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Vestibular-evoked reflexive head movements and their dependence on the body's orientation in space

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Abstract-**When the body is passively moved in space the mass of the head imposes force on the cervical spinal column. Reflexive activation of the neck musculature during whole body motion is hypothesized to function to counteract the inertial forces of the head. However, even when the body is stationary in space gravitational acceleration imposes force on segments of the body. Counteracting this force is complicated because it changes as the body's orientation changes with respect to gravity. In this study, we have focused on a subset of vestibulo-collic reflexes that act to stabilize the head when the whole body is rotated. The kinematics of reflexive head movements produced in response to whole body rotation were recorded from Squirrel Monkeys. The orientation of the body was sequentially manipulated to determine how gravity influences the kinematics of the reflexive head movements. Only small changes in reflexive head movement gain were observed at low stimulus frequencies. In contrast, larger changes in gain were observed at higher stimulus frequencies. These results suggest the vestibular system compensates for the body's orientation in space while regulating the postural stability of the head with respect to the trunk during low frequency perturbations of the body.**

I. INTRODUCTION

Postural reflexive mechanisms evolved when mammals began to ambulate in order to counteract the inertial forces produced by the mass of the body [1, 2]. The cervical spinal column is particularly vulnerable to the inertial forces caused by the mass of the head when the body moves in space [3-6]. Several collic reflexes are thought to protect the cervical spinal column from injuries that could arise due to these forces [7-10]. The fundamental principle of these reflexes is to transform sensory signals into motor signals which act to stiffen the neck musculature to compensate for the forces produced by the head's inertia.

Both vestibular- and proprioceptive-evoked reflexes are known to activate the neck musculature [7, 8]. The vestibulo-collic reflexes (VCR) receive input from the vestibular labyrinths and convey sensory information via the vestibulospinal pathways to the cervical neck motor nuclei. The cervico-collic reflexes (CCR) receives input from muscle spindles and activate the neck musculature either directly though a cervical stretch reflex, or indirectly through proprioceptive inputs converging on the vestibulospinal pathways. Both reflexes are coordinated to compensate for the inertia of the head during movement of the body [11-17].

Gravitational acceleration also imposes forces on the body. The direction of gravitational acceleration is constant; however, the force it imposes on a segment of the body dynamically changes with respect to the body's orientation in space. The goal of the present work was to determine how gravitational acceleration influences the kinematics of vestibular reflexes which compensate for the inertia of the head.

A series of experiments were carried out in awake Squirrel Monkeys to characterize the effects of gravitational acceleration on the kinematics of yaw head movements produced during horizontal rotation of the body. The orientation of the animal's body in space was manipulated to quantify the gravitational influence on head movement kinematics. The results show that the primary influence of gravity occurs during high frequencies of rotations such that the head movements with respect to the trunk are larger compared to an upright orientation. At low stimulus frequencies, the head movement kinematics were remarkably unaltered by the direction of the gravitational force exerted on the head. These results suggest that the neural substrate of the vestibulocollic reflexes activates the neck musculature differently depending on the orientation of the body in space, presumably using otolith inputs, in order to compensate for differences in the gravitational forces exerted on the head.

II. METHODS

A. Surgical preparation

Four adult squirrel monkeys were surgically prepared for chronic recordings of head movements. A cap constructed of dental acrylic was attached to the cranium using small stainless steel bolts. A keyed bolt was embedded in the acrylic, which was used to attach the animal's head to the apparatus. All surgeries were carried out under isoflourane anesthesia. All procedures were approved by the University Committee for Animal Resources (UCAR).

B. Experimental setup

Squirrel monkeys were seated in a chair on a multi-axis rotator (Fig. 1A) that was used to rotate the animal's whole

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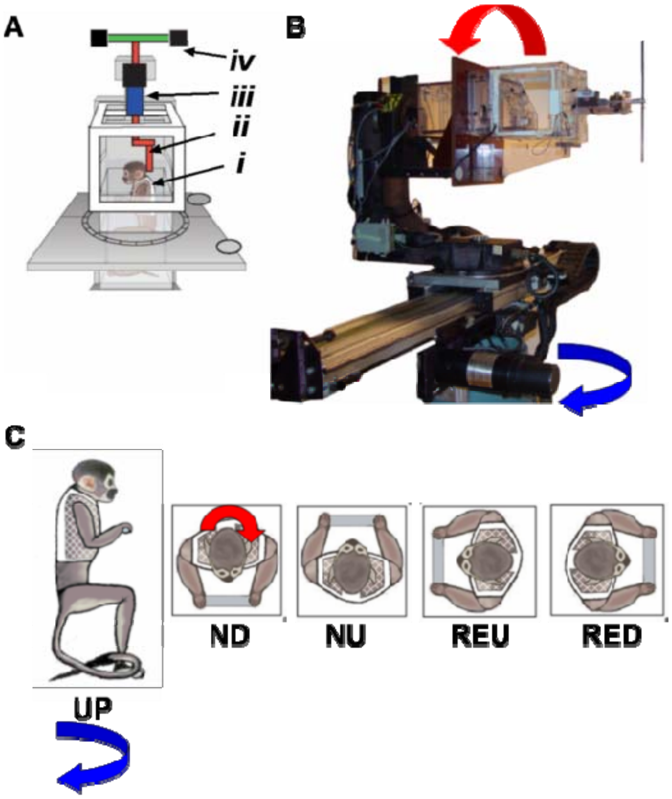

Fig. 1**A.** Monkeys are seated upright in a chair. Each animal wore a jacket (*i*) to restrict trunk movements. Its head was connected to a rod which only allowed yaw head movements (*ii*). The rod was connected to a rotational torque sensor (*iii*) and load (*iv*). **B.** Experimental apparatus has two motors for rotating the subject about the earth-horizontal axis (*red arrow*) and the earth vertical axis (*blue arrow*). The experimental box (**A**) could be oriented along the earth-vertical or -horizontal (shown) axes. **C.** Frontal views of the different body orientations tested (colored arrows denote motor used and corresponding direction of rotation). *Abbreviations: ND, nose-down, NU, nose-up, REU, Right ear up, and RED, Right ear down.*

body in yaw. The multi-axis rotator contains two rotational motors, one that rotates about an earth-vertical axis (Fig. 1B, *blue arrow*) and a second that rotates about an earth-horizontal axis (Fig. 1B, *red arrow*). Two experimental conditions were used including: 1) the animal was oriented vertically and was rotated in yaw about the *earth-vertical axis* and 2) the animal was repositioned horizontally so that its body could be rotated in yaw about the *earth-horizontal axis*. Four conditions were studied while the body was in the horizontal position. The body's position with respect to gravity was sequentially reoriented in yaw using a sundial mechanism. Yaw rotations were imposed while the nose was up (NU) or down (ND) and while the right or left ear was up (REU, RED).

A system for applying passive torque to the neck was used. Two symmetrically-located masses (25g.) were attached to a light-weight horizontal rod (Fig. 1A, *iv*) 3.5 inches from the center of rotation of the vertical rod through a rotational torque sensor (Lebow, 1701; Fig. 1A, *iii*). When the whole body was rotated the two masses produced a torque that was proportional to rotational acceleration and the square of the distance of the masses from the vertical rod. The system was balanced using two symmetrically-located masses so that the torque it produced was not affected by its orientation in space.

C. Experimental paradigm

The monkeys were seated upright within the chair in all experiments. Two experimental conditions were used including: 1) the animal's chair was oriented upright and was rotated in yaw about the *earth-vertical axis* (Fig. 1C, *UP condition*) and 2) the animal's chair was repositioned and oriented horizontally so that its body could be rotated in yaw about the *earth-horizontal axis* as illustrated in Fig. 1B (*red arrow*). The animal's initial orientation in yaw was sequentially manipulated by rotating the earth-horizontal axes in 90º increments (Fig. 1C) so that yaw rotations were imposed while the nose was up (NU) or down (ND) and while the right ear was up or down (REU, RED). Then the animal was sinusoidally rotated (0.5-1.5Hz, 20º/s) in yaw about each orientation. Stimuli were chosen because they are close to the resonant frequency of reflexive head movement in squirrel monkeys. The animal's head position, head torque and the position and velocity of the multi-axis rotator were recorded using A/D converters of a National Instruments data acquisition system (sampling rate, 500Hz).

D. Data Analysis

Analysis was carried out using software written in Matlab. Records of head and table velocity were averaged with respect to the stimulus cycle. Averaged records were fit using a sinusoidal function in order to compute the amplitude and phase of the reflexive head movement and the average torque imposed on the head. Records in which voluntary head movements were produced were eliminated from the analysis prior to signal averaging.

III. RESULTS

When the whole body was in an upright posture and rotated, only small compensatory head movements were produced in Squirrel Monkeys. The gain of the head movement with respect to the trunk in this orientation was typically smaller than 0.3. To study the influence of the inertia of the head, mass was added to the rotational axis of the head in order to increase the head movements that were produced. Two masses (25g.) were added to the horizontal bar at a radius of 3.5 inches from the center of rotation of the head (Fig. 1A). In all cases, the masses and their location were the same. Head movements were then recorded while the body was upright and rotated in yaw about the earth-vertical axis and while the whole body was horizontal and rotated in yaw about the earth-horizontal axis. Four orientations including: nose up (NU), nose down

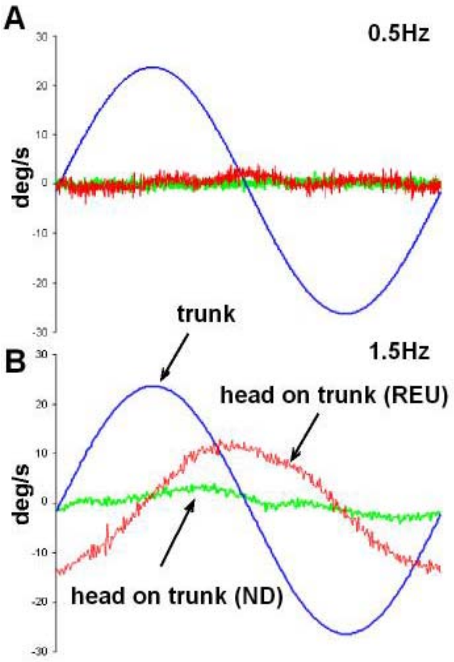

Fig. 2. Data records averaged with respect to each cycle. Each plot contains the trunk and head on trunk velocity produced during whole body rotations at: (**A**) 0.5Hz and (**B**) 1.5Hz whole body rotations for both the nose down (ND, *green*) and right ear up conditions (REU, *red*).

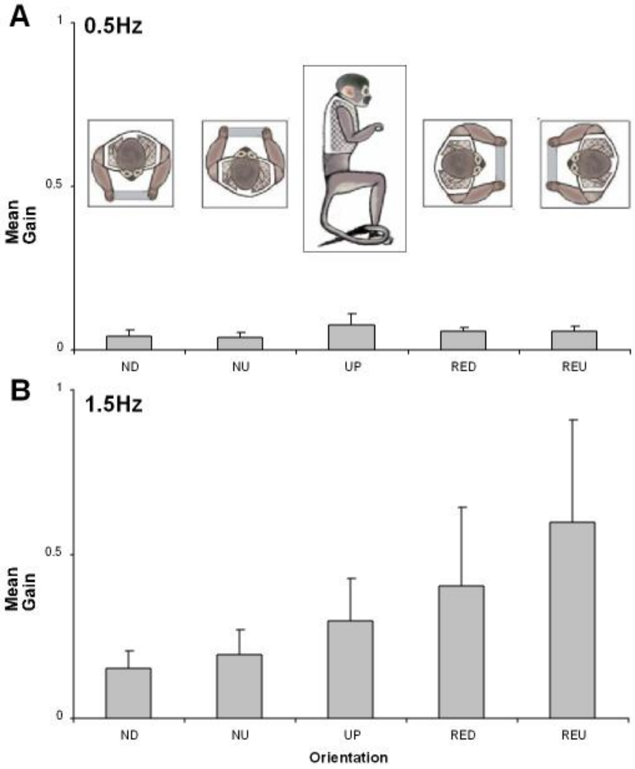

Fig. 3. Averaged gains (Head on Trunk/Trunk) for each body orientation for: (**A**) 0.5Hz and (**B**) 1.5Hz whole body rotations. Error bars are standard errors. *Abbreviations: ND, nose-down, NU, nose-up, REU, Right ear up, and RED, Right ear down.*

(ND), right ear up (REU) and right ear down (RED) were studied while the body was oriented horizontally.

When the body was sinusoidally rotated at low frequencies (0.5 Hz), very small head movements were produced regardless of the animal's orientation in space. Fig. 2A shows the average head movement of one monkey during 0.5Hz sinusoidal whole body yaw rotation while the nose was oriented downwards (green) and while the right ear was oriented upward (red). In each condition when the animal's body was horizontal and rotated in yaw about the earth-horizontal axis, the gain was small and the animal was capable of stabilizing its head with respect to its trunk regardless of the head's initial orientation in space.

At higher stimulus frequencies, the monkeys failed to stabilize their head with respect to the trunk in all orientations. Fig. 2B shows the average head movement of one monkey during 1.5Hz sinusoidal whole body yaw rotation while the nose was oriented downwards (green) and while the right ear was oriented upward (red). When the nose was up or down the gain of the head on trunk movement varied on an individual basis but on average was smaller than when the animal's body was upright and rotated about the earth-vertical axis. However, when the right ear was up or down, the gain of the head movement was larger than when the animal's body was upright and rotated about the earth-vertical axis (*red trace in* Fig. 2B). In addition, the head on trunk movement was almost always in phase with whole body acceleration.

Fig. 3 is a bar graph summarizing the mean gains of the head on trunk movement for 0.5Hz and 1.5Hz for all body orientations tested. At low frequencies, the largest gains were observed during upright whole body rotations about the earth-vertical axis. However, in general the gains were small for all orientations when the the body was rotated at 0.5Hz. At higher frequencies, the gain of the head on trunk movements were always the highest when the right ear was up or down (Fig. 3B).

IV. CONCLUSIONS

Studies in humans have shown that the kinematics of yaw head movements are maintained during horizontal rotation of the whole body even when weight is added to the head [13]. A fundamental question addressed in this study was whether the kinematics of reflexive head movements were affected by gravitational forces exerted on the body. These forces are particularly important because the body's orientation in space dictates the magnitude and direction of the gravitational force exerted on the body. A novel experimental paradigm was designed to determine if head movement reflexes were affected by gravitational forces.

In each circumstance, the whole body was rotated in yaw while the body's orientation in space was sequentially manipulated. In each orientation, the gain of the reflex remained small during low frequency stimuli. These results indicate that the kinematics of reflexive head movements produced in the yaw plane were maintained and unaffected by the direction of gravitational acceleration at low frequencies. When the stimulus frequency was increased we observed large changes in the kinematics of yaw head movements as a function of the body's orientation in space. In particular, the gain of the reflex was smaller in the nose up and nose down orientations during yaw rotations about the earth horizontal axis in comparison to an upright orientation during rotations about the earth vertical axis. In addition, the gain of the reflex was always higher during the right ear up or right ear down orientations during yaw rotations about the earth horizontal axis. The results indicate that the inertia of the head is more significant during high frequencies of rotation.

In conclusion, the addition of passively applied torque provides a novel method by which to study the interactions between the VCR and the CCR. Current investigations are underway to determine what central pathways contribute to the signal processing underling the generation of these unique head movements. Such work may provide insight as to how reflexive head movements adapt during development or during changes in the homeostasis of the vestibular endorgans.

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