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Gravity matters: Motion perceptions modified by direction and body position

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ABSTRACT

Motion coherence thresholds are consistently higher at lower velocities. In this study we analysed the influence of the position and direction of moving objects on their perception and thereby the influence of gravity. This paradigm allows a differentiation to be made between coherent and randomly moving objects in an upright and a reclining position with a horizontal or vertical axis of motion. 18 young healthy participants were examined in this coherent threshold paradigm. Motion coherence thresholds were significantly lower when position and motion were congruent with gravity independent of motion velocity ($p = 0.024$). In the other conditions higher motion coherence thresholds (MCT) were found at lower velocities and vice versa ($p < 0.001$). This result confirms previous studies with higher MCT at lower velocity but is in contrast to studies concerning perception of virtual turns and optokinetic nystagmus, in which differences of perception were due to different directions irrespective of body position, i.e. perception took place in an egocentric reference frame. Since the observed differences occurred in an upright position only, perception of coherent motion in this study is defined by an earth-centered reference frame rather than by an ego-centric frame.

1. Introduction

Perception of visual motion is essential for differentiating between moving and static objects. It helps objects to be perceived in three-dimensional vision, e.g. when we stand on the coast and see two ships crossing on the horizon, it will tell us which ship is nearer and what direction each ship is travelling in.

The coherent threshold paradigm is a well-established tool to measure perception of visual motion (Barton, Rizzo, Nawrot, & Simpson, 1996; Braddick, 1995; Moutoussis, Keliris, Kourtzi, & Logothetis, 2005). We were interested in examining the influence of gravity on visual motion perception.

In this context we aimed to find out what is the possible role of vestibular input, in particular gravity, on motion perception. On the vestibular basis, signals from otoliths and semicircular canals are combined to estimate the gravity vector (Angelaki, Shaikh, Green, & Dickman, 2004; Merfeld, Zupan, & Peterka, 1999). Animal experiments have revealed projections from the brainstem vestibular nuclear complex to the "inner cortical vestibular circuit", involving the parieto-insular vestibular cortex (PIVC) as well as temporal areas (Akbarian, Grüsser, & Guldin, 1993). Furthermore, visual stimuli led to a response in multisensory neurons in the vestibular cortex (Guldin & Grüsser, 1998).

Extracellular recordings from single neurons in monkeys have shown that the dorsal medial temporal area (MSTd) contributes to visual motion perception and that MSTd neurons have a greater sensitivity with congruent visual and vestibular input. Neuronal activity in MSTd was significantly correlated with perceptual decisions with no difference in the vestibular condition. Thus, the MST is important for the motion coherence paradigm, for visual and vestibular input, and for their interaction (Gu, DeAngelis, & Angelaki, 2007). Single-cell recordings in the PIVC, ventral intraparietal area (VIP) and MSTd during three-dimensional movements of macaque demonstrated that the strongest direction tuning, fastest response latency and strongest acceleration response were observed in PIVC, whereas velocity response was strongest in MSTd. Consequently, these results indicate a hierarchy in cortical vestibular processing, in which PIVC is most proximal and MSTd most distal (Chen, DeAngelis, & Angelaki, 2011). Sensitivity to motion signals of MST and the perturbation of perception by its

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stimulation has been reported before (Celebrini & Newsome, 1994; Britten & van Wezel, 1998, 2002).

Functional brain imaging studies also looked at congruent information between vestibular and visual cues. Some studies showed activity during motion coherence in the middle temporal area (Braddick et al., 2001; Snowden & Kavanagh, 2006), which was supported by former lesion studies in the MST of the macaque brain with less effect on other visual functions (Newsome & Paré, 1988; Snowden, 1994). In a study by Indovina et al. (2013) vertical self-motion under gravity showed activation in the posterior insula, ventral premotor areas, pre-SMA and cingulate cortex, thalamus, dorsal striatum, cerebellar cortex and vermis. The above-mentioned brain regions were also activated during perception of objects moving vertically under gravity (Indovina et al., 2005). The network includes the bilateral insula, the left lingual gyrus and the brain stem and had the strongest activity when targets moved congruent to gravity. Targets with constant velocity led to the second largest activity and the target moving at $-1g$ induced the lowest activity (Lacquaniti et al., 2013; Maffei, Macaluso, Indovina, Orban, & Lacquaniti, 2010).

In humans, Senot, Zago, Lacquaniti, and McIntyre (2005) examined the effect of gravity when intercepting virtual objects moving downward and upward. The objects were either accelerated by $1g$ or decelerated by $1g$ or at constant velocities ($\sim$8 m/s). Subjects had the highest success rate at constant velocities with higher rates when objects came from above. Furthermore, success rates in accelerating and decelerating conditions were high when objects moved congruently to natural gravity. In terms of response time, the downward condition (i.e. objects moving downward) elicited faster responses than the upward condition. When changing visual cues by turning the virtual scene by 90 deg, the effect of direction-dependent responses vanished. For pitch-rotating optic flow, a significantly stronger pitch sensation was observed for a downward compared to an upward pitch stimulus. In the yaw optic-stimulation, there was no difference in the sensation for different directions (Young, Oman, & Dichgans, 1975). In monkeys, Matsuo, Cohen, Raphan, de Jong, and Henn (1979) saw the same asymmetry in vertical optokinetic nystagmus (OKN) and added a tilted asymmetry when monkeys were tilted sideways. Thus, the asymmetry is defined in the egocentric reference frame.

Vidal, Amorim, McIntyre, and Berthoz (2006) demonstrated a difference in perception of pitch turns in an upright position and in pitch and yaw turns in a reclining position, i.e. the relative angular error of the estimated turn angle was higher in downward turns in an upright and in downward and rightward turns (downward in egocentric frame reference) in a reclining position. Thus, the results are in line with other studies (Matsuo et al., 1979), proposing an asymmetry of OKN. When subjects were instructed to stay on a fixation point, turns were underestimated for pitch and yaw in the upright position and asymmetry occurred similar to the experiment with normal pursuit. When only static pictures of the turn were presented, asymmetry of perception was far less for pitch turns in the upright position compared to visual cues rather corresponding to OKN. Thus, it was concluded that asymmetry in OKN is responsible for pitch asymmetry. Geometry-based perception is asymmetric to some extent and cognitive effects (i.e. fear of falling) increased the estimated turn angle in the direction of gravity.

Kalla et al. (2011) showed that healthy subjects and patients with bilateral vestibulopathy (BVP) were able to differentiate more easily between objects moving at higher velocities than at lower velocities, which was the case for objects moving in both horizontal and vertical directions.

In the current study, we examined healthy subjects with a motion coherence paradigm for vertical and horizontal moving objects in an upright and a reclining position. Inspired by prior research (Vidal et al., 2006), we aimed to investigate whether the perception of moving objects shows a similar asymmetry in pitch motion (i.e. vertical task) as it shows in the study of turn perception by Vidal et al. (2006). We included the reclining position to evaluate whether the motion coherence paradigm is more defined by the egocentric or the earth-centered reference frame. The aim was to study the role of the vestibular and visual input on motion coherence thresholds. Because of the different perception-thresholds found at different velocities in the study by Kalla et al. (2011), we examined a wide range of different velocities.

2. Methods

2.1. Patients

We examined 18 healthy subjects (11 female, 26.83 ±6.82 years). All of them had normal or corrected-to-normal vision. Approval for the study was granted by the local ethics committee and the study was performed in accordance with the Helsinki II Declaration. All participants gave their written informed consent before participating in the study.

2.2. Study design

Subjects were positioned on an examination couch in front of a computer screen (eye-screen distance 50 cm). In an area of 30 × 30 deg, centered on the computer screen (refresh rate: 100 Hz, gray background), 1320 randomly positioned white dots were presented. During the task, the dots were displayed for 0.6 s, during which a percentage moved coherently in one direction and the remaining dots moved randomly. Dots faded to the background-colour progressively in the last 6 deg of the coherent motion axis. The task was tested at a speed range from 0.1 to 25 deg/s (0.1, 0.2, 0.4, 0.8, 1.6, 3.2, 6.25, 12.5 and 25 deg/s). Cogent toolbox for Matlab was used for programming (http://www.vislab.ucl.ac.uk/cogent.php).

At the beginning of the experiment, subjects were asked to fixate a '+' sign centrally presented on the screen. By pressing an arrow key, subjects indicated the perceived direction of the coherently moving dots. Two training blocks of 32 trials with slow and moderately fast moving dots (0.8 and 12.5 deg/s) were performed to accustom subjects to the experiment. For the experiment, subjects were divided into two groups. Nine subjects (5 females, aged 26–35 years, mean 28.8 ± 2.8 years) did the vertical task and had to differentiate whether the dots moved coherently upward or downward. The experiment was performed in two different positions, i.e. sitting in an upright position and lying sideways on the left side (Fig. 1A–B).

The second group of nine subjects (6 females, aged 18–48 years, mean 25.00 ± 9.01 years) did the horizontal task and had to differentiate whether the dots moved coherently to the right or left. The two different positions were the same as in the vertical task (Fig. 1C–D).

For each speed, the motion coherence threshold was established by using a single-interval, two-option, forced-choice procedure. Patients had to indicate the direction of the coherent motion. The signal-to-noise ratio was one to one at the beginning. A correct answer led to a decrease of the signal-to-noise ratio by 1 dB, whereas an incorrect answer increased the signal-to-noise ratio by 3 dB. For each speed, 128 trials were conducted. Subsequently, the proportion of correct responses was calculated. The level at which subjects are expected to judge 75% correctly is defined as the coherence level. To find the coherence level for each speed and direction, a probit analysis was conducted.