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RESEARCH ARTICLE

Walking without optic flow reduces subsequent vection

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Abstract This experiment investigated the effect of walking without optic flow on subsequent vection induction and strength. Two groups of participants walked for 5 min (either wearing Ganzfeld goggles or with normal vision) prior to exposure to a vection-inducing stimulus. We then measured the onset latency and strength of vection induced by a radially expanding pattern of optic flow. The results showed that walking without optic flow transiently yielded later vection onsets and reduced vection strength. We propose that walking without optic flow triggered a sensory readjustment, which reduced the ability of optic flow to induce self-motion perception.

Keywords Vection · Self-motion perception · Adaptation · Sensory readjustment

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Introduction

Multiple senses contribute to the perception of self-motion, including vision, the vestibular system of the inner ear, the proprioceptive estimation of limb/joint movement and position, the somatosensory system of cutaneous receptors and even audition (Gibson 1966; Howard 1982). While the inputs of these different "self-motion" senses appear to be integrated (Rieser et al. 1995), vision is thought to play a particularly important role in the perception of self-motion (see Dichgans and Brandt 1978; Howard 1982; Riecke 2011). In fact, exposure to a visual motion field that mimics the retinal flow produced by locomotion typically induces a compelling illusion of self-motion (referred to as "vection"—Fischer and Kornmüller 1930). For example, when a train begins to move out from the station, it is common for stationary observers nearby to misperceive that they themselves are in motion (rather than the train—Seno and Fukuda 2012).

A number of recent studies suggest that such visually-mediated self-motion perceptions can be facilitated by

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physically moving the observer in a manner consistent with the visual simulation (Berger et al. 2010; Wong and Frost 1981; Wright 2009; Bubka and Bonato 2010) or by incorporating active head motions of the observer directly into the self-motion display (Ash et al. 2011a, b).[1] When taken together, such findings suggest that consistent multisensory stimulation may produce a more compelling overall experience of self-motion than visual self-motion stimulation alone.

But what happens when the multisensory patterns of self-motion stimulation are inconsistent with each other based on past experience? Given the vection enhancements outlined above during consistent multisensory stimulation conditions, one might expect to see large vection impairments. However, several recent studies appear to show that visually induced vection is surprisingly tolerant to a number of so-called sensory conflict situations (Ash and Palmisano 2012; Ash et al. 2011a, b; Kim and Palmisano 2008, 2010; Palmisano et al. 2011). For example, we have found that compelling vection can still be induced even when visual and non-visual self-motion stimulations are 180 degrees out of phase or indicate self-motion along completely different axes (Ash and Palmisano 2012). One possible explanation for such findings is that during prolonged exposure to these types of "sensory conflict" conditions, the brain may engage in some sort of sensory/multisensory readjustment in order to minimize the (assumed) conflicts between the different self-motion senses. Such sensory/multisensory readjustments could in principle have been generated in a number of different ways (e.g. via habituation, adaptation, sensory reweighting or sensory recalibration).

In the past, several investigators have searched for an objective index for such sensory changes. However, it has proven difficult to find. In one such study, Harris et al. (1981) proposed that visual motion aftereffects (MAEs) might provide an objective index of sensory recalibration. MAEs refer to the illusory motion of a physically stationary scene which is experienced after prolonged exposure to sustained visual movement. In the Harris et al. study, participants viewed optic flow displays simulating self-motion in depth while either stationary or seated on a trolley that moved during the display. The trolley motions either generated consistent or inconsistent multisensory self-motion stimulation (i.e. the trolley moved in the same or the opposite direction to the visually simulated self-motion). Harris and colleagues predicted that if the brain recalibrates during sensory conflict, and if MAEs serve as an index of this sensory recalibration, then stationary conditions and inconsistent trolley motions should produce stronger visual MAEs than consistent trolley motions. However, only partial support was found for these hypotheses. Consistent trolley motions were found to strongly suppress the MAEs generated by forward-simulated self-motions (compared with those generated during stationary viewing). However, consistent trolley motions did not significantly suppress the MAEs generated by simulated backwards self-motion. Furthermore, these MAEs were not enhanced by putting the visually simulated and trolley-based self-motions into conflict. Since similar patterns of results had previously been found by Wallach and Flaherty (1975), these findings weaken the case for a MAE-based index of sensory recalibration.

Based on previous findings of surprisingly compelling vection during situations of (assumed) sensory conflict, we hypothesized that the nature of the vection experience depends on: (1) relative influence of visual inputs in the multisensory processing of self-motion perception and (2) that this influence might be reduced (compared with that of the non-visual senses) by prolonged exposure to self-motion without optic flow.

To investigate this idea, we compared the vection induced directly after 5 min of walking either with normal vision or while wearing Ganzfeld goggles that removed all visual flow without affecting overall luminance. We hypothesized that compared with the Control condition, optic flow deprivation during the Ganzfeld walking condition should lead to a reduction in participants' susceptibility to vection, which (if it was due to sensory readjustment) should fade quickly following repeated exposure to the optic flow.

Methods

Ethics statement

Our experiments were pre-approved by the Ethics Committee of Kyushu University, and informed verbal consent was obtained from each participant prior to testing. The experimental protocol adhered to the Declaration of Helsinki.

Participants

Twenty-five volunteers participated in this experiment. Participants included both graduate and undergraduate students, as well as assistant professors (they were 14 males and 11 females ranging in age from 21 to 45 years). All participants reported normal vision and no history

[1] There are, however, examples where consistent cross-modal stimulation does not enhance but rather reduce vection: For example, adding velocity-matched linear treadmill walking to a visual forward motion simulation has been shown to reduce vection (Ash et al. 2012; Kitazaki et al. 2010; Onimaru et al. 2010), whereas linear treadmill walking was found to enhance vection when the visual velocity was 30 times faster than the walking velocity (Seno et al. 2011a, b).

Fig. 1 The translucent Ganzfeld goggles used in this experiment and an illustration of how the experimenter used a *wooden bar* to guide participants

of vestibular system diseases. None of them were aware of the purpose of the experiment, although all had previously participated in vection experiments. Participants were randomly divided into two groups (Ganzfeld and Control conditions): twelve participants (seven males, five females; mean age 24.3) were assigned to the Ganzfeld condition, and thirteen participants (seven males, six females; mean age 26.9) were assigned to the Control condition.

Stimuli

The vection-inducing stimuli were generated and controlled by a computer (Apple MacBook Pro) and presented on a plasma display (3D Viera 70 inch, Panasonic, Japan) with 1,024 × 768 pixel resolution at a 60-Hz refresh rate, presented without stereo mode. The display showed radially expanding patterns of optic flow simulating forward self-motion at 20 m/s (simulated display depth was 20 m). As the dots in these displays disappeared off the edge of the screen, they were replaced at the far depth plane, thereby creating an endless optic flow display. Approximately 1,240 dots were presented in each frame. There was no fixation point, but participants were asked to look at the centre of the optical expansion. The viewing distance was 57 cm, yielding a visual field of view of 100° × 72°.

Procedure

Apparatus

Two conditions were tested in this between-subjects-designed experiment: a walking condition with Ganzfeld viewing (Ganzfeld) and a normal viewing walking condition (Control). The Ganzfeld goggles were constructed from two ping-pong balls (sliced in half) and attached to a metal frame. These goggles prevented the participant from seeing any details of the outside world (he/she only saw a blank bright field without any specific visual features—Fig. 1). The Ganzfeld condition was used (rather than a blindfold) to avoid very different dark adaptation. Even though there were luminance differences, these were minimal.

Participants initially walked for 5 min around the ground floor of the Kyushu University building in which the experimental vection testing chamber was located. The room for the walking was normally lit. Participants in both the Ganzfeld and the Control conditions walked quite slowly (<1 m/sec on average) and were always accompanied by the experimenter. As illustrated in Fig. 1, the participant and the experimenter held opposite ends of the same 25-cm-long wooden bar, which was used by the experimenter to lead the participants safely when walking in Ganzfeld conditions and to control walking speeds in both conditions.[2]

At the end of this 5-min walking period, participants in both the Ganzfeld and Control conditions were directly led to the dark experimental vection testing chamber and seated in front of the visual self-motion display. They were then immediately exposed (sequentially) to four vection-inducing trials—on each trial of these trials they were presented with a computer-generated visual self-motion display for 30 s. In the Ganzfeld condition, participants wore the goggles until just before the optic flow stimulus presentation. Note that in order to avoid any potential context-specific influences, the Ganzfeld and Control conditions were conducted in the same corridor and lighting conditions during the walking phase and the same darkened test room and stimuli for the vection testing.

When viewing the computer-generated radially expanding pattern of optic flow, participants were asked to press a

[2] Even though the experimenter endeavoured to have participants walk at the same pace in both conditions, participants were (not surprisingly) somewhat more cautious when walking during Ganzfeld conditions.

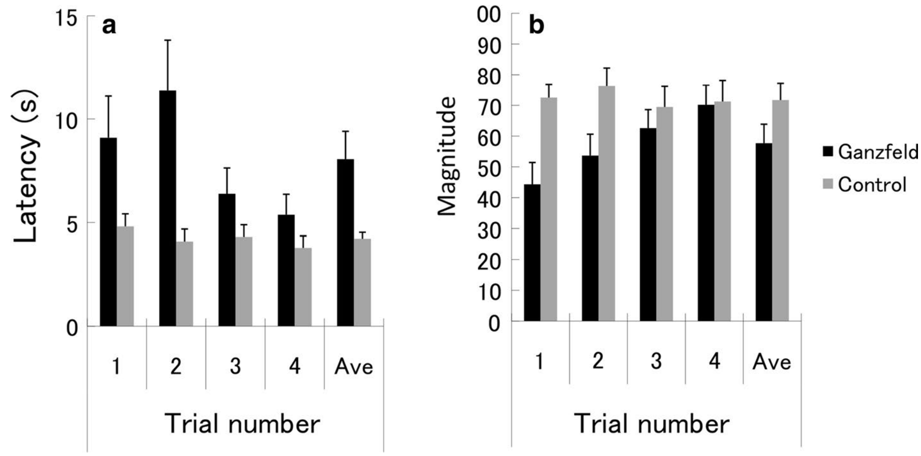

Fig. 2 Mean vection latency (**a**) and magnitude (**b**) for each of the four trials per person. The *black* and *grey bars* indicate the Ganzfeld and the Control conditions, respectively. *Error bars* indicate standard errors. "*Ave*" indicates the average values over the four trials

designated button as soon as they perceived forward self-motion. After each trial, the participants rated the subjective vection strength using a 101-point rating scale ranging from 0 (no self-motion was perceived) to 100 (very strong perceived self-motion). Immediately after the observer's verbal response, the visual stimulus for next trial was presented on the screen, i.e. there was no rest period between the four trials.

Results

We measured both vection onset latency and verbal ratings of vection strength. The vection onset latency was the time taken from the start of exposure to the optic flow until the participant's button press. Stronger vection tends to have both shorter onset latencies and higher estimated magnitudes.[3]

Figure 2 shows the two vection measures (onset and strength—averaged across participants) as a function of the vection trial for the two different walking conditions (Ganzfeld vs. Control).[4] We conducted Split-plot ANOVAs [Two walking conditions (between-subjects factor: Ganzfeld vs. Control) and four trial repetitions (within-subjects factor)]. Importantly, the interactions between these two factors were found to be significant for both latency, $F(3, 66) = 3.00$, $p = .04$, $\eta_G^2 = .06$, and magnitude, $F(3, 69) = 3.02$, $p = .04$, $\eta_G^2 = .02$. There were also significant main effects of walking condition on both the vection latency, $F(1,22) = 7.49$, $p = .01$, $\eta_G^2 = .16$, and vection strength data, $F(1,23) = 81.84$, $p < .0001$, $\eta_G^2 = .75$. In addition, there was also a significant main effect of trial repetition on vection latency, $F(3,66) = 4{,}07$, $p = .01$, $\eta_G^2 = .08$, but not on vection strength, $F(3, 69) = .92$, $p = .43$, $\eta_G^2 = .01$. These statistical results were interpreted as follows. Overall, vection occurred later and was rated as being weaker in the Ganzfeld condition compared with the Control condition. However, the significant interaction indicates that the effects of Ganzfeld (vs. Control) walking on subsequent vection induction were greater during the first two vection testing trials (trials 1 and 2) than during the latter two trials (trials 3 and 4)—see Fig. 2. This interaction was further investigated by conducting a series of post hoc comparisons (using Ryan's method, significance level was controlled at 5 %). These revealed that in the Control condition, there were no significant differences in either latency or vection strength ratings across the four trials. By contrast, in the Ganzfeld condition, significant differences were found between the first two trials (trials 1 and 2) and the last two trials (trials 3 and 4) in both vection latency and vection strength. There were also significant differences between the Control and Ganzfeld conditions in the first and second trials in terms of both vection latency and magnitude. However, there were no significant differences between the Control and Ganzfeld conditions in the third and fourth trials for any of the vection indices.[5]

Discussion

Prolonged periods of physical self-motion without corresponding visual motion (Ganzfeld conditions) were found

[3] Note there were vection dropouts (i.e. periods of "no vection") in some cases after vection induction.

[4] Latency data for one trial were lost for one participant in the Control condition. Therefore, we excluded his latency data from these analyses.

[5] The effect sizes here were larger for vection magnitude than for vection latency. This might be related to the fact that the changes in vection are easier for observer to respond to in terms of strength (compared to latency). In our previous studies, vection strength ratings were typically most reliable and sensitive measure of the changes of vection (e.g. Seno et al. 2013).

to strongly reduce the ability of optic flow to subsequently induce vection (compared with Control conditions which provided consistent visual and non-visual information about self-motion). Specifically, 5-min optic flow deprivation while walking was sufficient to strongly reduce the vection induced in the first and second vection test trials, indicated by delayed vection onset and reduced vection strength. Importantly, both types of (relative) vection reduction[6] were rather short-lived and lasted only for two trials. No significant differences were found between the Ganzfeld and Control walking conditions on either vection measure during the third and fourth test trials.

As indicated in the introduction, multiple sensory systems are known to be involved in self-motion perception. Here, we proposed that prolonged self-motion stimulation without optic flow might temporarily decrease the influence of visual (compared with non-visual) self-motion inputs in this multisensory integration process. The vection reductions observed in the Ganzfeld (compared with the Control) walking conditions are consistent with a sensory (or possibly even a multisensory) readjustment, which favoured the non-visual self-motion inputs and/or suppressed the visual self-motion inputs. Since the self-motion illusions examined in this experiment were purely visually induced (i.e. they were experienced by physically stationary observers), when the relative influence of visual inputs were decreased, vection induction should have been reduced as well, which is exactly what we observed (i.e. increased vection onset latencies and reduced vection strength ratings). The assumption was that these effects might have a cortical origin. They might even share similar origins to previous reports of reciprocal visual-vestibular interactions during perceived self-motion (e.g. Brandt et al. 1998; Deutschländer et al. 2004; Wenzel et al. 1996). These studies suggest that: (a) cortical activity in vestibular areas (such as *PIVC*) is suppressed in stationary subjects experiencing vection and (b) cortical activity in a wide variety of visual areas (including *MSTd*) is suppressed during vestibular caloric stimulation (Brandt et al. 1998; Deutschländer et al. 2004; Wenzel et al. 1996). However, the actual mechanisms underlying these transient effects are currently unclear—they could in principle have arisen via habituation, adaptation, sensory reweighting or sensory recalibration.

Importantly, we also predicted that if a sensory readjustment was responsible for the above effects, then the Ganzfeld walking conditions should only temporarily reduce vection.[7] Consistent with this prediction, the recovery of vection following Ganzfeld walking can be clearly seen over the course of the four successive test trials on both vection measures (these measures were not statistically different for Ganzfeld and Control conditions on the third and fourth testing trials). Since the time taken to complete each vection test trial was about 1 min (which includes not only the 30-s exposure to the optic flow display, but also the time taken for the participant to make their overall vection strength response for the trial, and the interstimulus interval), vection recovery for both measures appeared complete only 2 min after Ganzfeld walking. It appears thus that any sensory readjustment generated by the Ganzfeld walking was quite short-lived, at least in the case of 5-min adaptation.

In the introduction, we proposed that sensory readjustment is likely to occur when we are selectively deprived of the information provided by one or more of self-motion senses. Intriguingly, it is not just the Ganzfeld walking conditions (walking without optic flow), but also the vection testing conditions (optic flow without walking) in the current experiment that meet this criterion for sensory readjustment. However, we expected sensory readjustments to occur in opposite directions in these different situations—the former case should favour non-visual self-motion inputs, whereas the latter case should favour visual self-motion inputs. It was therefore possible that the vection recovery from Ganzfeld walking seen in the third and fourth testing trials might also (in part at least) reflect the occurrence of a second sensory readjustment process—this time favouring the visual-only self-motion testing conditions. However, as can be seen in Fig. 2, trial-based vection improvements were only seen in the Ganzfeld walking conditions (not in the Control conditions), which suggests that our four 30-s-long vection testing conditions were not sufficient to initiate their own sensory readjustment process.

Self-motion perception is primarily a multisensory experience (e.g. Gibson 1966; Rieser et al. 1995; Seno et al. 2011a, b; Allison et al. 2012; Riecke and Schulte-Pelkum 2013). While vection is often considered a purely visual illusion of self-motion, one cannot hope to fully understand self-motion perception by examining the role that vision plays in it alone. It is important to also examine the consequences of providing consistent and inconsistent

[6] While it is possible that prior walking with optic flow facilitated subsequent vection, it is more likely that prior walking without optic flow either inhibited vection induction or resulted in a sensory/multisensory cue reweighting so as to favour non-visual cues. However, in order to rule out the possibility that prior walking with optic flow facilitated subsequent vection, we would need a Control condition where the participant was stationary for 5 min prior to exposure to the optic flow.

[7] If there was a perceptual effect of the Ganzfeld viewing on vection we would have expected it to be transient. It is possible however that if there had instead been a cognitive or experimental demand based effect of Ganzfeld viewing then this might have been more likely to be long (or longer) lasting.

multisensory self-motion stimulations.[8] Past research has shown that the vection experience can be increased, reduced or unaffected by these different types of multisensory self-motion stimulation. Unfortunately, it is difficult to directly investigate multisensory processing underlying these self-motion perceptions at the cortical level (since the observers in brain imaging studies are by necessity always physically stationary—e.g. Pitzalis et al. 2013). Here we report perceptual/behavioural evidence (i.e. not based on brain imaging) that strongly supports the notion that sensory readjustment can occur during adaptation to unusual/inconsistent patterns of multisensory self-motion stimulation.

Since we did not have access to an objective index of sensory readjustment and were concerned with carry-over between the Ganzfeld and Control condition, we deliberately chose to use a between-subjects (as opposed to within-subjects) design for this experiment. Participants were only ever exposed to one of the different adaptation conditions (Ganzfeld or Control) and were not even aware of the other condition. Thus, this between-subjects design eliminated possible carry-over effects between these two adaptation conditions and minimized the likelihood of either participant cognitions or any experimental demands influencing their vection experience.

What are the implications of the current findings? In many "real world" situations, the visual and non-visual senses are thought to provide consistent information about self-motion, and thus the integration of this information presumably occurs in a straight-forward fashion. However, in other situations, such as driving an automobile along a straight expressway for an extended period, the self-motion perception may be predominantly determined by the available visual information. In such situations, it would seem likely that there will be a modulation in the driver's self-motion perception (e.g. directly after driving). The current study appears to show that such atypical combinations of self-motion sensations can trigger sensory readjustments, which can (at least transiently) affect/alter subsequent self-motion perceptions.

Conclusion

This study suggests that sensory readjustment occurs when observers walk without any exposure to optic flow. We propose that the relative influence of visual self-motion inputs was reduced in these conditions compared with normal walking conditions, the result being that vection induction and strength was strongly, but only temporarily, diminished. These findings confirm that vection is mediated by a multisensory integration process, which can be significantly affected by prior sensory readjustment.

[8] It should also be noted here that we believe that our results were not a result of dark adaptation but were mediated by sensory readjustment as we hypothesized. In future, we should also examine potential effects of walking with eye closed or walking in the complete dark room.

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