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Up-down asymmetry in vertical vection

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ABSTRACT

To investigate whether up-down asymmetry similar to that reported in vertical optokinetic nystagmus (OKN), that is, larger OKN responses for upward motion than for downward motion, would appear in vertical vection, we conducted three experiments. In all three experiments, participants viewed a vertically moving random-dot pattern. In Experiments 1 and 2, participants reported vection using a joystick. After each trial, they were also asked to rate the vection magnitude experienced during the stimulus presentation. In Experiment 3, eye movements and vection magnitude (rated after each trial) in response to the stimulus were measured. The results of Experiment 1 showed larger vection magnitude for the upward motion of the stimulus than for the downward motion of it. However, vection onset latency did not change much with stimulus motion direction. Experiment 2 revealed that the up-down asymmetry in vection manifested progressively during the latter part of the stimulus presentation period. Experiment 3 showed clear up-down asymmetry in both OKN and vection magnitude. These results not only indicate that up-down asymmetry similar to that reported in vertical OKN appears in vertical vection, but they also support the notion that the mechanisms underlying vection and OKN are closely related to each other.

1. Introduction

When a visual stimulus occupying a large part of the observer's visual field moves uniformly, observers often perceive illusory body movements in the opposite direction of the stimulus motion. This phenomenon is referred to as "vection" (Fischer & Kornmüller, 1930; Mach, 1906/1959). A familiar example of vection in daily life is that, when a person inside a stationary train views an adjacent moving train, the person feels as if his/her train is moving. During locomotion of the observer's body, vestibular organs rapidly create self-motion perception. However, as vestibular organs respond only to the acceleration of body movements, it is reasonable to assume that visual information of the counter-motion of the scene associated with body movements contributes to the sustained perception of self-motion.

Many studies have pointed out close relations between mechanisms mediating vection and optokinetic nystagmus (OKN) (Brandt, Dichgans, & Büchele, 1974; Brandt, Dichgans, & Koenig, 1973; Ebenholtz, 2001; Flanagan, May, & Dobie, 2002; Seno & Sato, 2009; see also, Seno, Ito, Sunaga, & Nakamura, 2010), and it is expected that vection should be stronger in stimulus conditions that are more effective in eliciting OKN than in those that are not. OKN refers to reflective eye movements in response to a stimulus motion, and consists of a series of slow phase movements for stabilizing retinal images of a large moving pattern and quick-phase movements for resetting eye position. OKN responses (e.g., slow-phase velocity and quick-phase frequency) increase with increasing stimulus size (Murasugi & Howard, 1989) and velocity (Murasugi & Howard, 1989; Seya, Ishihara, & Imanaka, 2015; van den Berg & Collewijn, 1988), which is consistent with vection studies that have shown stronger vection with increasing stimulus size (e.g., Brandt et al., 1973; Telford & Frost, 1993) and stimulus velocity (e.g., Nakamura & Shimojo, 1999; Seya, Tsuji, & Shinoda, 2014).

Seno and Sato (2009) examined the relationship between vection and OKN by measuring vection with horizontally moving stimuli presented at different retinal positions (nasal and temporal retinas). They assumed that stronger vection would be perceived when vection-inducing stimuli moved in the temporonasal direction (e.g., rightward motion in a left eye) than in the nasotemporal direction (e.g., leftward motion in a left eye), particularly when they were presented on the nasal retina, because several OKN studies have reported asymmetry in horizontal OKN between the two directions (Ohmi, Howard, & Eveleigh, 1986; van den Berg & Collewijn, 1988). Their results support the prediction, indicating that the mechanisms underlying vection and OKN are closely related to each other. It should be noted that the previous findings

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of correlation between vection and OKN do not mean that they are causally related (see Ebenholtz, 2001).

A large number of OKN studies have reported that upward motion elicits vertical OKN more effectively than downward motion does (Garbutt et al., 2003; Matsuo & Cohen, 1984; Murasugi & Howard, 1989; Takahashi, Sakurai, & Kanzaki, 1978; van den Berg & Collewijn, 1988). By contrast, although many studies have measured vertical vection (e.g., Giannopulu & Lepecq, 1998; Ito & Fujimoto, 2003; Ito & Takano, 2004; Kitazaki & Sato, 2003; Lepecq, Giannopulu, Mertz, & Baudonnière, 1999; Nakamura & Shimojo, 1998; Telford & Frost, 1993), no study has reported on differences in vertical vection. For example, Lepecq et al. (1999) examined the relationships between vestibular thresholds and vection. In their study, vestibular thresholds for detection of upward accelerations and vection onset latency to upward or downward motion presented on displays located on each side of a participant's head were assessed. Their results showed a negative correlation between vestibular threshold and vection latency. However, no up-down asymmetry in vection onset latency was found (see also Giannopulu & Lepecq, 1998). Telford and Frost (1993) investigated various factors affecting vection such as depth structure, stimulus motion direction, and restriction of central or peripheral vision, and reported no significant difference in vertical vection between upward and downward stimulations. Ito and Takano (2004) measured vection by using upward- or downward-inducing stimuli overlaid with dynamic visual noise, and reported no significant difference between the two directions, although there was a tendency for stronger vection in upward stimulus motion than in downward stimulus motion.

In light of the reviewed literatures, we decided to investigate further whether up-down asymmetry similar to that found in vertical OKN would appear in vertical vection. The motivation was twofold. First, we wanted to examine up-down asymmetry by measuring vection magnitude. In general, the slow phase of OKN consists of two components—that is, a cortically mediated fast OKN mechanism and subcortically mediated slow OKN mechanism (e.g., Cohen, Matsuo, & Raphan, 1977; Murasugi & Howard, 1989). The fast OKN mechanism produces rapid ocular following in response to motion (e.g., Kawano & Miles, 1986; Miles & Kawano, 1986; Miles, Kawano, & Optican, 1986), whereas the slow OKN mechanism produces slow buildup or decay of OKN. Several studies have suggested that up-down asymmetry reflects the slow OKN mechanism (e.g., Murasugi & Howard, 1989). Stronger vection is therefore likely to be perceived for upward stimulation of the stimulus than for downward stimulation of it, particularly during the latter part of stimulus presentation. Vection onset latency and vection duration are assumed to reflect vection magnitude; nonetheless, these measures may not be sensitive to detecting vection up-down asymmetry in the slow OKN mechanism. Second, we wanted to examine vertical vection by using stimuli similar to that used in studies reporting clear up-down asymmetry in vertical OKN. Although the majority of previous OKN studies have supported a preference in OKN for upward motion, mixed results have also been reported (for a review, see Knapp, Proudlock, & Gottlob, 2013); a preference for downward eye movements (e.g., Schor & Narayan, 1981) or no asymmetry (e.g., Knapp, Gottlob, McLean, & Proudlock, 2008; Seya & Mori, 2007) have been reported. It is therefore possible that the inducing stimuli used in previous research may not have been effective in eliciting up-down asymmetry in vertical OKN. Indeed, most previous studies measuring vertical vection (Ito & Fujimoto, 2003; Ito & Takano, 2004; Kitazaki & Sato, 2003; Telford & Frost, 1993) used inducing stimuli consisting of small dots at relatively low density, which were similar to those used in Seya and Mori (2007) showing no OKN asymmetry.

In the present study, we used a vertically moving random-dot pattern similar to that used by Seya et al. (2015), who investigated the relationship between induced motion (i.e., illusory motion of a fixated object induced by background motion, Duncker, 1929/1938) and OKN suppression (see also Lott & Post, 1993; Seya & Mori, 2007) and found clear up-down asymmetry in vertical OKN. In Experiment 1, we measured vection magnitude in the presence or absence of a fixation stimulus. We also measured vection onset latency to see whether the present results align with previous findings (Giannopulu & Lepecq, 1998; Lepecq et al., 1999). The effect of the fixation stimulus presence or absence was examined, as several vection studies have reported that OKN suppression in the direction opposite to the inducing stimulus motion (and slow phase of OKN) can induce vection in the same direction as the inducing stimulus motion (e.g., inverted vection, Nakamura, 2004; Nakamura & Shimojo, 2000, 2003). According to the OKN suppression hypothesis, vection should become smaller in the presence of the fixation stimulus than in the absence of the fixation stimulus. This is expected because vection in the direction opposite to that of the inducing stimulus would be partially cancelled by vection induced by the OKN suppression in the same direction as the inducing stimulus motion. In Experiment 2, we investigated the time course of vection magnitude, to examine directly whether vection would align with the activities of the slow OKN mechanism. In Experiment 3, we measured eye movements to examine whether the inducing stimulus used in the present study would produce up-down asymmetry in vertical OKN.

2. Experiment 1

2.1. Method

2.1.1. Participants

Eighteen individuals participated (16 men and 2 women; mean age = 22.8 years; range = 19–25 years). Participants had no knowledge as to the purpose of this study and had normal or corrected-to-normal vision. Participants gave written informed consent prior to their participation. The experimental protocol was approved by the ethics committee of Ritsumeikan University. The study was performed in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki).

2.1.2. Apparatus and stimuli

A personal computer (Apple Mac Pro Early 2009) was used to control the experiment and generate stimuli that were front-projected onto a white screen (200 cm × 150 cm in width and height) using a projector (Vivitek D795WT) with a refresh rate of 100 Hz. Stimuli were viewed binocularly from a distance of

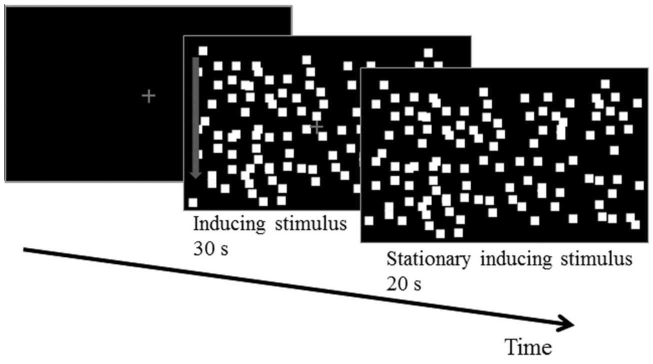

Fig. 1. Example of the stimulus display (fixation present condition) used in the experiment.