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Effect of head position on postural orientation and equilibrium

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Abstract This study examined (1) how changes in head position affect postural orientation variables during stance and (2) whether changes in head position affect the rapid postural response to linear translation of the support surface in the horizontal plane. Cats were trained to stand quietly on a moveable platform and to maintain five different head positions: center, left, right, up, and down. For each head position, stance was perturbed by translating the support surface linearly in 16 different directions in the horizontal plane. Postural equilibrium responses were quantified in terms of the ground reaction forces, kinematics, dynamics (net joint torques), body center of mass, and electromyographic (EMG) responses of selected limb and trunk muscles. A change in head position involved rotation of not only the neck but also the scapulae and anterior trunk. Tonic EMG levels were modulated in several forelimb and scapular muscles but not hindlimb muscles. Finally, large changes in head orientation in both horizontal and vertical planes did not hamper the ability of cats to maintain postural equilibrium during linear translation of the support surface. The trajectory of the body’s center of mass was the same, regardless of head position. The main change was observed in joint torques at the forelimbs evoked by the perturbation. Evoked EMG responses of forelimb and scapular muscles were modulated in terms of magnitude but not spatial tuning. Hindlimb responses were unchanged. Thus, the spatial and temporal pattern of the automatic postural response was unchanged and only amplitudes of evoked activity were modulated by head position.

Key words Balance · Sensorimotor transformation · Neck proprioception · Vestibular system · Cat

Introduction

Control of postural orientation and equilibrium is believed to involve the integration of information from multiple sensory channels including somatosensory (primarily proprioceptive), vestibular, and visual (reviewed by Horak and Macpherson, 1996). It has been hypothesized that the position of the trunk in space may be an important controlled variable for balance, in part because the trunk contains most of the body mass (Gurfinkel et al. 1981; Inglis and Macpherson 1995). According to Mergner’s model (Mergner et al. 1997), the position of trunk in space may be derived from two sources, (1) proprioceptive inputs from successive body segments, beginning with those in contact with the support surface (usually the feet); and (2) vestibular “head-in-space” inputs combined with neck proprioceptive “head-on-trunk” inputs, with appropriate matching of the sensory dynamics. Under dynamic conditions, the pattern of stimulation of vestibular and neck afferents will depend upon head position yet the combination of these signals should still yield an accurate representation of “trunk-in-space.”

Automatic postural responses to unexpected perturbations tend to minimize the displacement of the body’s center of mass. The nervous system must use sensory information to assess current body position and configuration as well as the direction and velocity of the disturbance. Different head positions will result in different sensory signals from both head and neck evoked by a perturbation, even if the change in head position does not alter the position of the body center of mass. For example, when a cat stands with its head in the forward, neutral position and the support surface is translated anteriorly, the otoliths will detect a linear acceleration whose net vector points along the sagittal axis of the head in an occipitofrontal direction. Neck proprioceptors will be stimulated symmetrically on left and right sides. If the head is rotated to the right in yaw by 60° and the animal is subject to the same anterior translation relative to the feet, the otoliths will now detect a linear acceleration whose main vector points along an axis that is rotated in the horizontal plane.
by 60° toward the right ear. Acceleration of the head will result in an asymmetric stimulation of neck afferents. Nevertheless, the motor response evoked by the translation must be similar in both cases, because the body’s center of mass is accelerated in the same direction relative to the animal’s base of support. This study addresses the questions of how the standing animal achieves different head positions kinematically and how the dynamic postural system copes with different head positions that result in different combinations of vestibular and neck proprioceptive inputs. This study represents the first in a series that examines the influence of head position and head movement on postural equilibrium.

Materials and methods

Experimental paradigm

These experiments were conducted with the approval of the institutional animal care and use committee and conformed to the guidelines established by the NIH for the care and use of animals. Four cats were used in this study, three males (Go, Rg, and Rb) and one female (So), ranging in weight from 3.6 to 4.3 kg. Each cat, under anesthesia, received implants of chronically indwelling EMG electrodes consisting of pairs of multisstranded stainless steel wire coated with Teflon insulation; sterile techniques were used. The recorded muscles are listed below, with the numbers in parentheses indicating the number of cats.

1. Left hindlimb: gluteus medius (3), vastus lateralis (2), anterior sartorius (2), rectus femoris (2), lateral gastrocnemius (2), tibialis anterior (2), caudal semimembranosus (2)
2. Left forelimb and scapula: supraspinatus (3), infraspinatus (2), teres major (1), spinotrapezius (1), levator scapulae (2), brachialis (3), triceps brachii – lateral head (3), triceps brachii – long head (3)
3. Trunk: longissimus dorsi at T5 (2), T12 (2), and L5 (2)

The animals were trained using food and positive verbal reinforcement, to stand unrestrained on four force plates mounted on a moveable platform, with their weight equally distributed on left and right sides. In addition, they were trained to assume each of five different head positions as required and to maintain that head position during both stance and perturbations to stance. The required head orientation was indicated by the presence of a food bowl as visual target and by auditory and visual cues provided by one of the experimenters. The five head positions are shown in Fig. 1 and consist of the center position with head level and facing forward, and four rotated positions, right, left, up, and down. Head position was monitored visually and perturbations were delivered only when the head was in the correct position. If the animal moved its head prior to or during the disturbance, the trial was discarded. For the last cat, Rb, head position in space was recorded using a 6-df magnetic tracking device (Fastrak; Polhemus) with a transmitter mounted approx. 20 cm above the head of the cat and a receiver on the electromyographic (EMG) connector that was cemented to the skull. These measures verified that visual inspection was effective in monitoring head position. Furthermore, it was confirmed that the change in head orientation was large. Yaw position with head forward (0°) had a standard deviation of 9° (n=80); the mean value of a turn to the left was –74° (±23°, n=80) and a turn to the right, +75° (±15°, n=80). Pitch position with head forward had a standard deviation of 10°; the mean excursion in downward pitch was 50° (±14°, n=80) and upward pitch, –52° (±5°, n=80).

Each animal stood at a constant fore-hindpaw distance for all head positions. For each cat, this was its preferred distance as determined during free stance on the laboratory floor. During periods of quiet stance, the animals were given repeated trials of linear ramp-and-hold translations of the support surface in each of 16 directions in the horizontal plane, spaced at 22.5° intervals. The reference coordinate system for translation direction is shown in Fig. 1. The amplitude ranged linearly from 2.5 cm for lateral translations to 4.0 cm for longitudinal (mean peak velocity of 16 cm/s). The postural reactions of the animals were quantified in terms of the 3D forces exerted by each paw against the support, EMG activity, and 3D positions of the body segments on the animal’s left side (Optotrak; Northern Digital). The Optotrak system was used to calculate a coordinate transform for the Fastrak magnetic data such that both position systems used the same coordinate reference frame based on the platform axes (lateral axis x, and longitudinal axis y) and the gravity vector (z). Thus, pitch was defined as a rotation about the x-axis (positive nose down), roll about the y-axis (positive left ear down), and yaw about the z-axis (positive nose to the right), as shown in Fig. 1.8.

The kinematic markers were placed over the joint centers. For those joints over which the skin has more motion (shoulder, scapula, and knee), markers were placed with the aid of palpation while the animal was standing on the platform. Because the joint angle changes during translation are small (usually less than 6°), skin slippage was not considered to be a significant problem for estimating joint centers.

Data collection consisted of 1-s trials with 160 ms of quiet stance preceding the platform translation. Force, EMG, and platform position data were recorded at 500 samples and kinematic data at 100 samples. EMGs were bandpass filtered (300 Hz and 2 kHz), full-wave rectified and low-pass filtered at 35 Hz prior to digitization. Only one head position was tested in a single session. Within a session, five trials were collected in sequence for each direction of perturbation (total 80 trials per session). One or two sessions were recorded for each of the five head positions on successive days. A more detailed description of the equipment and the paradigm can be found in previous publications (Fung and Macpherson 1995; Macpherson et al. 1987).