

Velocity not acceleration of self-motion mediates vestibular – visual interaction

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Abstract. We investigated the influence of vestibular stimulation with different angular accelerations and velocities on the perception of visual motion direction. Constant accelerations resulting in different angular velocities and constant angular velocities obtained at different accelerations were combined in twenty healthy subjects. Random-dot kinematograms with coherently moving pixels and randomly moving pixels were used as visual stimuli during whole-body rotations. The smallest percentage of coherently moving pixels leading to a clear perception of motion direction was taken as the perception threshold. Perception thresholds significantly increased with increasing angular velocity. Increased acceleration, however, had no significant effect on the perception thresholds. We conclude that the achieved angular velocity, and not acceleration, is the predominant factor in the processing of vestibular – visual interaction.

1 Introduction

Perception of visual motion is impaired by concurrent vestibular stimulation. These vestibular – visual interactions were found to occur for both rotational self-motion (Brandt 1982; Brandt et al 1990; Büchele et al 1980; Buizza et al 1980; Degner and Brandt 1981; Mergner et al 1992; Probst and Wist 1990) and translational (linear) self-motion (Dichgans and Brandt 1978; Pavard and Berthoz 1977; Probst et al 1984, 1987).

Perception of visual motion direction is impaired by concurrent body rotations about the vertical axis when visual and vestibular motion directions are incongruous because visual and vestibular stimulations are in the same direction (Probst et al 1995). In accordance with this, visual motion-direction evoked potentials decrease in amplitude during rotation of subjects about their vertical axis, when visual and vestibular motion directions are incongruous (Loose et al 1999).

However, the perception of visual motion direction is not influenced significantly by concurrent translational (linear) self-motion (Loose et al 1996; Probst et al 1996). It was, therefore, concluded that translational self-motion mediating self-motion perception mainly via the otolithic system plays only a minor role in vestibular – visual interaction regarding the perception of motion direction. Obviously, this vestibular – visual interaction is caused by stimulation of the semicircular canals.

Angular acceleration is an adequate stimulus for the semicircular canals. With increasing angular acceleration the intensity of vestibular – visual interaction increases (Loose et al 1996; Probst et al 1995). In these investigations constant accelerations with constant stimulus duration were used. However, angular velocity is also changed with variable acceleration under a constant stimulus duration. In the present investigation the acceleration and velocity of rotation were varied systematically. The vestibular – visual interaction in the detection of visual motion direction was measured.

2 Methods

2.1 Subjects

Twenty volunteers, ten female and ten male, aged between 18 and 42 years, served as subjects. All subjects were without any neurological and otological impairments. They signed an informed consent statement to indicate their understanding of the experiment and their willingness to participate. The study has been approved by the local ethics committee.

2.2 Apparatus

A hydraulically driven, digitally servo-controlled multi-axes rotary chair was used (Probst et al 1993). Rotations of an inner rotary frame turned the sitting subject about his/her longitudinal z -axis (figure 1). Subjects were fastened in a sports-car seat secured with a 6-point-belt. The feet rested safely in a foot support. The legs were restrained both near the hip joints and near the knees, with an additional padded support between the inner sides of the knees. The head was kept in the centre of rotation, tilted 25° nose-down with respect to the Reid horizontal (Blanks et al 1975), with a rugged support for the back and the sides of the head and held by a forehead strap.

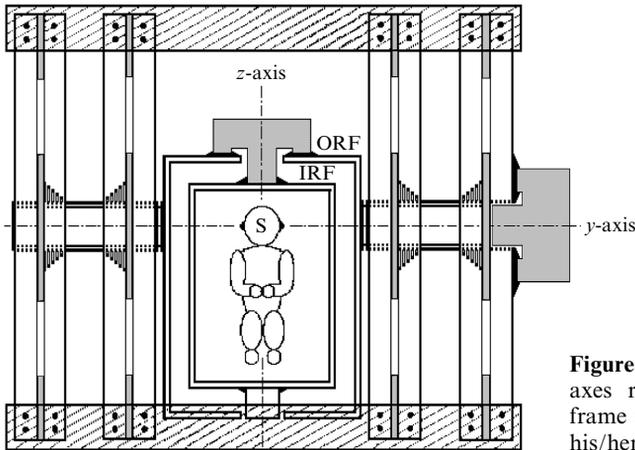


Figure 1. Schematic diagram of the multi-axes rotation device. The inner rotary frame (IRF) rotated the subject (S) about his/her vertical z -axis.

2.3 Visual stimulus

The visual stimulus was computer-generated and presented on a monitor with paper-white phosphor. The monitor was installed in the inner rotary frame in front of the subject and moved with him/her. During vestibular stimulation, the subjects had to fixate a small black dot in the centre of the stimulus in order to keep the eyes stable within the head (suppression of the vestibulo-ocular reflex). A dynamic random-dot kinematogram $10 \text{ deg} \times 10 \text{ deg}$ in size, with a pixel density of 25% (pixel size 0.05 deg , number of pixels 10 000), was used as the basis of the visual motion-direction stimulus. The intensity of the visual motion direction was varied by changing the percentage of pixels coherently moving to the left within an otherwise randomly moving random-dot background without any motion-direction information (figure 2). Coherent pixel motion was presented for 640 ms in each trial. Velocity of coherently moving pixels was 1 deg s^{-1} . The motion-direction stimulus corresponds to the one designed by Niedeggen and Wist (1992, 1998). The percentage of coherently moving pixels which resulted in the just noticeable coherent motion direction was taken as the threshold. Threshold measurement was performed by the modified binary search (MOBS) method which allows reliable threshold determination with fewer stimulus presentations as compared to conventional staircase methods (Tyrrell and Owens 1988).

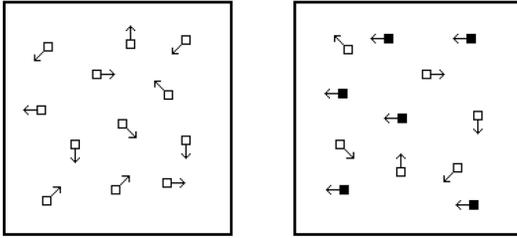


Figure 2. Schematic depiction of the visual stimulus. In a random-dot kinematogram the pixels move randomly with respect to their direction of motion but with the same constant step width (random walk, left panel). In the right panel, 50% of pixels move coherently to the left within random-walk motion of the residual pixels. Motion direction intensity was varied by changing the percentage of pixels coherently moving to the left.

2.4 Stimulations

The subjects were rotated about their longitudinal z -axis in both directions with two different constant angular accelerations of 30 and 60 deg s^{-2} . With an acceleration of 30 deg s^{-2} , an angular velocity of 60 deg s^{-1} was reached in 2 s and 120 deg s^{-1} in 4 s. With an acceleration of 60 deg s^{-2} , a velocity of 60 deg s^{-1} was attained after 1 s and 120 deg s^{-1} after 2 s. Thus acceleration and velocity was combined in such a way that constant accelerations resulted in different velocities and constant angular velocities were attained with different accelerations. Deceleration was always 120 deg s^{-2} (figure 3). The order of presentation of the 8 conditions (2 motion directions, 2 accelerations, 2 velocities) was randomised.

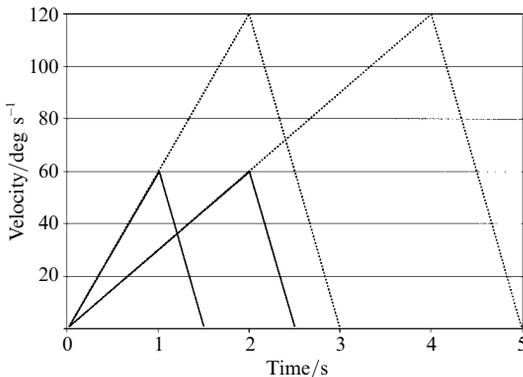


Figure 3. Velocity profiles for the two constant acceleration levels (30 and 60 deg s^{-2}) leading to angular peak velocities of 60 and 120 deg s^{-1} for the two acceleration levels, respectively. Therefore, acceleration and velocity was combined in such a way that constant accelerations resulted in different velocities and constant angular velocities were attained with different accelerations.

Thresholds for the perception of visual motion direction were obtained under combined vestibular and visual stimulus conditions. At constant accelerations of the rotary chair, the angular velocity changed during presentation of the visual motion stimulus lasting 640 ms. However, mean velocity during visual motion stimulation was 60 and 120 deg s^{-1} in the two acceleration conditions, respectively. This was achieved by starting the visual motion-direction stimulus 1680 and 3680 ms after vestibular motion onset (30 deg s^{-2}) or 680 and 1680 ms after vestibular motion onset (60 deg s^{-2}), respectively. By using a joystick, the subjects decided whether or not they clearly perceived the visual motion direction. The decision was made after ending of the visual direction stimulus, usually during deceleration of the rotary chair. The single trials were separated by a 12 s pause (standstill), in order to ensure the disappearance of all possible motion aftereffects.

2.5 Results

Mean motion-direction thresholds and standard errors for each experimental condition are given in table 1. The visual motion-direction thresholds for concurrent rotations to the left were significantly higher than those for rotations to the right ($p < 0.001$, Wilcoxon test). Thresholds increased significantly ($p < 0.001$) with increasing velocity (figure 4). No significant influence on the thresholds was found for the acceleration levels ($p = 0.588$).

Table 1. Means (M) and standard errors (SE) of the visual motion-thresholds in percentages of coherently moving pixels for all conditions.

Acceleration/deg s ⁻²	Rotation to the left: velocity/deg s ⁻¹		Rotation to the right: velocity/deg s ⁻¹	
	60	120	60	120
30				
M	29.23	47.83	8.67	15.43
SE	4.43	4.15	2.23	3.12
60				
M	26.75	54.65	9.5	17.3
SE	4.94	3.68	1.93	3.41

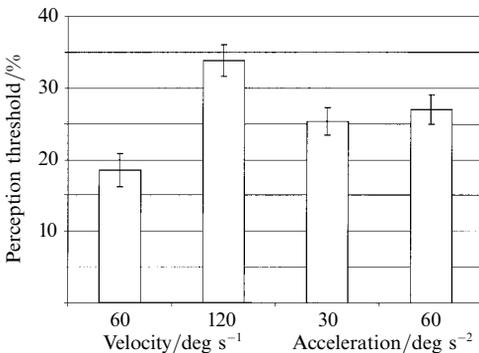


Figure 4. Means and standard errors of the visual motion-direction thresholds expressed as the percentage of coherently moving pixels. Thresholds increased significantly with increasing velocity of the rotary chair. No statistically significant effect was found for the acceleration level.

3 Discussion

3.1 Motion direction

The visual motion-direction thresholds were found to be significantly higher for rotations to the left. Visual motion direction was to the left in all cases. Visual motion-direction processing is obviously inhibited if physiologically incongruent stimulation occurs. Normally, locomotion or rotation is constantly combined with retinal image motion opposite in sign. The data of the present investigations replicate the results of Probst et al (1995), who found impaired visual motion-direction perception for self-rotations to the left if the visual stimuli moved leftwards, as well as for self-rotations to the right if the visual stimuli moved rightwards. Electrophysiological evidence for direction-specific vestibular–visual interaction was recently obtained. Amplitudes of visual motion-direction evoked potentials significantly decreased during physiologically incongruent stimulation (Loose et al 1999).

Direction-specific results may be explained on a postnatal developmental basis. It is hypothesised that cortical processes are responsible for interactions between the vestibular and visual systems (Straube and Brandt 1987). Cerebral blood flow in the occipital cortex is decreased during caloric vestibular stimulation. This was shown by transcranial Doppler sonography (Tiecks et al 1996) and positron emission tomography

(Wenzel et al 1996). Cortical development occurs mainly postnatally (Atkinson 1984; Bronson 1974). Perception of visual motion direction during concurrent rotation in the same direction is therefore inhibited, because this combination of directions hardly occurs, ie the systems are not calibrated for these combinations.

Some models try to explain errors in visual speed perception. The estimation of retinal image velocity was found to be affected by several stimulus properties including spatial frequency, dot density, contrast, and chromatic content (Freeman and Banks 1998). Turano and Heidenreich (1999) found that, when an observer's eyes moved in the same direction as a distal stimulus, the latter appeared slower than when the observer's eyes were still. The speed judgments were relatively close to the predictions generated by the retinal-motion model; the effects of eye movements on the retinal-image motion were not compensated. These models, however, cannot be used to explain the results of the present examination, because there were no changes in the visual stimulus properties and the subjects did not move their eyes. Therefore, perceived object motion depends not only on retinal speed and eye velocity, but also on vestibular inputs. Wertheim (1994) suggested that perception of object motion is related to eye velocity in space which corresponds to the vectorial addition of eye velocity in the head and head velocity in space. Perception of motion direction and velocity then depends on the ratio between retinal-image velocity and eye velocity in space. Wertheim's model explains similar results in investigations in which eye movements and vestibular stimulation are used. It is, however, important to distinguish object motion perception and visual motion-direction perception. For example, object motion is inhibited by concurrent translational (linear) self-motion (Dichgans and Brandt 1978; Pavard and Berthoz 1977; Probst et al 1984, 1987), whereas visual motion-direction perception is not influenced by concurrent linear self-motion (Loose et al 1996; Probst et al 1996). Perception of visual motion direction was investigated not by the movement of a single object, but with a global motion-direction sensation produced with random-dot kinematograms. Therefore, different mechanisms could be involved.

We agree with Wertheim's (1994) emphasis on the importance of distinguishing between percepts of relative motion and percepts of absolute motion. If we consider our subjects perceiving the visual motion direction within the stimulus frame or in relation to the fixation point, we may assume that our paradigm implies relative motion. Wertheim (1994) postulated that relative motion is independent of the reference signal including vestibular information. This would explain the differences in the perception of object motion (absolute motion) and visual motion direction (relative motion) during concurrent linear self-motion. It then remains unclear, however, why perception of visual motion direction is strongly inhibited by concurrent angular self-motion as shown in the present investigation replicating previous results (Loose et al 1996, 1999; Probst et al 1995). A direction-specific effect may result from illusory motion of the visual frame or fixation point, but the subjects never reported such illusions. We therefore suggest that relative motion perception can also be influenced by vestibular signals.

3.2 *Acceleration and velocity*

Visual motion-direction thresholds increased significantly with increasing velocity, while there was no significant influence found for acceleration. These results seem to be surprising, because angular acceleration, not velocity is the effective stimulus for the semicircular canals. With constant velocity, the cupula in the semicircular canals returns to the starting position. After a few seconds subjects would not perceive this rotation with eyes closed. Motion profiles with constant accelerations of a few seconds used in the present investigation, however, produced movements of the cupula which look like the velocity profile. Short acceleration and velocity profiles are much closer approximations

to natural head movements. Therefore, the semicircular canals can be referred to as velocity transducers (Guedry 1974). It is possible that vestibular–visual interactions mediated by higher cortical areas are influenced by acceleration through the use of velocity information and information about time, but the results of the present investigation are contrary to this assumption. Our results are in accordance with Wertheim's (1981) demonstration that during smooth-pursuit eye movements retinal and extraretinal signals are compared in terms of velocity. This is well-grounded, because in the natural environment retinal and extraretinal information caused by eye movements is set off against extraretinal vestibular information. Therefore, the signals should be present in the same unit.

A sensory interaction model postulates that the medial superior temporal area (MST) inhibits the middle temporal area (MT) during sensation of self-motion (Loose et al 1999). The perception of visual motion direction is processed particularly in area MT or homologous V5 in humans (Britten et al 1993; Grüsser and Landis 1991; Rodman and Albright 1989; Stoner et al 1990; Stoner and Albright 1992). Area MST is specifically activated by visual and vestibular direction stimulations (Thier and Erickson 1992). Area MST receives input from the vestibular cortex and is reciprocally connected with area MT. Therefore, neurons in area MST and MT are conceivable candidates mediating both vestibular–visual and visual–vestibular interactions on the cortical level. Additionally, it is thought that area MT is involved in the perception of motion contrast (Murakami and Shimojo 1996). Both area MT and area MST are activated, when subjects attend to moving stimuli (O'Craven et al 1997). The same regions are activated during galvanic vestibular stimulation (Dieterich and Brandt 2000). Therefore both areas seem to play a critical role whenever visual or vestibular motion is involved. A physiological model of reciprocal sensory–sensory interaction was introduced by Dieterich and Brandt (2000). The model is based on functional imaging studies showing decreased activation in the visual cortex (areas 17, 18, and 19) during vestibular caloric stimulation (Wenzel et al 1996), and decreased activation in the vestibular cortex (parieto insular vestibular cortex) during visual motion stimulations (Brandt et al 1998).

In our examination, a similar mechanism may be active as in the freezing illusion (Mesland and Wertheim 1996). In this illusion, moving gratings were perceived as stationary relative to a monitor when the observer was moved relative to the monitor or when the monitor was moved relative to the observer. The effect was stronger when the retinal velocity of the gratings was in the same direction as that of the monitor. Accordingly, the perceived velocity of the grating was underestimated when the grating and the subject's eye moved in the same directions in space. The authors assumed that their effect has a visual explanation, because the illusion happened when moving the monitor instead of the subject. It remains speculative if there is a similar mechanism for these direction-specific effects and the present interaction. It is, however, clear that the physiological cause for the interaction in the present investigation was the stimulation of the semicircular canals, because there were no changes in the retinal motions in the different conditions. The vestibular signals may be interpreted as relative eye motion in space if the head is kept stationary and the vestibulo-ocular reflex is suppressed. A simple physical explanation of the cupula movement in the vestibular organs, however, demonstrates that velocity, not acceleration mediates vestibular–visual interaction in the present examination.

In conclusion, perception of visual motion direction is direction specifically impaired during concurrent vestibular stimulation. This vestibular–visual interaction depends on the angular velocity and is probably mediated by cortical structures, possibly including area MST and area MT.

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