as evident in the raster plots of Fig. 7*B*, which show forelimb force angles for all directions of rotation and translation. All four cats showed a strong linear relationship of force angle with platform displacement in sagittal and frontal planes, and the slopes of the regressions were in the same direction for rotation and translation (Fig. 8, *A*, *B*, and *C*; Tables 1 and 2). Two exceptions were observed: for cats *An* and *Wo*, the regression for force angle was significant for the hindlimb during rotations in the frontal and not the sagittal plane, but was significant for the forelimb in both planes.

Interestingly, the rate of change in force angle was slower for rotation as it took 5–10 ms longer for the net force angle to reach the same magnitude as that observed for translation at 20 ms after onset of the perturbation. This is consistent with the smaller

amplitude and longer latency of EMG response observed for rotation. Overall, the change in ground-reaction force angle is a robust indicator of the direction of impending CoM destabilization relative to the feet, regardless of the type of perturbation.

No other variables showed similar directional tuning (slope of the same sign) for rotation and translation in both sagittal and frontal planes. Some variables like CoP (Fig. 9) showed a significant regression with platform displacement but the slopes were of opposite sign for rotation and translation and, therefore opposite directional tuning. Most kinematic variables showed opposite directional tuning for rotation and translation for the most part, as illustrated for MTP, MCP, and hip joint-angle changes (Fig. 10). Sagittal wrist, elbow, and knee joint angles exhibited the same directional tuning in the sagittal plane but not in the frontal plane (Fig. 10, Tables 1 and 2). Therefore these joint-angle changes cannot encode direction of perturbation for the full range of platform motion. Even joints that have full range of motion in the frontal plane (shoulder and hip) did not show a significant relationship to frontal plane platform displacement for either rotation or translation primarily because the trunk tends to roll after frontal plane perturbations as previously described for translation (Macpherson and Fung 1999). These results suggest there is no apparent combination of kinematic variables that could encode direction for the complete set of paired rotations and translations.

Short-latency EMG bursts, probably due to muscle stretch, were usually evoked during rotation and less often for translation, but when present, the directions that evoked stretch in a particular muscle were opposite for the two perturbation types. Figure 3*B* illustrates a stretch response in plantaris (PLAN) for a rotation at 67° when the platform pushed up against the left hindlimb, causing it to flex and increasing the loading on the limb; a similar stretch response might also be observed in PLAN for a translation in the opposite direction, 247° (not illustrated). Such short-latency stretch responses were unrelated to the later automatic postural response. The relative infrequency of short-latency EMG responses during translation precluded a regression analysis of directional tuning.

Rotations and translations were matched according to direction of CoM displacement with respect to the feet, so we asked whether the directional tuning appeared early enough to encode direction for the postural response. The regression for initial change in CoM position with respect to the feet was significant and in the same direction for rotation and translation for only two cats and only in the sagittal plane, making CoM an unreliable variable for directional coding. One source of variability in the initial CoM displacement may be due to the normal, continual sway of the cat during quiet stance. At the time the perturbation began, the animal could have been swaying in any direction, assisting, opposing, or orthogonal to the direction of CoM displacement induced by the disturbance. The relationship between the initial velocity of the CoM and the velocity imparted by the perturbation influenced the time at which the body began to sway in the expected direction due to the perturbation. Therefore the amplitude and direction of CoM displacement during the initial phase after the perturbation onset was quite variable for any given direction of disturbance and could not provide a reliable indicator of perturbation direction within the initial 30–45 ms.

Even though early CoM motion was not reliable, could head acceleration in space and, therefore vestibular inputs provide

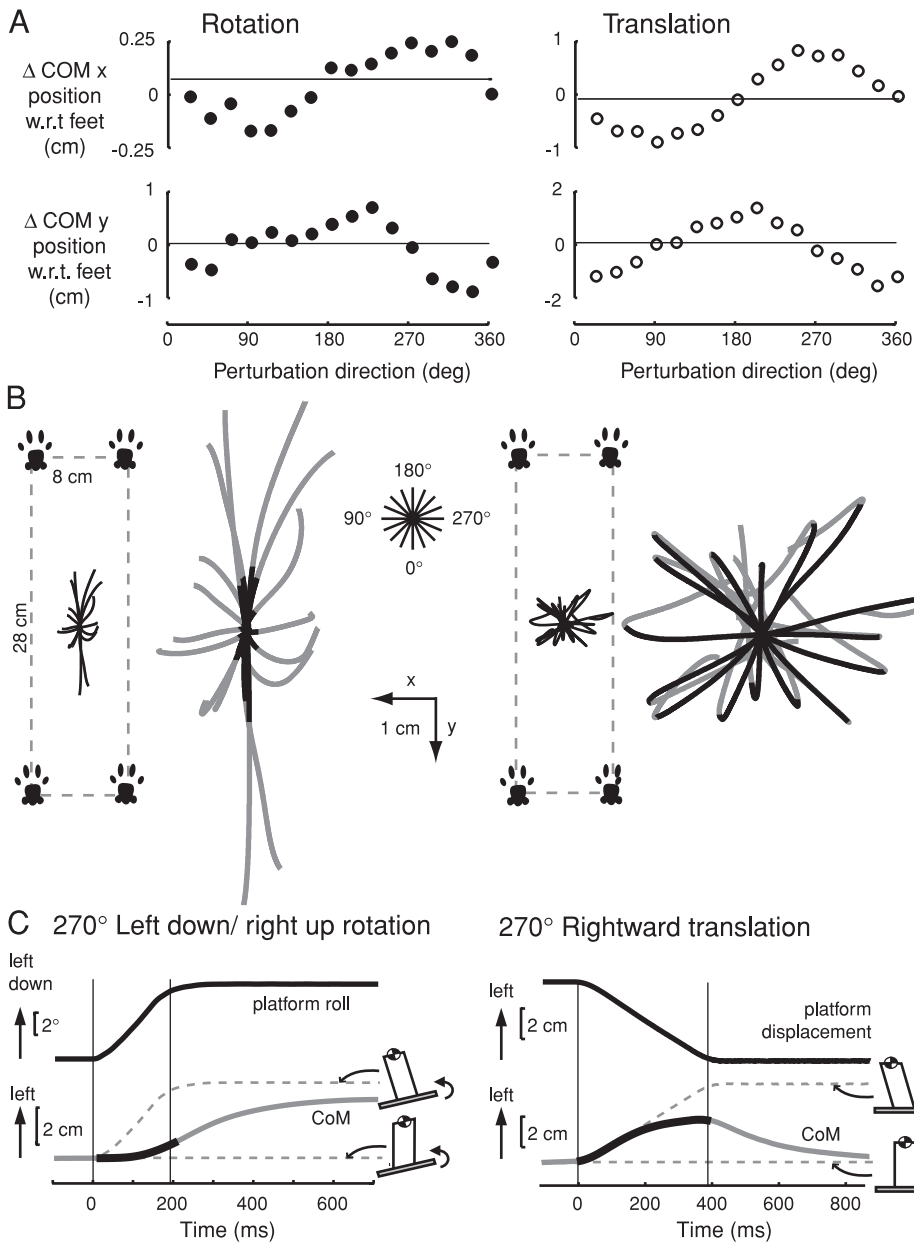


FIG. 6. *A*: average displacement with respect to the feet of the x and y components of the center of mass (CoM) at 150 ms after the onset of platform movement for *cat An* plotted against the direction of perturbation for rotations (*left*, filled circles) and translations (*right*, open circles). Note the similar directional tuning of CoM displacement evoked by rotation and translation. *B*: trajectories of the CoM with respect to the feet, in the horizontal plane, with traces from all directions of perturbation superimposed on the same origin. The trajectories are drawn to scale on the base of support and then expanded for clarity. The initial part of the trajectories (black portions) show displacement up to the end of platform movement; gray portions, from the end of platform movement to the end of the trial, as illustrated in *C*. Note that the trajectories continue along their path after the end of rotations but return toward the center after translations. The trajectory amplitudes are asymmetrical, being longer along the longitudinal axis for rotations and along the lateral axis for translations. *C*: example ramp-and-hold perturbation profiles showing CoM displacement for a matching direction of rotation and translation, 270°. Dashed lines, CoM trajectories that would occur with the kinematic profile schematized to the right of each trace. During rotation, the CoM initially paralleled the bottom dashed-line trajectory in which the limbs rotated only slightly to the left and the CoM displacement was small and to the left with respect to the feet. After the platform stopped rotating, the CoM continued moving downhill (toward the top dashed-line trajectory) as the limbs oriented to the platform-normal and the body moved downhill—the postural response. During translation, the CoM initially followed the top dashed-line trajectory as the feet moved to the right and the body and CoM remained behind. In effect, the CoM moved to the left with respect to the feet. After the platform stopped translating, the CoM returned toward the center with respect to the feet (bottom dashed-line trajectory) as the limbs oriented to the platform-normal and the body moved back over the feet—the postural response.

directionally tuned information about platform motion? Although the CoM moved in the same direction *with respect to the feet* for rotation and translation, the body and head moved in the opposite direction in space, negating a role for vestibular inputs in the directional tuning of the postural response. Head linear and angular displacement showed no significant relationship to platform displacement in either sagittal or frontal planes during the initial, passive period (Table 1). Figure 11 illustrates schematically that a right-up rotation of the platform results in a small leftward movement of the head in space, whereas a rightward translation carries the body and head to the right, in space, even though the CoM moves to the left *with respect to the feet* in both these disturbances. Therefore vestibular inputs cannot provide the directional trigger for the postural response to rotation and translation.

In summary, the automatic postural response to multiple directions of rotation and translation of the support surface was

similar when the two perturbation types were paired appropriately. During the early part of the disturbance, prior to the EMG response, only ground-reaction force angle showed a consistently similar directional tuning for the two perturbation types. All other variables exhibited opposite directional tuning or no significant directional changes.

DISCUSSION

The results of this study suggest that the key variable for shaping the directional tuning of the automatic postural response to sudden movement of the support is the change in ground-reaction force angle, which is equivalent to the ratio of shear and loading forces. The most likely inputs for detecting change in force angle are the directionally specific cutaneous receptors in the paw pads, suggesting that cutaneous sensors

TABLE 2. Early variable changes with the same slope relationships to rotation and translation perturbations

Variable	Perturb Plane		An		Kn		Ve		Wo	
			Rotation	Translation	Rotation	Translation	Rotation	Translation	Rotation	Translation
Sagittal force angle, forelimb	S	Slope	-0.07	-0.17	-0.06	-0.16	-0.09	-0.20	-0.08	-0.16
		r ²	0.85	0.93	0.89	0.94	0.92	0.93	0.88	0.91
Frontal force angle, hindlimb	F	Slope	-0.06	-0.19	-0.03	-0.22	-0.03	-0.23	-0.05	-0.28
		r ²	0.58	0.95	0.51	0.95	0.71	0.96	0.61	0.93
Sagittal force angle, forelimb	S	Slope	NS	-0.20	-0.05	-0.18	-0.02	-0.25	NS	-0.27
		r ²	NS	0.91	0.74	0.95	0.46	0.91	NS	0.94
Frontal force angle, hindlimb	F	Slope	-0.05	-0.21	-0.02	-0.19	-0.03	-0.28	-0.05	-0.36
		r ²	0.58	0.94	0.57	0.93	0.56	0.97	0.63	0.97
F _x amplitude, Forelimb	F	Slope	0.004	0.03	0.003	0.03	NS	0.03	NS	0.04
		r ²	0.20	0.96	0.18	0.95	NS	0.97	NS	0.94
F _x Hindlimb	F	Slope	0.01	0.03	0.003	0.03	NS	0.04	NS	0.05
		r ²	0.21	0.95	0.17	0.94	NS	0.98	NS	0.95
Summed F _x amplitude	S	Slope	0.02	0.12	0.01	0.13	NS	0.15	0.01	0.17
		r ²	0.56	0.97	0.67	0.97	NS	0.99	0.16	0.96
Sagittal CoM displ	S	Slope	0.004	0.02	0.01	0.02	0.01	NS	-0.004	0.02
		r ²	0.28	0.67	0.448	0.88	0.26	NS	0.10	0.72
Sagittal wrist angle	S	Slope	0.02	0.02	0.06	0.02	0.03	NS	0.06	0.03
		r ²	0.28	0.09	0.62	0.33	0.14	NS	0.28	0.20
Sagittal elbow angle	S	Slope	-0.02	-0.02	-0.01*	-0.02	NS	-0.01	-0.03	NS
		r ²	0.12	0.23	0.05*	0.64	NS	0.04	0.37	NS
Sagittal knee angle	S	Slope	-0.07	-0.02	-0.04	-0.03	NS	-0.01	-0.07	-0.02
		r ²	0.75	0.56	0.61	0.90	NS	0.32	0.63	0.68

S, sagittal plane platform displacement: pitch rotation/AP translation. F, frontal plane platform displacement: roll rotation/ML translation. NS, no significant relationship. *, significant to $P < 0.05$, all other values significant to $P < 0.01$.

play a more important role in rapid balance corrections than was previously thought.

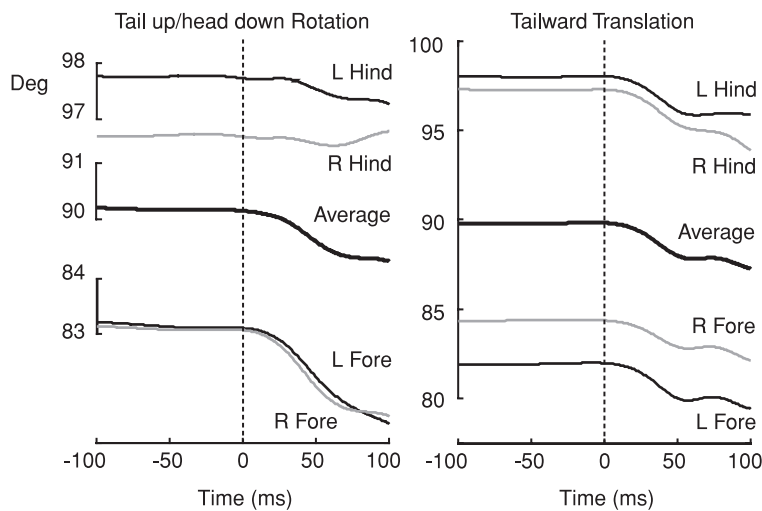
A long-standing question in the field of postural control is the identity of the sensory inputs that shape the directional tuning and amplitude of the initial phase of the automatic postural response to disruptions of balance. Various receptor types have been suggested, including muscle stretch and force sensors, joint receptors, cutaneous receptors, and vestibular and visual sensors. When a subject sways on a solid surface, either naturally during quiet stance or voluntarily, all the sensory signals are generally in agreement regarding the excursion of the CoM. In contrast, when the support surface is moved under the subject, the signals conveyed by various receptors depend on the nature of the surface motion, as demonstrated in the current study. There is generally not a simple mapping between a single sensory signal and the direction of CoM displacement relative to the moving support base. A support surface can move in many different ways such as translating, rotating, dropping, or elevating all disrupting balance. Because the postural response to a disturbance must occur within a short time window for balance to be maintained (Stapley et al. 2002), it is vital that the nervous system be able to rapidly estimate the direction of the impending displacement of the center of body mass, well before the mass has undergone any significant motion. We propose that change in angle of the ground-reaction force provides an unambiguous estimate of the direction of impending motion of the CoM that is induced by a disturbance of the support surface and that cutaneous receptors in the body segment that contacts the support surface may be the receptors that encode this variable. The evidence for this assertion comes from the comparison of the response to rotation and translation of the support surface and depends on the finding that both perturbation types evoke the same postural strategy.

Robust strategy for balance control

Our data suggest that the nervous system uses a single, robust strategy for stabilizing the body that is effective after both rotation and translation perturbations. Because EMG activity reflects the neural output signal, the similarity across many muscles in EMG tuning for rotations and translations suggests that the same neural strategy was used for both perturbation types even though many of the initial kinetic and kinematic effects induced by the perturbations differed substantially. That the same neural strategy is common to rotation and translation corresponds with the directional similarity of imposed displacement of the CoM. The mechanical outcome of the neural strategy was the same for rotations and translations in terms of the pattern of forces at the ground under each limb, i.e., the tuning of force amplitude changes and the force constraint in the horizontal plane (Macpherson 1988a). This robust solution for balance control parallels the notion that similar neuronal circuits can be used to coordinate muscles for multiple tasks as, for example, the spinal circuits that evoke various locomotor modes, scratching, and paw shake (Baev et al. 1991; Buford and Smith 1993; Carter and Smith 1986a,b).

The absence of some flexor muscle activity during rotations is the main deviation from the neural strategy observed in translations, but this may reflect an adaptation of the original strategy to a change in biomechanical task conditions rather than a new, different strategy. In rotations, the postural response consists of a displacement of the body toward the downhill limbs and an increase in extensor activity to accommodate the increased weight support. Because gravity assists the motion of the body, flexor activation in the uphill limbs is not required. The nervous system, therefore, incorporates the contribution of the force of gravity and modifies the postural strategy by reducing the drive to the flexor muscles. In contrast, during translations, the limbs exhibiting flexor responses ac-

A Sagittal force angle for 0° perturbation



B Left forelimb force angles

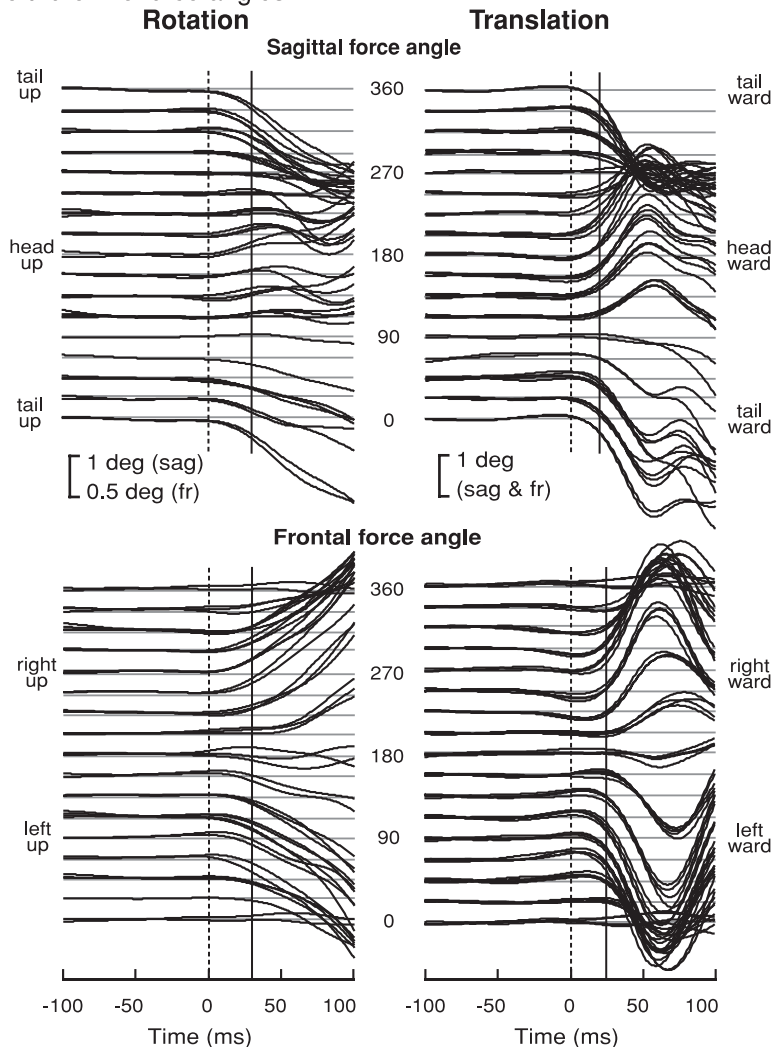
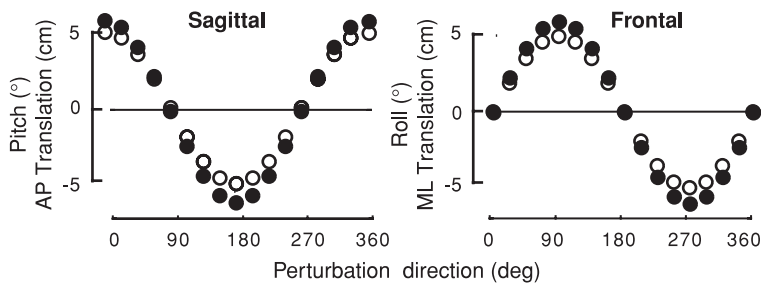


FIG. 7. *A*: mean ground-reaction force angles (platform-based coordinates) for all 4 limbs and the average force angle across all 4 limbs in the sagittal plane during a 0° rotation (*left*) and translation (*right*) for *cat Kn*. All the limbs showed an initial decrease in force angle for both perturbation types. L, left; R, right. *B*: force vector angle from the left forelimb, in the sagittal (*top*) and frontal (*bottom*) planes, plotted for 100 ms before and after onset of rotation (*left*) and translation (*right*) for each direction of perturbation in *cat Kn*. Note that the initial change in angle is in the same direction for the 2 perturbation types, but the rate of change is slower for rotations. Several trials are superimposed for each direction and traces are ordered by perturbation direction from 0° (*bottom*) to 360° (*top*). Solid line, the time point at which data were selected for the plots in Fig. 8. Recorded force traces were filtered with a 4-pole low-pass digital filter with cutoff at 20 Hz to remove high-frequency transients. Vector angles were calculated from the filtered data.

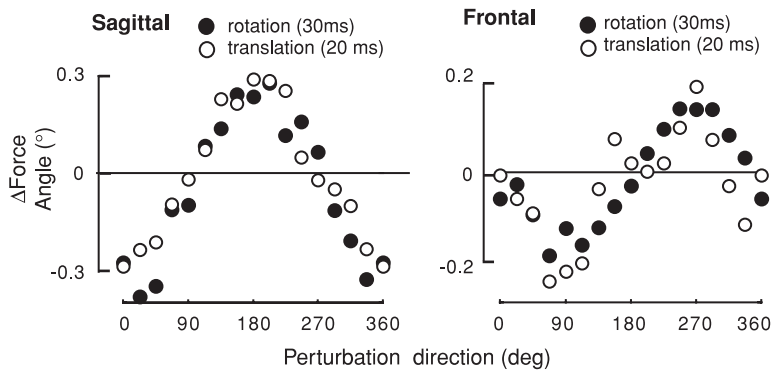
tively pull the body back toward the original position relative to the feet in a direction that is orthogonal to the gravity vector and so the force of gravity does not contribute to the response. The idea that the postural response is slightly modified by the

biomechanical conditions is supported by the fact that the active force response was so similar in rotations and translations in spite of the lack of some flexor EMG responses. Postural adaptation to differing environmental conditions is not

A Platform displacements



B Average force angle tuning curve



C Initial force angle regressed onto platform displacement

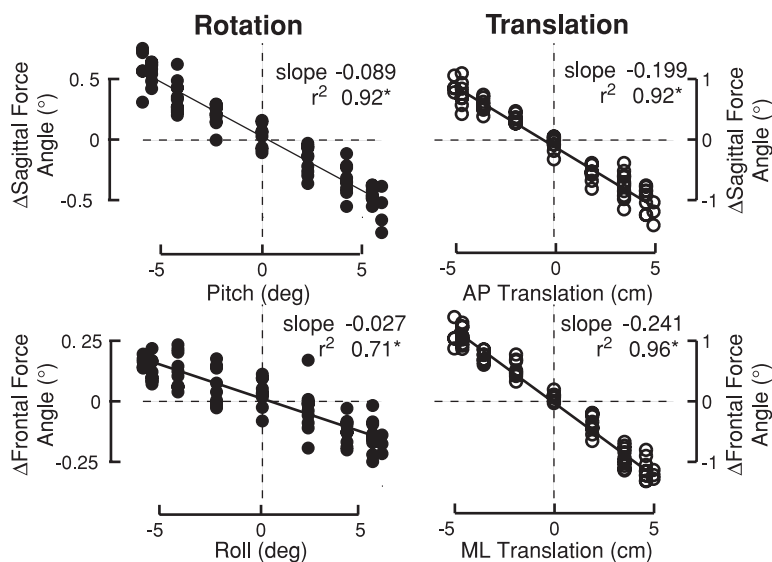


FIG. 8. A: platform displacements in the sagittal and frontal planes in rotations (●) and translations (○). The displacement amplitude in each plane was maximum when the perturbation direction was parallel to the plane and minimum when the perturbation direction was orthogonal to the plane (e.g., platform sagittal displacement was maximum for perturbations at 0 and 180° and 0 for perturbations at 90 and 270°). B: change in average force-angle direction in *cat Kn* for rotations (●) and translations (○). The force-angle change in translation was plotted for 20 ms after onset of perturbation, which is about one-half the latency of the EMG responses. The time at which the change in force angle for rotation reached the same amplitude as that shown for translation was slightly longer (30 ms). C: regression of force angle vs. perturbation displacement for the right forelimb of *cat Ve*.

uncommon; for example, during translations in seated versus standing posture, activity in trunk muscles is similar, but activity in lower leg muscles is absent in seated postures (Forssberg and Hirschfeld 1994; Horak et al. 1992). In standing humans, flexor muscles are recruited in the postural response to both rotations and translations, probably reflecting the different biomechanics of bipedal versus quadrupedal stance (Carpenter et al. 1999; Henry et al. 1998).

Force angle may trigger postural responses

We propose that the initial change in frontal and sagittal ground-reaction force angle provides a robust local signal for

specifying direction of the automatic postural response. Given that the postural responses to rotation and translation originate from the same neural strategy, a parsimonious inference is that there is a common input signal for shaping and initiating the balance response. Our results show that the only initial events common to the two perturbation types across all directions are change in ground-reaction force angle and CoM displacement with respect to the feet.

Force angle is the more likely input for signaling direction, which was surprising because the postural response was *not* predicted by amplitude changes in the individual ground-reaction force components either globally (net force) or locally

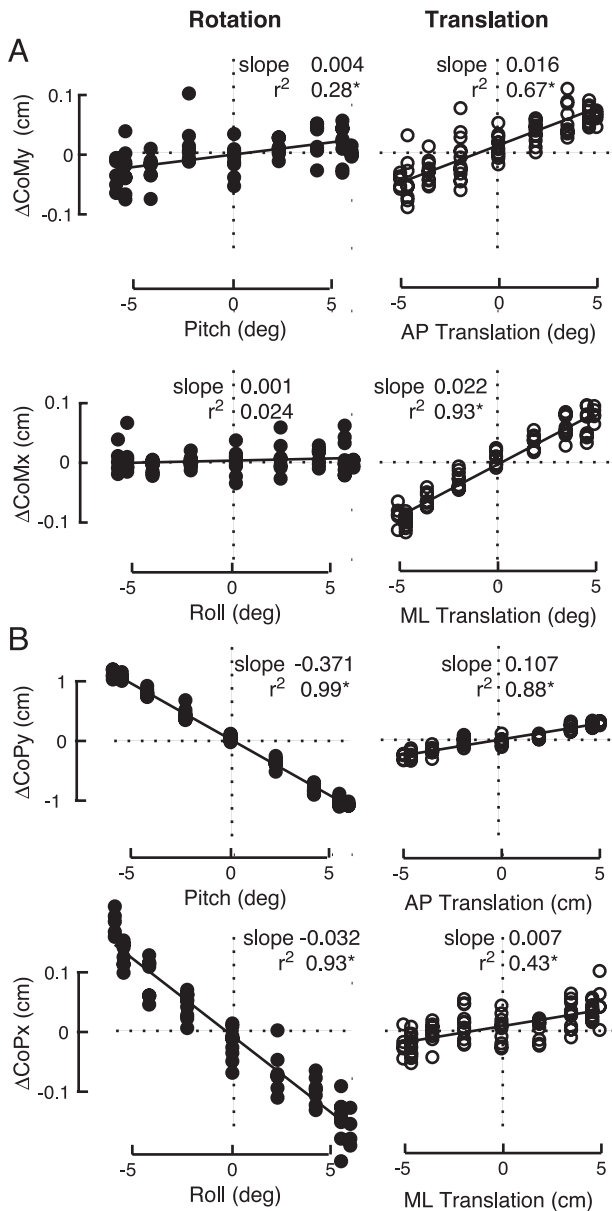


FIG. 9. Initial CoM displacement (A) and center of pressure (CoP) displacement (B) with respect to the feet regressed against perturbation amplitude in the sagittal and frontal planes (*cat An*). Displacements were taken at 25 ms after onset of translations, and 40 ms after onset of rotations. The slopes and coefficients of determination (r^2) are shown for each plot with statistically significant relationships indicated (*). Note that the initial CoM displacement during rotation is quite small and does not have a significant relationship to perturbation amplitude. In contrast, CoP displacement shows a strong relationship to perturbation amplitude that is opposite in rotations compared with translations.

(under any 1 limb). Force angle is related to the ratio of horizontal (shear) and vertical (load) force components, and even though each individual force component changed differently for rotation and translation, the resultant force vector rotated in the same direction immediately after the onset of perturbation for all four paws. Therefore the same change in force angle could occur under conditions of either limb loading or unloading. During stance, the initial change in force angle under the paws is related to the net torque generated about the CoM because the magnitude of the ground-reaction force is

dominated by weight support. Therefore change in force angle may provide the nervous system with an accurate estimate of the direction of the forthcoming destabilization induced by a perturbation. When the support surface moves as a unit, the local angle change under each paw is in the same direction as the change in net force vector. When the limbs are differentially perturbed (Dietz et al. 1989; Rushmer et al. 1987), the postural response in any one limb is likely determined by the local force angle change under that limb. Alternatively, the postural response in all limbs could be shaped by the change in ground-reaction force angle averaged across the limbs, a global variable that would require integration of the local inputs from all the limbs.

The initial displacement of the CoM with respect to the feet may not be a reliable directional signal because the amplitude is quite small and the onset time of motion in the direction related to the perturbation is variable, depending on the direction and velocity of postural sway at the time of the perturbation. Furthermore, the CoM is not a fixed point within the body, and it is not clear what sensory inputs might contribute to the computation of CoM displacement. Vestibular and visual sensory signals provide information about the relative motion of the head in space and likely contribute to computation of trunk in space, which provides a rough estimate of CoM in space (Mergner and Rosemeier 1998). However, in translations and rotations evoking similar postural responses, the motion of the head and body in space is opposite, and therefore the vestibular and visual signals during those perturbations would also be opposite. Moreover, vestibular and visual signals are not necessary for the appropriate timing and directional tuning of the automatic postural response to support surface translation in either humans or cats (see INTRODUCTION).

What sensory inputs might encode change in ground-reaction force angle? The most likely answer is cutaneous receptors in the paw pads. Directional coding of shear force has been demonstrated in the afferents of both slowly and rapidly adapting cutaneous receptors in the fingertips (Birznieks et al. 2001). Cutaneous receptors with similar properties to those in the fingers are found in the glabrous skin of the paw pads in cats (Ferrington 1985; Janig 1971) and the foot sole in humans with observations of directional sensitivity in the latter (Kennedy and Inglis 2002). Slowly adapting cutaneous receptors are particularly sensitive to skin stretch rather than compression and show directional tuning (Leem et al. 1993; Vierck 1979). Thus cutaneous afferents could be instrumental in sensing the rapid initial change in ground-reaction force angle during postural perturbations, and this is consistent with the finding that somatosensory loss causes significant delays in the timing of postural responses in cats (Stapley et al. 2002) and in humans with peripheral somatosensory loss (Bloem et al. 2000, 2002; Inglis et al. 1994).

Cutaneous receptors contribute to the ability to regulate the ratio of slip-to-grip forces in finger-pinch tasks that is essential to avoid slipping of a grasped object (Johansson et al. 1992b). Such receptors appear to subservise the rapid response in finger muscles to sudden slips of a grasped object (Johansson and Westling 1987). An entirely analogous mechanism may underlie the rapid postural response to sudden slips of the support surface (Winstein et al. 2000). Johansson and colleagues have suggested that grip responses are triggered by changes in load (shear) force and that there is a minimum threshold of 0.19 N

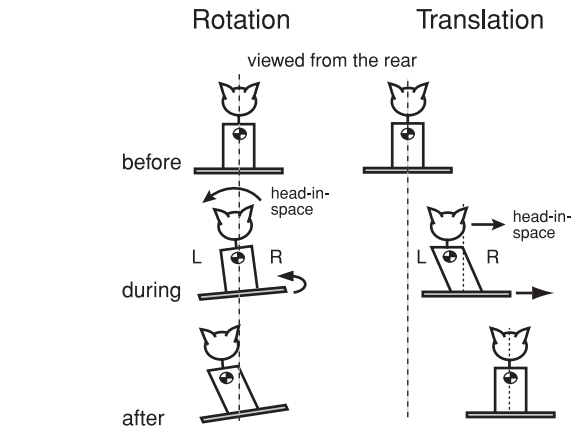
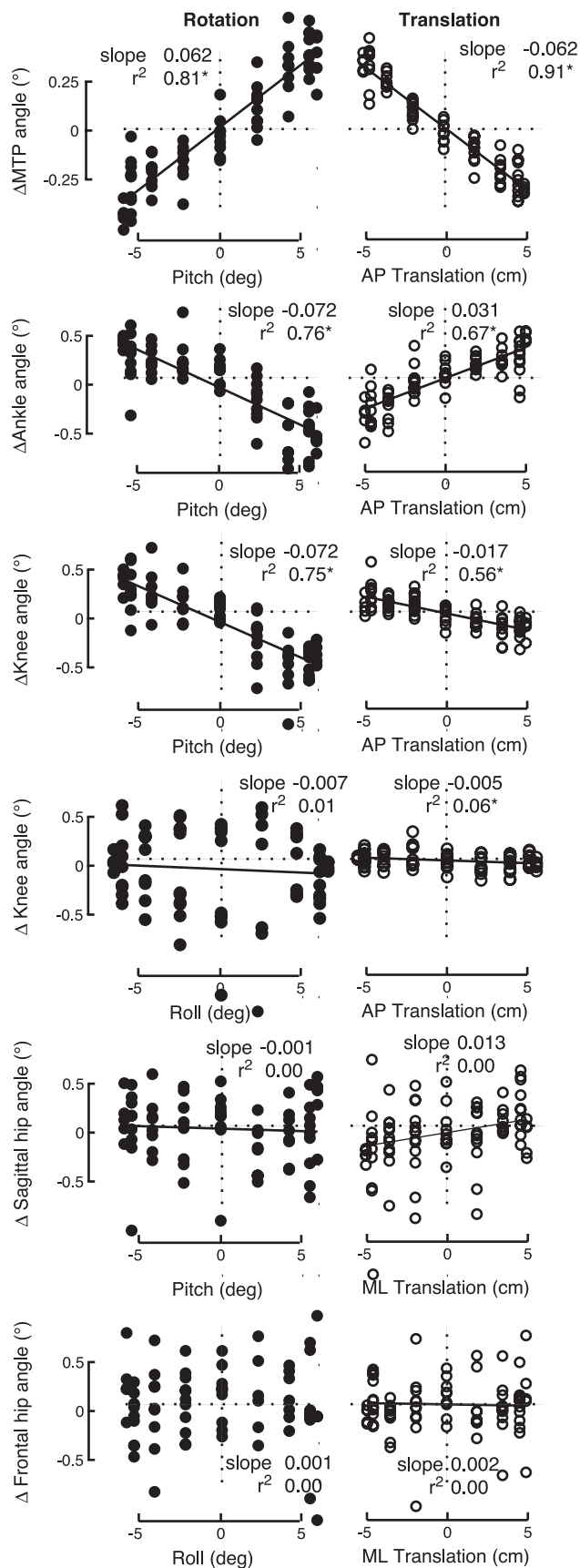


FIG. 11. Schematic illustration of the CoM motion with respect to the feet and with respect to an Earth-fixed reference (vertical dashed line). These 2 coordinate reference systems are the same for rotation but not for translation. In this example of rotation, the CoM moves left with respect to both the feet and to the Earth reference. In translation, however, the CoM moves leftward with respect to the feet but rightward with respect to an Earth-fixed reference as the platform translates to the right.

at which the slip is detected (Johansson et al. 1992a). During translations in the current study, the net horizontal (shear) force under each paw reached the value of 0.19 N at ~15–20 ms after the onset of platform acceleration; this is early enough to have elicited the postural response. However, our results showed that the change in shear force cannot be the trigger signal for the postural response as the vector direction is opposite for translations and rotations having the same postural response, at least in the anteroposterior direction. Furthermore, during rotations, the shear force amplitude often did not reach the threshold value of 0.19 N prior to the active postural response. Instead, the key variable for the postural response seemed to be change in shear to load force ratio.

It is interesting that a simple shear-force threshold mechanism fails to explain the difference in onset time of active grip responses that are evoked for different *directions* of slip in the finger-pinch task. For example, when the slip force is in the same direction as the force of gravity, the grip response is elicited earlier than when the same slip force acts opposite to the gravity vector (HagerRoss et al. 1996). Perhaps it is change in force-vector angle rather than slip-force amplitude that is the key trigger for the slip-grip response in grip tasks. In support of this idea, the ratio of normal to tangential forces, or resultant force angle, appears to be tightly regulated during grip responses (Birznieks et al. 1998; Burstedt et al. 1999). The net force is the vector sum of the applied slip force and the component of force due to gravity acting on the object. When the slip disturbance is applied in the same direction as gravity, it is possible that the change in net force angle could reach the critical threshold sooner than when the slip disturbance is applied in the opposite direction. In the case of postural

FIG. 10. Initial changes in joint angle regressed against perturbation amplitude for *cat An*. Note that the MTP angle shows the opposite sign in the relationship to perturbation amplitude but similar slope magnitude for rotation compared with translation. The only variable that demonstrates slope of the same sign for rotation and translation is the sagittal plane knee angle. However, the regression is significant only for the sagittal plane platform displacement ($P < 0.01$) and not frontal plane displacement. Neither sagittal nor frontal hip angle was significantly correlated to perturbations in either the sagittal or frontal planes.

responses, we observed a longer latency of evoked EMG after rotation compared with translation, which corresponds to the slower rate of change in force angle in the initial phase of rotation compared with translation.

Postural studies in humans and animals have shown that modifying cutaneous input from the feet can affect balance, but the exact role of these inputs has not been clear (Horak and Macpherson 1996). For example, anesthesia or cooling of the foot soles decreased postural stability during quiet stance (Magnusson et al. 1990; Mori et al. 1970; Perry et al. 2000; Thoumie and Do 1996), but the effects seemed rather small perhaps because other sensory signals provide information about body sway that is congruent with foot sole inputs. Cutting cutaneous nerves in the cat hindpaw resulted in small but lasting effects on locomotion, especially under challenging conditions such as ladder-walking (Bouyer and Rossignol 2003), but specific effects on balance control were not analyzed. To test the effects of cutaneous loss on postural reactions in our paradigm is technically challenging—all four paws would have to be denervated because of the redundant nature of the ground-reaction force angle inputs. Furthermore, such denervation is not restricted to the cutaneous inputs from the paw pads.

In studies of human subjects, direct cutaneous stimulation of the foot sole during quiet stance, which mimics motion of the CoP, caused postural sway congruent with an illusion of CoM motion (Kavounoudias et al. 1998; Roll et al. 2002). However, pin-cushion stimulation of a region of the foot sole while the support surface was being rotated did not affect the excursion of CoP or CoM, leading the authors to question the role of cutaneous inputs in standing balance (Maurer et al. 2001). However, this finding supports our assertion that change in CoP is not the critical input for detecting disturbances to balance because the movement of the CoP is not always correlated with the disturbance to CoM, for example, in the case of rotation versus translation of the support surface. The particular stimulus used in the latter study likely produced only orthogonal forces relative to the foot sole, and so there was not likely any illusion of change in ground-reaction force angle. Finally, anesthesia of the feet by use of compression cuffs at the ankle was reported to induce a change in postural strategy in standing subjects, from the ankle sway response to the hip strategy, which is typically used when the support surface is unstable and cutaneous inputs from the foot sole unreliable (Diener et al. 1984; Horak et al. 1990). Indeed it has been suggested that weighting among the various sensory channels changes when inputs from the feet are no longer reliable or the support surface is no longer stable (Peterka 2002). Cutaneous afferents other than from the foot sole along with proprioceptive afferents throughout the body must also provide information regarding postural equilibrium because subjects with lower limb proprioceptive loss are still able to stabilize posture by activating distal muscles, despite abnormally long latencies of evoked postural response (Bloem et al. 2000, 2002). However, these findings speak only to the adaptability of the postural-control system under altered conditions, and they do not negate the importance of cutaneous afferents from the foot sole for shaping the automatic postural response under conditions of normal stance on a firm surface.

Finally, we propose that cutaneous inputs responding to change in ground-reaction force angle are responsible for the

directional tuning of the automatic postural response. Other receptors such as muscle spindles or Golgi tendon organs may provide additional information about the dynamics of a disturbance and may contribute to the timing and amplitude of the initial burst of the postural response. Thus several types of inputs could contribute to the triggering of the automatic postural response, but only cutaneous inputs could encode the directional component within the conditions of our experiment.

In conclusion, a single neural strategy for postural control appears to stabilize balance under two widely varying perturbation conditions. The trigger that specifies direction of this automatic postural response may be the change in angle of the ground-reaction force that directly reflects the direction of impending destabilization of the CoM with respect to the feet. The input that encodes force angle likely arises from a population of cutaneous receptors in the foot sole or glabrous skin of the paw.

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REFERENCES

- Baev KV, Esipenko VB, and Shimansky Yu P. Afferent control of central pattern generators: experimental analysis of locomotion in the decerebrate cat. *Neuroscience* 43: 237–247, 1991.
- Birznieks I, Burstedt MKO, Edin BB, and Johansson RS. Mechanisms for force adjustments to unpredictable frictional changes at individual digits during two-fingered manipulation. *J Neurophysiol* 80: 1989–2002, 1998.
- Birznieks I, Jenmalm P, Goodwin AW, and Johansson RS. Encoding of direction of fingertip forces by human tactile afferents. *J Neurosci* 21: 8222–8237, 2001.
- Bloem BR, Allum JH, Carpenter MG, and Honegger F. Is lower leg proprioception essential for triggering human automatic postural responses? *Exp Brain Res* 130: 375–391, 2000.
- Bloem BR, Allum JH, Carpenter MG, Verschuuren JJ, and Honegger F. Triggering of balance corrections and compensatory strategies in a patient with total leg proprioceptive loss. *Exp Brain Res* 142: 91–107, 2002.
- Bouyer LJ and Rossignol S. Contribution of cutaneous inputs from the hindpaw to the control of locomotion. I. Intact cats. *J Neurophysiol* 90: 3625–3639, 2003.
- Bufoed JA and Smith JL. Adaptive control for backward quadrupedal walking. III. Stumbling corrective reactions and cutaneous reflex sensitivity. *J Neurophysiol* 70: 1102–1114, 1993.
- Burstedt MKO, Flanagan JR, and Johansson RS. Control of grasp stability in humans under different frictional conditions during multidigit manipulation. *J Neurophysiol* 82: 2393–2405, 1999.
- Carpenter MG, Allum JH, and Honegger F. Directional sensitivity of stretch reflexes and balance corrections for normal subjects in the roll and pitch planes. *Exp Brain Res* 129: 93–113, 1999.
- Carpenter MG, Allum JHJ, and Honegger F. Vestibular influences on human postural control in combinations of pitch and roll planes reveal differences in spatiotemporal processing. *Exp Brain Res* 140: 95–111, 2001.
- Carter MC and Smith JL. Simultaneous control of two rhythmical behaviors. I. Locomotion with paw-shake response in normal cat. *J Neurophysiol* 56: 171–183, 1986a.
- Carter MC and Smith JL. Simultaneous control of two rhythmical behaviors. II. Hindlimb walking with paw-shake response in spinal cat. *J Neurophysiol* 56: 184–195, 1986b.

- Diener HC, Dichgans J, Guschlbauer B, and Mau H.** The significance of proprioception on postural stabilization as assessed by ischemia. *Brain Res* 296: 103–109, 1984.
- Dietz V.** Evidence for a load receptor contribution to the control of posture and locomotion. *Neurosci Biobehav Rev* 22: 495–499, 1998.
- Dietz V, Gollhofer A, Kleiber M, and Trippel M.** Regulation of bipedal stance: dependency on “load” receptors. *Exp Brain Res* 89: 229–231, 1992.
- Dietz V, Horstmann GA, and Berger W.** Interlimb coordination of leg-muscle activation during perturbation of stance in humans. *J Neurophysiol* 62: 680–693, 1989.
- Ferrington DG.** Functional properties of slowly adapting mechanoreceptors in cat footpad skin. *Somatosens Res* 2: 249–262, 1985.
- Forsberg H and Hirschfeld H.** Postural adjustments in sitting humans following external perturbations—muscle activity and kinematics. *Exp Brain Res* 97: 515–527, 1994.
- Gollhofer A, Horstmann GA, Berger W, and Dietz V.** Compensation of translational and rotational perturbations in human posture: stabilization of the centre of gravity. *Neurosci Lett* 105: 73–78, 1989.
- Hager Ross C, Cole KJ, and Johansson RS.** Grip-force responses to unanticipated object loading: load direction reveals body- and gravity-referenced intrinsic task variables. *Exp Brain Res* 110: 142–150, 1996.
- Henry SM, Fung J, and Horak FB.** EMG responses to maintain stance during multidirectional surface translations. *J Neurophysiol* 80: 1939–1950, 1998.
- Horak FB and Macpherson JM.** Postural Orientation and Equilibrium. In: *Handbook of Physiology. Exercise: Regulation and Integration of Multiple Systems.* New York: Am. Physiol. Soc., 1996, sect. 12, p. 255–292.
- Horak FB, Nashner LM, and Diener HC.** Postural strategies associated with somatosensory and vestibular loss. *Exp Brain Res* 82: 167–177, 1990.
- Horak FB, Nutt J, and Nashner LM.** Postural inflexibility in parkinsonian subjects. *J Neurol Sci* 111: 46–58, 1992.
- Inglis JT, Horak FB, Shupert CL, and Jones-Rycewicz C.** The importance of somatosensory information in triggering and scaling automatic postural responses in humans. *Exp Brain Res* 101: 159–164, 1994.
- Inglis JT and Macpherson JM.** Bilateral labyrinthectomy in the cat: effects on the postural response to translation. *J Neurophysiol* 73: 1181–1191, 1995.
- Jacobs R and Macpherson JM.** Two functional muscle groupings during postural equilibrium tasks in standing cats. *J Neurophysiol* 76: 2402–2411, 1996.
- Janig W.** Morphology of rapidly and slowly adapting mechano-receptors in the hairless skin of the cat’s hind foot. *Brain Res* 28: 217–231, 1971.
- Johansson RS, Hager C, and Riso R.** Somatosensory control of precision grip during unpredictable pulling loads. II. Changes in load force rate. *Exp Brain Res* 89: 192–203, 1992a.
- Johansson RS, Riso R, Hager C, and Backstrom L.** Somatosensory control of precision grip during unpredictable pulling loads. I. Changes in load force amplitude. *Exp Brain Res* 89: 181–191, 1992b.
- Johansson RS and Westling G.** Signals in tactile afferents from the fingers eliciting adaptive motor-responses during precision grip. *Exp Brain Res* 66: 141–154, 1987.
- Kavounoudias A, Roll R, and Roll JP.** The plantar sole is a “dynamometric map” for human balance control. *Neuroreport* 9: 3247–3252, 1998.
- Kennedy PM and Inglis JT.** Distribution and behaviour of glabrous cutaneous receptors in the human foot sole. *J Physiol* 538: 995–1002, 2002.
- Lacquaniti F and Maioli C.** Independent control of limb position and contact forces in cat posture. *J Neurophysiol* 72: 1476–1495, 1994.
- Leem JW, Willis WD, and Chung JM.** Cutaneous sensory receptors in the rat foot. *J Neurophysiol* 69: 1684–1699, 1993.
- Macpherson JM.** Strategies that simplify the control of quadrupedal stance. I. Forces at the ground. *J Neurophysiol* 60: 204–217, 1988a.
- Macpherson JM.** Strategies that simplify the control of quadrupedal stance. II. Electromyographic activity. *J Neurophysiol* 60: 218–231, 1988b.
- Macpherson JM.** The force constraint strategy for stance is independent of prior experience. *Exp Brain Res* 101: 397–405, 1994.
- Macpherson JM and Fung J.** Weight support and balance during perturbed stance in the chronic spinal cat. *J Neurophysiol* 82: 3066–3081, 1999.
- Macpherson JM, Lywood DW, and Van Eyken A.** A system for the analysis of posture and stance in quadrupeds. *J Neurosci Methods* 20: 73–82, 1987.
- Magnusson M, Enbom H, Johansson R, and Pyykko I.** Significance of pressor input from the human feet in anterior-posterior postural control. The effect of hypothermia on vibration-induced body-sway. *Acta Otolaryngol* 110: 182–188, 1990.
- Maurer C, Mergner T, Bolha B, and Hlavacka F.** Human balance control during cutaneous stimulation of the plantar soles. *Neurosci Lett* 302: 45–48, 2001.
- Mergner T and Rosemeier T.** Interaction of vestibular, somatosensory and visual signals for postural control and motion perception under terrestrial and microgravity conditions—a conceptual model. *Brain Res Rev* 28: 118–135, 1998.
- Mori S, Reynolds PJ, and Brookhart JM.** Contribution of pedal afferents to postural control in the dog. *Am J Physiol* 218: 726–734, 1970.
- Nashner LM.** Adapting reflexes controlling the human posture. *Exp Brain Res* 26: 59–72, 1976.
- Perry SD, McIlroy WE, and Maki BE.** The role of plantar cutaneous mechanoreceptors in the control of compensatory stepping reactions evoked by unpredictable, multi-directional perturbation. *Brain Res* 877: 401–406, 2000.
- Peterka RJ.** Sensorimotor integration in human postural control. *J Neurophysiol* 88: 1097–1118, 2002.
- Roll R, Kavounoudias A, and Roll JP.** Cutaneous afferents from human plantar sole contribute to body posture awareness. *Neuroreport* 13: 1957–1961, 2002.
- Runge CF, Shupert CL, Horak FB, and Zajac FE.** Role of vestibular information in initiation of rapid postural responses. *Exp Brain Res* 122: 403–412, 1998.
- Rushmer DS, Macpherson JM, Dunbar DC, Russell CJ, and Windus SL.** Automatic postural responses in the cat: responses of proximal and distal hindlimb muscles to drop of support from a single hind- or forelimb. *Exp Brain Res* 65: 527–537, 1987.
- Stapley PJ, Ting LH, Hulliger M, and Macpherson JM.** Automatic postural responses are delayed by pyridoxine-induced somatosensory loss. *J Neurosci* 22: 5803–5807, 2002.
- Thoumie P and Do MC.** Changes in motor activity and biomechanics during balance recovery following cutaneous and muscular deafferentation. *Exp Brain Res* 110: 289–297, 1996.
- Vierck CJ.** Comparisons of punctate, edge and surface stimulation of peripheral, slowly adapting, cutaneous, afferent units of cats. *Brain Res* 175: 155–159, 1979.
- Winstein CJ, Horak FB, and Fisher BE.** Influence of central set on anticipatory and triggered grip-force adjustments. *Exp Brain Res* 130: 298–308, 2000.