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Vestibular signals of self-motion modulate global motion perception

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ABSTRACT

Certain visual stimuli can have two possible interpretations. These perceptual interpretations may alternate stochastically, a phenomenon known as bistability. Some classes of bistable stimuli, including binocular rivalry, are sensitive to bias from input through other modalities, such as sound and touch. Here, we address the question whether bistable visual motion stimuli, known as plaids, are affected by vestibular input that is caused by self-motion. In Experiment 1, we show that a vestibular self-motion signal biases the interpretation of the bistable plaid, increasing or decreasing the likelihood of the plaid being perceived as globally coherent or transparently sliding depending on the relationship between selfmotion and global visual motion directions. In Experiment 2, we find that when the vestibular direction is orthogonal to the visual direction, the vestibular self-motion signal also biases the direction of onedimensional motion. This interaction suggests that the effect in Experiment 1 is due to the self-motion vector adding to the visual motion vectors. Together, this demonstrates that the perception of visual motion direction can be systematically affected by concurrent but uninformative and task-irrelevant vestibular input caused by self-motion.

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1. Introduction

Human vision creates an impressively coherent and reliable perception of the external world despite the poor quality of the retinal image. One of the limits inherent in the retinal image is that it underspecifies the external world and as a consequence, a given image could arise from an infinite number of real-world stimuli. In trying to solve this puzzle, the visual system makes constraining assumptions to restrict the set of possible solutions (Marr, 1982; Ullman, 1979). However, conditions may arise which defeat the brain's ability to obtain a single coherent percept, as occurs when two highly probable interpretations are simultaneously possible. In such cases, the two perceptual interpretations alternate over time in an irregular fashion each few seconds, with individual dominance durations usually drawn from a gamma distribution (Brascamp, van Ee, Pestman, & van den Berg, 2005). This class of phenomena is known as bistable perception and reveals the visual system's inability to resolve the visual input into a single unique solution (Alais & Blake, 2015).

Another problem in visual processing is that our representation of the world is built up from isolated local cues which may be ambiguous. The so-called aperture problem is an example of this

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problem in the domain of motion perception. When a moving line is viewed through an aperture such that its endpoints are not visible, only the motion component perpendicular to the line's direction can be observed (Stumpf, 1911; Todorovic, 1996; Wuerger, Shapley, & Rubin, 1996). Because of the small size of receptive fields in the early visual cortex, this problem is ubiquitous in direction-tuned motion-sensitive neurons (Marr & Ullman, 1981). The resolution of ambiguity in local motion measurements therefore requires an integrative, global process. So-called *plaid* stimuli have been extensively studied to investigate the interaction of local and global signals in motion perception. Plaids are formed by superimposing two grating patterns drifting in different directions. Being a one-dimensional pattern, each grating on its own is ambiguous and has an infinite number of possible velocities due to the aperture problem. However, when both gratings are combined and cohere, there is only one motion vector consistent with the motion of both gratings. This unique solution is known as the intersection of constraints direction and usually observers perceive the gratings as a coherent two-dimensional pattern drifting in this direction (Adelson & Movshon, 1982).

Plaids are also a class of perceptually ambiguous stimuli. If the angular difference between the component motions is large, for example greater than about ±60°, plaids are bistable and alternate over time between being a coherent two-dimensional percept and an incoherent one in which the gratings are seen to drift transparently over each other in their own directions (Kim & Wilson, 1993)





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Various other visual parameters can be systematically varied to bias an observer's tendency to perceive a plaid as moving coherently or transparently, including for example spatial frequency and speed of the components (Adelson & Movshon, 1982; Movshon, Adelson, Gizzi, & Newsome, 1985). Recently, studies have used bistable stimuli to investigate whether an unambiguous signal in one sensory modality can help perceptually resolve stimulus ambiguity present in another modality. Several studies using binocular rivalry have shown that an auditory or a tactile stimulus congruent with one of two images engaged in rivalry can help resolve visual ambiguity (Hsiao, Chen, Spence, & Yeh, 2012; Lunghi, Morrone, & Alais, 2014; Van Ee, van Boxtel, Parker, & Alais, 2009).

One way to disambiguate bistable plaid stimuli is to provide motion information in a different (non-visual) sensory modality. Here, we investigate how the interpretation of a bistable plaid stimulus is influenced by the addition of vestibular signals. Vestibular signals are known to be integrated with visual motion signals in order to establish the observer's direction of selfmotion (for a review, see (Fetsch, DeAngelis, & Angelaki, 2013). In particular, visual optic flow information and input from the otolith organs of the vestibular system are both processed in several extra-striate visual areas, including MST in particular (Chen, DeAngelis, & Angelaki, 2011; Gu, Watkins, Angelaki, & DeAngelis, 2006), to calculate the observer's heading direction. In addition to visual motion contributing to the calculation of self-motion, the interaction might also manifest as an effect in the opposite causal direction: vestibular signals affecting the interpretation of visual motion. Indeed, because self-motion creates visual motion signals not associated with movement of objects in the outside world in the form of optic flow, it makes sense that the nervous system would use other information about self-motion to identify which motion signals result from self-motion and which result from self-propelled external objects. In this interpretation, there is a clear parallel with eye movements, which are also associated with a strong retinal motion signal in the absence of real movement in the outside world.

For eve movements, the spurious motion signal resulting from eye rotation is suppressed in perception (Krekelberg, 2010), and the shift in retinal coordinates is corrected by a process known as saccadic remapping (Duhamel, Colby, & Goldberg, 1992). When correction for retinal motion across saccadic eye movement is imperfect, two aligned objects presented before and after the saccade can appear misaligned (Szinte, Wexler, & Cavanagh, 2012). Similar corrective processes might play a role in interactions between vestibular input and visual motion processing, whereby vestibular information about self-motion could be used to correct the perceived motion vector of a visual object. If so, over- or undercorrection would lead to subtle changes in motion perception, dependent on the relationship between the visual motion vector and the vestibular motion vector. Importantly, such an effect would be especially apparent if the motion signal itself were weak or ambiguous. In the case of weak motion, the added vestibular component could either render the visual motion above or below perceptual threshold, or if the visual motion were ambiguous, the vestibular component could favour one interpretation over another. In the present study we investigate how vestibular input about self-motion affects visual motion processing using bistable plaid stimuli.

2. Experiment 1

In Experiment 1 we tested whether vestibular signals can influence the interpretation of moving plaid stimuli. For this, we used plaids whose component directions were broadly separated so as to be perceptually ambiguous. That is, with good alternation probability, but neither continually coherent nor continually sliding as two separate gratings. To provide vestibular input we use a CKAS 6-degrees-of-freedom motion simulator. The motion platform has a hemispherical pod mounted on it which encloses the observers and creates an immersive virtual visual environment. The platform and surrounding pod can be driven by motors to rotate around the three axes of roll, pitch, and yaw to provide vestibular input to the observer seated inside and viewing a widescreen visual display (see Fig. 1). Using this device, we will test whether vestibular motion signals, either aligned with the global motion vector or orthogonal to it, can influence the integration of local motion signals into a global motion vector.

2.1. Methods

2.1.1. Observers

Ten observers with normal or corrected-to-normal vision participated in the experiment. Observers were undergraduates recruited from The University of Sydney undergraduate Psychology subject pool; seven were male. All observers were naïve to the purposes of the experiment and gave informed consent prior to participation. All work was carried out in accordance with the declaration of Helsinki and was approved by the local ethics committee.

2.1.2. Apparatus

Observers were seated on a CKAS 6 degree-of-freedom motion platform system (CKAS Mechatronics, Australia) that was used in this experiment to rotate the observer in the horizontal and sagittal planes (Fig. 1). Observers were buckled into a racing chair with head support to ensure stability throughout these movements. No forehead or chinrest was used. Maximum displacement on either axis was 24° away from the central position (level, facing straight ahead). A large dome was rigidly mounted on the motion platform so that there were no optic flow signals when the observer was rotated. The only visual motion came from the video monitor displaying the plaid stimulus.



Fig. 1. Apparatus. Observers were seated in a CKAS 6-degree-of-freedom motion system. Stimuli were presented inside the pod on a projection screen mounted directly in front of the observer.

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