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HEAD MOVEMENT DURING WALKING IN THE CAT

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Abstract—Knowledge of how the head moves during locomotion is essential for understanding how locomotion is controlled by sensory systems of the head. We have analyzed head movements of the cat walking along a straight flat pathway in the darkness and light. We found that cats' head left-right translations, and roll and yaw rotations oscillated once per stride, while fore-aft and vertical translations, and pitch rotations oscillated twice. The head reached its highest vertical positions during second half of each forelimb swing, following maxima of the shoulder/trunk by 20–90°. Nose-up rotation followed head upward translation by another 40–90° delay. The peak-to-peak amplitude of vertical translation was ~1.5 cm and amplitude of pitch rotation was ~3°. Amplitudes of lateral translation and roll rotation were ~1 cm and 1.5–3°, respectively. Overall, cats' heads were neutral in roll and 10–30° nose-down, maintaining horizontal semicircular canals and utriculi within 10° of the earth horizontal. The head longitudinal velocity was 0.5–1 m/s, maximal upward and downward linear velocities were ~0.05 and ~0.1 m/s, respectively, and maximal lateral velocity was ~0.05 m/s. Maximal velocities of head pitch rotation were 20–50 °/s. During walking in light, cats stood 0.3–0.5 cm taller and held their head 0.5–2 cm higher than in darkness. Forward acceleration was 25–100% higher and peak-to-peak amplitude of head pitch oscillations was ~20 °/s larger. We concluded that, during walking, the head of the cat is held actively. Reflexes appear to play only a partial role in determining head movement, and vision might further diminish their role.

Key words: locomotion, posture, vestibular, head fixation point.

INTRODUCTION

To navigate successfully through complex natural environments, humans and animals depend on visual, vestibular, and somatosensory information about the orientation of their head and body. Vision is used to locate objects in the environment, determine the route of locomotion, and often to plan individual steps (e.g., Hollands and Marple-Horvat, 1996; Patla, 1997; Sherk and Fowler, 2001; Warren et al., 2001). The vestibular system provides information about the orientation of the head in respect to the vector of gravity, head rotation and acceleration (e.g., Peterson, 2004; Angelaki and Cullen, 2008). Additionally, vestibular and somatosensory mechanisms including vestibulo-collic and cervico-collic reflexes (e.g., Bilotto et al., 1982; Peterson et al., 1985; Wilson et al., 1995; Goldberg and Cullen, 2011), and vestibulo-ocular reflex participate in stabilizing gaze (Donaghy, 1980a,b; rev. in Raphan and Cohen, 2002). Jointly, information from receptors on the head is crucial for successful locomotion, and consequently the knowledge of how the head moves during locomotion is essential for understanding how locomotion is controlled by sensory systems of the head.

Movements of the head during locomotion were intensively studied in humans including during walking overground (Grossman et al., 1988; Pozzo et al., 1990, 1991; Cromwell et al., 2001, 2004; Imai et al., 2001; Kavanagh et al., 2005) and on the treadmill (Crane and Demer, 1997; Hirasaki et al., 1999), walking with different velocities and directions (Cappozzo, 1981; Hirasaki et al., 1999; Nadeau et al., 2003), and walking on irregular and inclined surfaces (Cromwell, 2003; Menz et al., 2003). One focus in these studies was on the relationship between the head vertical displacement and pitch (nose up-down) rotation. These movements are of substantial amplitudes and often are coupled so that the head upward displacement occurs simultaneously with nose-down rotation, while the downward displacement is simultaneous with nose-up rotation. Due to such relationship between these movements, a ''head fixation point" is maintained, which is a point in space where the occipito-nasal axes of the head coincide in space for different head positions during the step cycle (Pozzo et al., 1990; Hirasaki et al., 1999; Hirasaki and Kumakura, 2004). Having such a fixation point for the head is believed to assist in processing visual information during locomotion.

Studies of head movements during locomotion in quadrupeds are much fewer. They were conducted in monkeys and horses (Dunbar, 2004; Dunbar et al., 2004, 2008; Xiang et al., 2008), and showed that while movements of the head in quadrupeds and bipeds are similar in many aspects, there are important differences as well. For example, while walking bipeds (humans and non-human primates) typically have a head fixation point, the head of quadrupeds (monkeys and horses) often translates and rotates in the same direction during the stride (nose-up while translating upward and vice versa),

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resulting in no fixation point in front of the animal. This difference raises the question whether head contribution to gaze behavior is different between bipedal and quadrupedal locomotion.

It is quite surprising that head movements have not been intensely investigated in the cat, which has been the classic subject for studies of visual, vestibular, and motor systems for at least two centuries. Currently, there exist limited data on cat head movement during locomotion (Graf et al., 1995; Carlson-Kuhta et al., 1998; Fowler and Sherk, 2003; Beloozerova et al., 2010). The cat, however, is the animal closest to humans whose unconstrained locomotion behavior can be fully researched in a laboratory setting, including neuronal mechanisms of locomotion and posture (e.g., Beloozerova and Sirota, 1993; Drew, 1993; Matsuyama and Drew, 2000a,b; Karayannidou et al., 2009; Zelenin et al., 2010; Marigold and Drew, 2011; Farrell et al., 2014; Stout et al., 2015). Therefore, researching how cats move their head during walking is of significant interest.

While studying head movements of the walking cat, our first aim was to determine how cats hold the head in respect to the earth horizontal. This orientation is important, because it determines the efficacy of activation of vestibular receptors during locomotion. Studies by Graf and colleagues (1995) showed that, while cats may at times rotate their head substantially, most of the time they keep horizontal semicircular canals oriented within 5–15° of the earth horizontal. Unfortunately, the authors' quantity of data in respect to locomotion was limited. In humans, non-human primates, and horses, however, it was found that during most locomotor tasks the head rotation remains within a 20° range in all planes, providing a relatively stable spatial reference frame to the brain (Pozzo et al., 1990; rev. in Dunbar et al., 2008). We were interested in whether the head orientation of the walking cat complies with this rule.

Our second objective was to estimate the contribution of head mechanical properties and potential contribution of reflexes to head movement during walking. To accomplish this, we analyzed frequencies of head movements, their velocities, and accelerations. It is believed that during locomotion, reflexes participate greatly in establishing orientation of the head with respect to the earth horizontal and support surface, and in governing head movements. For example, rotation of the head around the intra-ural axis (in pitch), which in bipeds stabilizes the head fixation point in space, is considered to be a result of vestibulo-collic reflexes both in bipeds and quadrupeds (Hirasaki et al., 1999; Xiang et al., 2008). Therefore, we investigated whether rotational movements of the head in the cat during walking are a mechanical consequence of head translations, and whether velocities and accelerations of head translations and rotations are in the ranges that activate vestibulo-collic and cervico-collic reflexes.

Finally, we were interested in the role of light in head orientation and movement during locomotion. During walking under normal laboratory illumination there are many potential visual targets in the environment for the animal to look at, ranging from pieces of dirt on the walkway to objects in the laboratory. We previously found that cats look at closer points on the walkway when walking in the light than in darkness (Rivers et al., 2014). This is likely because in the light, proximal areas of the walkway were of interest to the cats. Therefore, to differentiate head movements related to viewing of the environment from those determined by other locomotor mechanisms, we examined head movement during walking in both light and complete darkness.

We found that during walking the head of the cat underwent small translations and rotations along all of its axes: the left-right translation, and roll and yaw rotations oscillated once per step cycle, while the fore-aft and vertical translations, and pitch rotation oscillated twice. During walking, the head was oriented nose-down so that horizontal semicircular canals and utriculi stayed within ±10° of the earth horizontal most of the time. Head velocities and accelerations were well in the activation range for vestibulo-collic and cervico-collic reflexes. Head rotation movements, however, could not be completely explained as reflexes of head translations. Illumination of the room caused cats to hold their head slightly higher and move it more. We concluded that, during walking, the head of the cat is held actively. However, reflexes appear to play only a partial role in determining head movement, and vision might further diminish their role.

A partial account of this study was published in abstract form (Rollando et al., 2012; Zubair et al., 2015).

EXPERIMENTAL PROCEDURES

Three adult cats were used in these studies: two females (Cat 1, 3.7 kg and Cat 3, 3.0 kg) and a male (Cat 2, 4.0 kg). The data were collected during our study of gaze behaviors in freely walking cats, which was reported previously (Rivers et al., 2014). These cats were also used for other studies (Marlinski et al., 2012a,b; Armer et al., 2013; Favorov et al., 2015). All experiments were conducted in accordance with NIH guidelines and with the approval of the Barrow Neurological Institute Animal Care and Use Committee.

Locomotor tasks

Food was used as positive reinforcement to adapt cats to the experimental situation and engage them in locomotor behavior (Skinner, 1938; Pryor, 1975). Cats walked in a chamber divided by a longitudinal wall into two corridors, a test- and return-corridor, each 2.5-m-long and 0.28-m-wide (Fig. 1A). Cats passed through the chamber sequentially and repeatedly in a counter-clockwise direction. The floor in the chamber was covered with rubberized black material. In the test corridor, one wall was constructed of clear acrylic plastic to permit recording of cat movements (see below), while other walls were opaque. The passage of the cat throughout the test corridor was monitored using photo-sensors paired with infrared light-emitting diodes (LEDs). LEDs had emission wavelengths