



# 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 self-motion 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 one-dimensional 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

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; Wuergler, 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  $\pm 60^\circ$ , 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 self-motion (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 eye 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 under-correction 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.

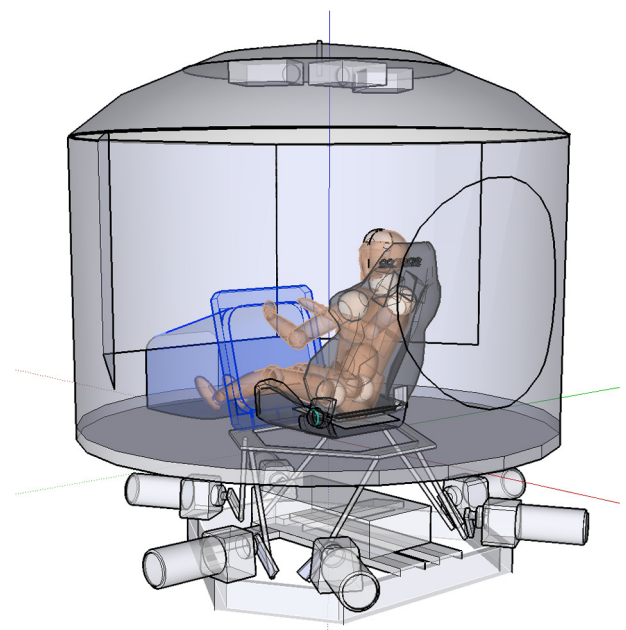
### 2.1. Methods

#### 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.

### 2.1.3. Stimuli

Visual presentation within the motion simulator was achieved by means of a BENQ projector (1280 × 1024, 60 Hz refresh) projecting the stimulus on a screen directly in front of the observer inside (and therefore moving along with) the motion simulator. The screen was placed at a distance of 130 cm from the observer and subtended 60° of horizontal visual angle.

The stimulus consisted of a moving plaid composed of two square-wave gratings presented on a black background (Fig. 2). The plaid was presented within a circular annulus (inner and outer radii 3.75° and 15°, respectively) surrounding a central fixation point. The wavelength of each square-wave grating was 4.7° (i.e., 0.21 cycles per degree), with a duty cycle of 0.38 such that individual light bars were 1.8° wide. Individually, each of the two gratings drifted at 4.7°/s. The motion vector of each of the two component gratings was rotated away from the global motion direction by 70.7° such that the relative motion vectors of the two components was separated by 141.4°. The global pattern therefore drifted with 11.7°/s.

### 2.1.4. Procedure

Plaids were presented for three seconds, drifting at constant velocity with the global plaid direction in one of four cardinal directions (right, down, left, or up). Concurrently with presentation of the plaid, observers themselves were rotated in one of four possible cardinal directions (yaw right, pitch down, yaw left or pitch up) or remained stationary in a fifth no-self-motion condition. Observers were rotated from the central starting position (level and facing straight forward) with a half-period sinusoidal velocity profile, terminating at maximum angular displacement (i.e., ±24° yaw or pitch). Angular displacement commenced concurrently with the appearance of the plaid and terminated concurrently with the offset of the plaid. Directly after each trial, the motion simulator returned to the central position with an identical but opposite motion profile in preparation for the subsequent trial.

The observers' task was to continuously report their percept of the bistable plaid during each 3 s trial. For this two conventional mouse buttons were used, one indicating that the plaid was moving as a globally coherent pattern, and the other indicating the two



**Fig. 2.** Stimulus. The plaid stimulus was composed of two square-wave gratings drifting in directions separated by 141°. Because of the large angular difference between the gratings, this plaid tended to be bistable over time and could be perceived either as the individual components drifting transparently over each other (solid arrows) or as a single surface, drifting in the global direction (dotted arrow). [Video](#) of example trial available online.

components were sliding transparently. Observers were instructed to keep the corresponding button pressed for the duration of the percept, switching keys whenever their percept switched, and to indicate their best guess when they were not sure.

Each observer participated in 3 experimental blocks, each of which consisted of 100 trials (4 global motion directions × 5 self-motion conditions × 5 trials per condition). This yielded a total of 15 3-s trials per condition per observer.

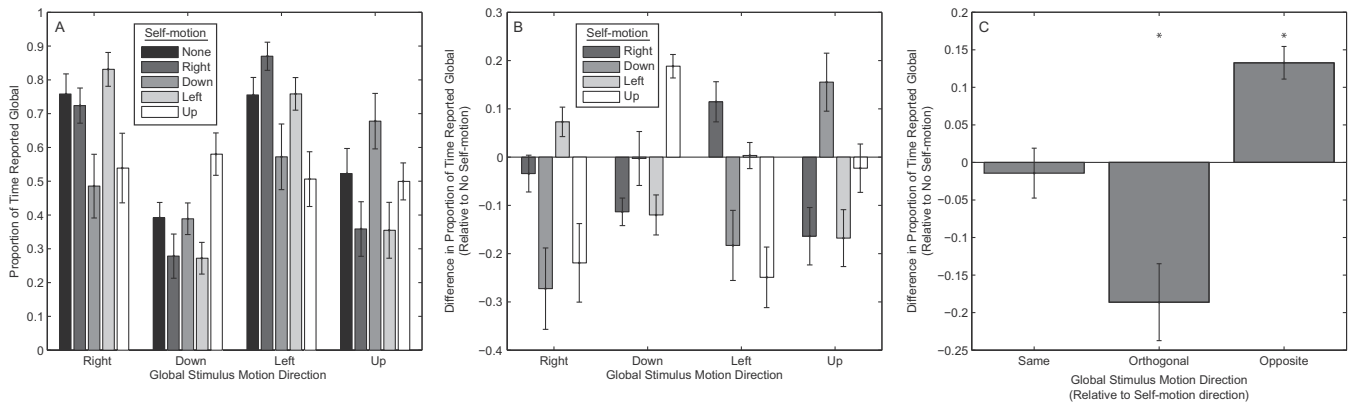
## 2.2. Results

For each condition, we calculated the proportion of time for which observers reported perceiving the plaid moving in its global motion direction as our dependent variable. Fig. 3A plots this measure as a function of both plaid global motion direction and self-motion direction. Plaids with horizontal global motion directions were perceived as coherent for a greater proportion of time than plaids with vertical global motion, consistent with previous reports (Hupé & Rubin, 2004). Before submitting results to statistical analysis, we therefore subtracted the proportions of global plaid motion in the No-Self-Motion conditions from each of the four Self-Motion conditions to correct for the baseline tendency to perceive global plaid motion. The remaining value (Fig. 3B) therefore reflects the change in proportion of global plaid motion caused by the addition of vestibular self-motion, independently for each of the plaid global directions and for each self-motion direction. These values were submitted to a 4 × 4 repeated-measures ANOVA, which revealed no main effects of either Global Plaid Motion direction ( $F = 1.95$ ,  $df = 3$ ,  $p > 0.14$ ) or Self-Motion Direction ( $F = 0.45$ ,  $df = 3$ ,  $p > 0.45$ ). There was, however, a strong interaction effect between the direction of Global Plaid Motion and Self-Motion direction ( $F = 11.7$ ,  $df = 9$ ,  $p < 0.001$ ).

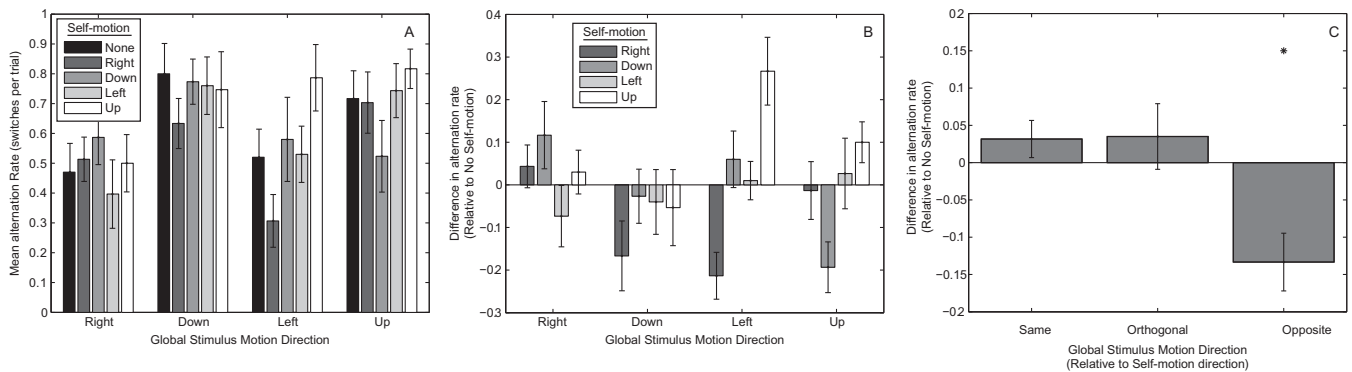
As shown in Fig. 3B, this interaction effect was characterized by an increase in perceived global motion when self-motion and global plaid motion were in *opposite* directions, a decrease in the perception of global motion when self-motion and global plaid motion were in *orthogonal* directions, and no change when self-motion and global plaid motion were in the *same* direction. To test these observations more formally, we reanalysed conditions according to self-motion direction *relative* to global motion direction, rather than absolute self-motion direction. In doing so, we collapsed the two orthogonal self-motion directions for each global motion direction. The resulting data were entered into a 4 × 3 repeated-measures ANOVA (4 Global Motion directions: right, down, left, and right × 3 Relative Self-Motion directions: same, orthogonal, or opposite). The ANOVA revealed no main effect of Global Motion direction ( $F = 1.53$ ,  $df = 3$ ,  $p = 0.23$ ), but did reveal a strong main effect of Relative Self-Motion direction ( $F = 14.8$ ,  $df = 2$ ,  $p < 0.001$ ).

In order to further test the direction of the effects of relative motion direction, we further collapsed the data across global motion direction and used two-tailed paired-samples t-tests to test the changes in proportion of global motion against 0 (no difference in proportion global dominance relative to baseline). As shown in Fig. 3C, when self-motion was in the same direction as global plaid motion, no effect on proportion of global plaid motion was observed ( $t = -0.42$ ,  $df = 9$ ,  $p = 0.68$ ). However, when self-motion was in a direction orthogonal to the global plaid motion, the proportion of global dominance was strongly reduced ( $t = -3.64$ ,  $df = 9$ ,  $p < 0.01$ ). Conversely, when self-motion was in the opposite direction to the global plaid motion, the proportion of global dominance was strongly increased ( $t = 6.11$ ,  $df = 9$ ,  $p < 0.001$ ).

In addition to relative dominance duration, we also investigated alternation rate. Across all conditions, observers reported an average of 1.62 perceptual epochs per trial, indicating an average of 0.62 alternations per trial. Fig. 4A plots alternation rate as a function of both plaid global motion direction and self-motion direc-



**Fig. 3.** Results of Experiment 1 showing group mean dominance duration for 10 observers. All error bars represent standard errors of the mean. (A) Proportion of total time that observers report perceiving global plaid motion plotted as a function of global motion direction (four cardinal directions) and self-motion direction (four cardinal directions, plus a 'no self-motion' control). (B) Difference in proportion reported global relative to the 'no self-motion' baseline condition (black bars in panel (A)). Values are consistently near zero when global and self-motion directions match, but deviate for other combinations. (C) Summary of the data in panel B showing the difference in proportion reported global when conditions are grouped by the direction difference between global and self-motion directions. Asterisks denote values significantly different from 0 ( $p < 0.05$ ) according to uncorrected one-sample  $t$ -tests.



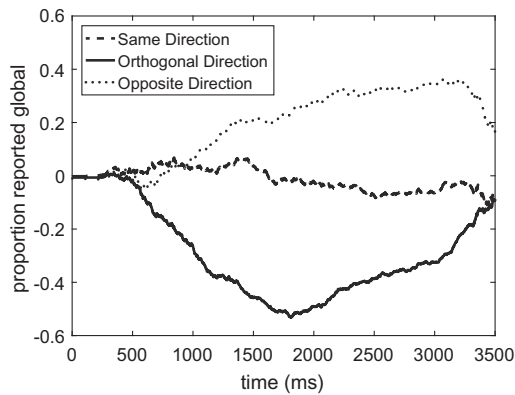
**Fig. 4.** Results of Experiment 1 showing group mean alternation rate for 10 observers. All error bars represent standard errors of the mean. (A) Mean number of alternations between reported percept per trial as a function of global motion direction (four cardinal directions) and self-motion direction (four cardinal directions, plus a 'no self-motion' control). (B) Difference in alternation rate relative to the 'no self-motion' baseline condition (black bars in panel A). (C) Summary of the data in panel B showing the difference in alternation rate when conditions are grouped by the direction difference between global and self-motion directions. Asterisks denote values significantly different from 0 ( $p < 0.05$ ) according to uncorrected one-sample  $t$ -tests.

tion. Similar to dominance duration, alternation rate was slightly lower for plaids with horizontal coherent motion than for plaids with vertical coherent motion, again consistent with previous reports (Hupé & Rubin, 2004). Further statistical analysis was carried out exactly as described above. After subtracting alternation rate in the No-Self-Motion condition (Fig. 4B), a  $4 \times 4$  repeated measures ANOVA revealed a significant effect of Self-Motion Direction ( $F = 6.37$ ,  $df = 3$ ,  $p = 0.002$ ) as well as an interaction between Global Motion Direction and Self-Motion Direction ( $F = 3.86$ ,  $df = 1$ ,  $p < 0.001$ ). We then re-analyzed alternation rates according to self-motion direction *relative* to global motion direction, rather than absolute self-motion direction, by collapsing the two orthogonal self-motion directions for each global motion direction as we did above for dominance duration. The resulting data were entered into a  $4 \times 3$  repeated-measures ANOVA (4 Global Motion directions: right, down, left, and right  $\times$  3 Relative Self-Motion directions: same, orthogonal, or opposite). The ANOVA revealed no main effect of Global Motion direction ( $F = 0.56$ ,  $df = 3$ ,  $p = 0.64$ ), but did reveal a strong main effect of Relative Self-Motion direction ( $F = 6.05$ ,  $df = 2$ ,  $p < 0.010$ ). Contrary to dominance duration, we also observed an interaction between Global Motion Direction and Relative Self-Motion Direction ( $F = 3.91$ ,  $df = 6$ ,  $p = 0.002$ ).

We further collapsed the data across global motion direction and used two-tailed paired-samples  $t$ -tests to test the changes in alternation rate against 0 (no difference relative to No-Self-Motion). As shown in Fig. 4C, when self-motion was in the same direction as global plaid motion, no effect on alternation rate was observed ( $t = 1.26$ ,  $df = 9$ ,  $p = 0.23$ ). Likewise, when self-motion was in a direction orthogonal to the global plaid motion, there was no effect on alternation rate ( $t = 0.79$ ,  $df = 9$ ,  $p < 0.44$ ). However, when self-motion was in the opposite direction to the global plaid motion, alternation rate was decreased ( $t = -3.44$ ,  $df = 9$ ,  $p < 0.007$ ).

Finally, we analyzed the time-course of the interpretation of the bistable plaid over the course of the trial. To do so, we computed the relative dominance of the two interpretations across all trials as a function of time, independently for each combination of stimulus motion and self-motion. Subsequently, as in our analyses of overall dominance and switch rate, we corrected the time-course of relative dominance in each of the self-motion conditions by subtracting the time-course of the corresponding No-Self-Motion condition. Finally, we collapsed the time-series across conditions, grouping the conditions according to the direction of self-motion relative to global stimulus motion direction: Same, Orthogonal, or Opposite (Fig. 5).





**Fig. 5.** Relative dominance of global and component interpretations over time, as compared to the no-self motion condition. The stimulus is presented from 0 to 3000 ms. Self-motion in the same direction as global stimulus motion does not introduce a systematic bias at any point in the trial. Self-motion in a direction orthogonal to the direction of global stimulus motion introduces a bias for the component interpretation, which develops during the first half of the trial, peaks midway, and then reduces to zero again. This time-course closely matches the velocity of the observer. Conversely, the effect of self-motion in the direction opposite to the global stimulus motion is monotonic, with a bias for the global interpretation gradually and continually developing over the course of the whole trial.

Consistent with our previous analysis of dominance duration and switch rate, self-motion in the same direction as global stimulus motion did not systematically affect the interpretation of the plaid at any given time-point, as compared to the No Self-Motion condition. However, we observed an interesting dissociation between Orthogonal and Opposite Self-Motion conditions. Over the course of the trial, self-motion in a direction orthogonal to global stimulus motion resulted in a steady decrease of the relative dominance of the global interpretation, with a minimum approximately midway the trial, after which the bias gradually disappeared again. Cumulatively, this produces an overall bias for the component interpretation in the orthogonal relative self-motion condition, as is evident in Fig. 3C. Over the course of the trial, the time-course closely matches the sinusoidal velocity profile of the observer's motion. Conversely, self-motion in a direction opposite to the global stimulus motion led to a bias for a global interpretation that continued to build over the course of the entire trial. This time-course produces the overall bias for a global interpretation as evident in Fig. 3C, but is also consistent with the reduction in alternation rate observed in this condition: if observers switched to a global interpretation in this condition, they did not frequently switch their interpretation a subsequent time during that same trial. In this, self-motion in the direction opposite to the direction of global stimulus motion had the effect of stabilizing the global interpretation.

### 3. Experiment 2

The results of Experiment 1 indicate that the perception of bistable plaid stimuli composed of individual components moving in different directions can be biased by the vestibular input provided by self-motion. Furthermore, this bias is systematic in that self-motion in the opposite direction to the global direction of the plaid increases the dominance of the global interpretation and results in a decrease in alternation rate of the bistable stimulus. Conversely, self-motion in a direction orthogonal to the global direction of the plaid (and therefore within  $20^\circ$  of one of the component motions) increases the dominance of the component interpretation in which the observer perceives two transparent bar patterns transparently sliding over one another.

It remains an open question whether these interactions with vestibular input reflect an interaction between the visual motion vectors and self-motion vectors at the stage where motion integration takes place, or whether it might bias the interpretation of bistability at a higher, decision-making stage. In other words, does vestibular input affect visual motion processing, or does it bias an observer's tendency to give a particular response? In Experiment 2, we contrast these two interpretations by investigating the effect of self-motion on the perceived motion direction of a simple moving pattern. If self-motion affects the perception of bistable plaids by biasing the way in which the ambiguous stimulus is interpreted, this should have no effect on the perceived direction of a simple moving pattern. Conversely, if self-motion influences visual motion processing at an earlier stage, for example through a weighted sum of the visual motion vector and the self-motion vector, then self-motion should affect the perceived direction of a simple stimulus translating in a single direction.

#### 3.1. Methods

##### 3.1.1. Observers

Five observers with normal or corrected-to-normal vision participated in the experiment. As in Experiment 1, all observers were undergraduates recruited from the University of Sydney undergraduate Psychology subject pool; four were male. None of the observers had previously participated in Experiment 1 and all observers were naïve to the purposes of the experiment and gave informed consent prior to participation. All observers gave informed consent prior to participation.

##### 3.1.2. Apparatus

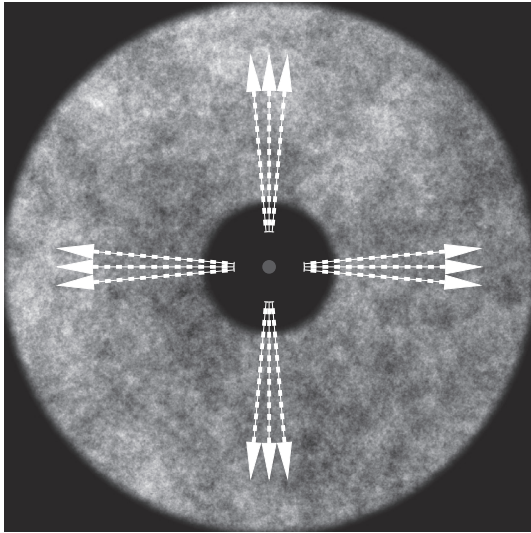
The observers were seated in the same CKAS 6 degree-of-freedom motion system (CKAS Mechatronics, Australia) that was used in Experiment 1.

##### 3.1.3. Stimuli

The presentation of the visual stimuli within the motion simulator was achieved using the same equipment as in Experiment 1. The stimulus consisted of a moving  $1/f$  noise pattern presented within the same annulus as in Experiment 1 (inner and outer radii  $3.75^\circ$  and  $15^\circ$  of visual angle, respectively) surrounding a central fixation point. The pattern moved within the annulus at a constant speed of  $5.6^\circ/s$  for 2 s. The pattern moved in one of twelve possible directions: one of the four cardinal directions, or either  $5^\circ$  clockwise or  $5^\circ$  counterclockwise from one of the four cardinal directions (Fig. 6). The slightly oblique motion vectors were included to avoid observers referencing the perceived motion vector to a cardinal direction.

##### 3.1.4. Procedure

In each trial observers viewed the moving texture for 2 s. Concurrently with the presentation of the texture, observers themselves were rotated in one of four possible cardinal directions (yaw left, yaw right, pitch up, or pitch down). Whereas in Experiment 1 observers were rotated with a sinusoidal velocity profile, in Experiment 2 observers were rotated at approximately constant angular velocity, from the central starting position (level and facing straight forward) to maximum angular displacement (i.e.,  $\pm 24^\circ$  yaw or pitch). The final position was reached 2 s after initial acceleration such that self-motion terminated concurrently with the presentation of the stimulus. A constant velocity profile was used in Experiment 2 (rather than sinusoidal, as in Experiment 1), because we anticipated that the magnitude of any effect of self-motion on perceived direction might be dependent on the speed of self-motion. In this case, applying a sinusoidal velocity profile to self-motion would cause the perceived direction of motion to



**Fig. 6.** The stimulus in Experiment 2 was a  $1/f$  noise pattern translating in a single direction presented within an annulus. The pattern moved with a constant velocity in one of 12 possible directions at or near one of the four cardinal directions. After each 2 s trial, observers indicated the perceived direction of movement by adjusting a centrally presented arrow. Video of example trial available online.

fluctuate over the course of the trial. This was avoided by keeping self-motion velocity constant.

After the stimulus disappeared (and upon reaching the final position of the observer) the observer was presented with a centrally presented line which the observer could rotate using a mouse to indicate the perceived direction of motion of the moving texture on that trial. This response was self-terminated by clicking the mouse, whereupon the observer was returned to the starting position following a velocity profile equal and opposite to the initial rotation.

Because we were interested in the effects of self-motion on perceived visual motion direction, not all combinations of self-motion and visual stimulus direction were tested. Rather, only orthogonal self-motion was combined with the various visual stimulus directions to determine whether this altered perceived visual direction. Observers completed 9 repetitions in each combination of 4 self-

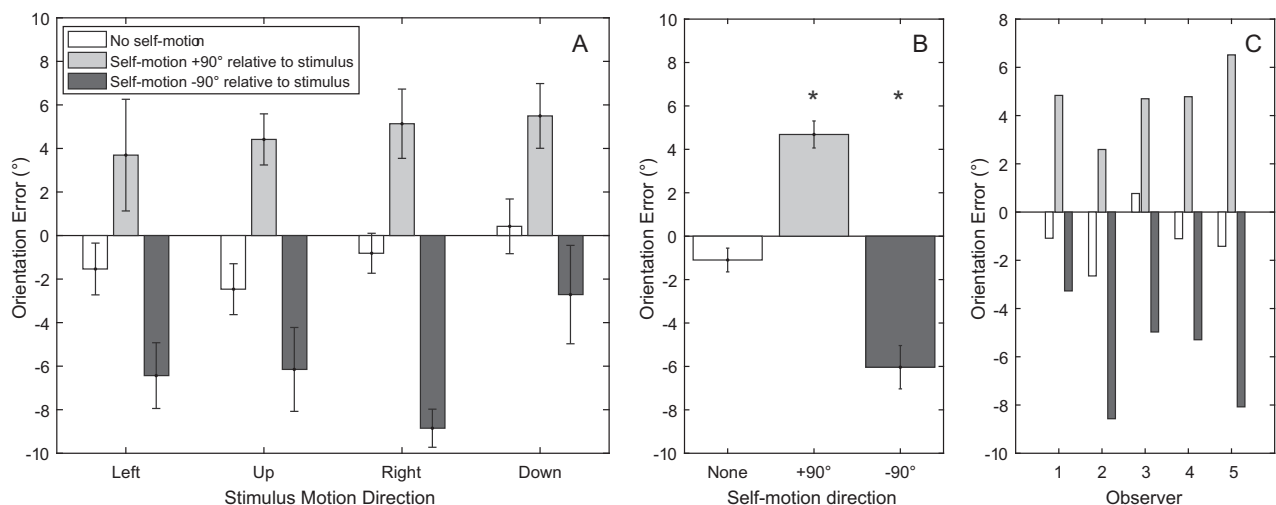
motion directions and 6 approximately orthogonal stimulus motion directions ( $-95^\circ$ ,  $-90^\circ$ ,  $-85^\circ$ ,  $85^\circ$ ,  $90^\circ$  and  $95^\circ$ ; see Fig. 6), as well as 9 repetitions of each of the 12 possible stimulus motion directions without any self-motion, for a total of 324 trials.

### 3.2. Results

For each trial, the response error was calculated as the difference between the indicated direction and the true direction of motion on that trial. Before analyzing the data, each cardinal direction of visual motion was combined with the trials  $\pm 5^\circ$  from that cardinal to collapse the 12 visual directions shown in Fig. 5 into four cardinal directions. Fig. 7A shows average response errors across all five observers for the four cardinal directions of visual motion and the three self-motion conditions (approximately  $90^\circ$  clockwise of the visual cardinal, approximately  $90^\circ$  counterclockwise of the visual cardinal, and static).

Response errors were submitted to a  $4 \times 3$  repeated-measures ANOVA with factors Stimulus Motion Direction (right, down, left, or up) and Relative Self-Motion Direction (none,  $90^\circ$  clockwise, and  $90^\circ$  counterclockwise). This revealed no main effect of Stimulus Motion Direction ( $F = 0.89$ ,  $df = 3$ ,  $p = 0.472$ ), and no interaction with Relative Self-Motion Direction ( $F = 1.58$ ,  $df = 6$ ,  $p = 0.196$ ). However, it revealed a strong main effect of Relative Self-Motion Direction ( $F = 77.4$ ,  $df = 2$ ,  $p < 0.001$ ). This effect was characterized by response errors towards the direction of self-motion (see Fig. 7): errors were positive when self-motion was in a direction rotated  $90^\circ$  relative to the stimulus motion vector, and negative when self-motion was in a direction rotated  $-90^\circ$  relative to the stimulus motion vector.

In order to formally test this characterization of the main effect of Relative Self-Motion Direction, we collapsed trials across Stimulus Motion Direction and submitted average response errors across observers to one-sample  $t$ -tests against a null hypothesis of zero mean response error (Fig. 7B). This revealed that there was no significantly non-zero mean response error in the no-motion condition ( $t = -2.0$ ,  $df = 4$ ,  $p = 0.12$ ), but did reveal a positive mean response error in the  $+90^\circ$  self-motion condition ( $t = 7.5$ ,  $df = 4$ ,  $p = 0.002$ ) and a negative mean response error in the  $-90^\circ$  self-motion condition ( $t = -6.0$ ,  $df = 4$ ,  $p = 0.004$ ). Self-motion therefore systematically biases the perceived direction of an orthogonal



**Fig. 7.** Results of Experiment 2. All error bars represent standard errors of the mean. (A) Mean direction error as a function of stimulus motion direction and relative self-motion direction across all five observers. (B) Mean direction error as a function of relative self-motion direction, collapsed across stimulus motion directions. Asterisks denote means significantly different from zero (two-tailed, one-sample  $t$ -tests,  $p < 0.01$ ). (C) Mean direction error as a function of relative self-motion direction for individual observers.

motion vector towards the direction of self-motion. These effects were evident in each of the five individual observers (Fig. 7C).

#### 4. Eye movements

The perception of bistable stimuli can be influenced by systematic differences in eye movements (Baker & Graf, 2010). In order to be able to evaluate the role of eye movements in Experiments 1 and 2, gaze direction was monitored for a subset of observers in both experiments using an Eyetribe remote eyetracker sampling monocular gaze position at 60 Hz (The Eyetribe, Copenhagen, DK). Although technical constraints of the motion simulator negatively impacted the quality of the resulting data, we analyzed the available data for evidence of two possible eye movement confounds: the optokinetic reflex (OKR) and vestibulo-ocular reflex (VOR).

A moving stimulus can elicit OKR, evident as a drift of gaze in the direction of stimulus motion whilst an observer is attempting to fixate. To avoid this, in the current experiments the stimulus was presented outside a 7.5° diameter annulus surrounding a clear and stable fixation point. Pilot testing using an Eyetribe eyetracker outside the motion simulator showed no evidence of OKR with this annulus size. We inspected data from 3 observers in Experiment 1 and 5 observers in Experiment 2, analyzing the mean gaze position averaged over all available trials as a function of stimulus motion direction. No systematic effect of stimulus motion direction on mean gaze direction was observed (Fig. 8). Most importantly, even if OKR did occur on some trials in some observers, it would not be able to explain our results, as OKR would be in the direction of stimulus motion in all cases, and independent of self-motion.

VOR is a reflexive eye movement elicited by head-movements. Although we cannot completely rule out the possibility that VOR affected our results, we do not believe it played a large role for two reasons. Firstly, the motion simulator is a fully immersive,

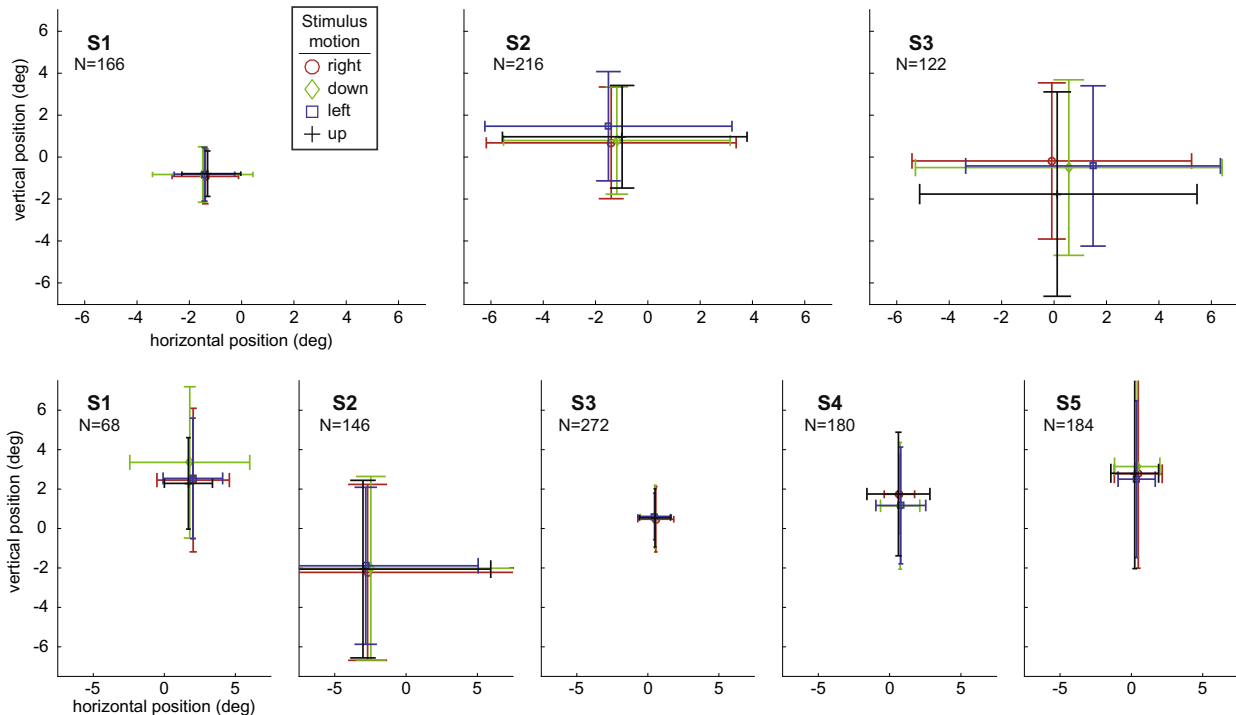
rigid environment that moves along with the observer. This provides a strong, full-field stationary retinal signal that stabilizes the observer within the reference frame of the simulator and helps him/her maintain fixation. Secondly, we analyzed mean gaze direction over all available trials in 3 observers in Experiment 1 and 5 observers in Experiment 2, and observed no systematic effect of self-motion direction on mean gaze direction (Fig. 9). Although technical limitations did not allow us to record eye position with the spatial and temporal resolution necessary to identify individual VOR episodes, this grand average analysis nevertheless gives us reasonable confidence that even if VOR did occur occasionally, it does not play a substantial causative role in our results.

Altogether, we are confident that the pattern of results observed in Experiments 1 and 2 is not due to systematic eye movements caused by either self-motion or stimulus motion.

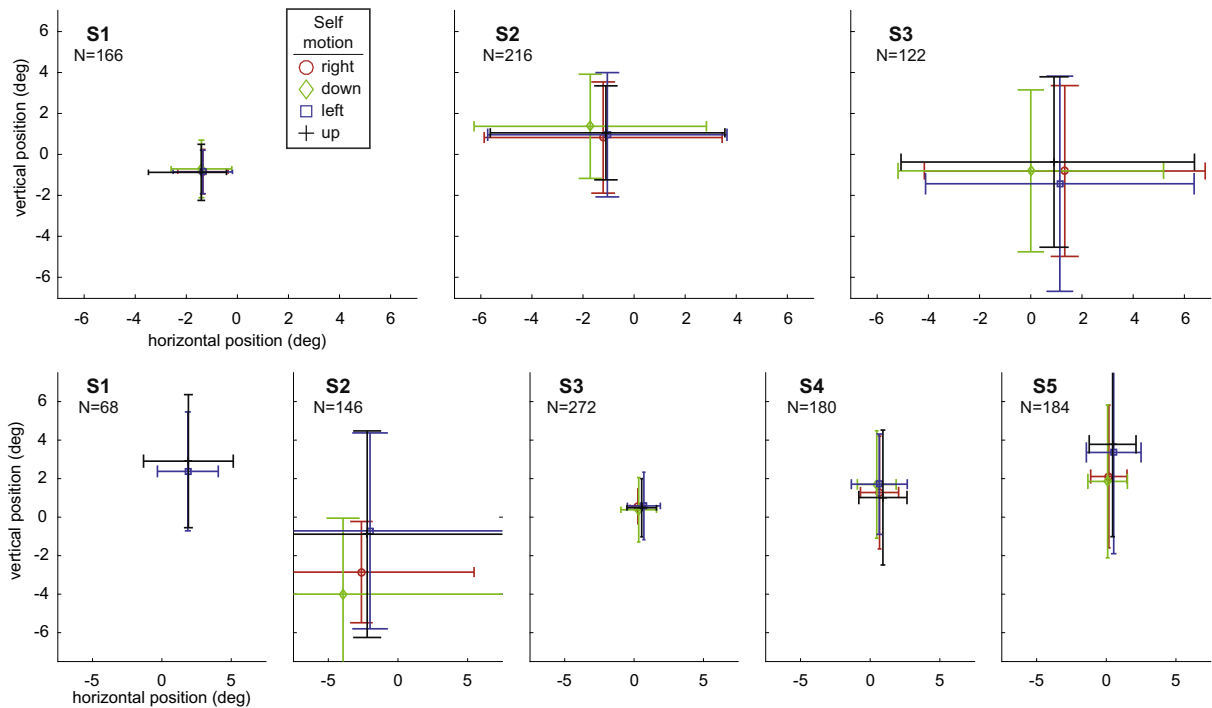
#### 5. General discussion

In two experiments we used a motion simulator to investigate the effect of self-motion on visual motion processing and sensory integration. In Experiment 1, we showed that self-motion systematically biased the perception of bistable plaid stimuli. Self-motion in the direction opposite to the global, integrated plaid direction caused the global percept to become more dominant, relative to the percept in which the separate components are seen to slide transparently over each other. Conversely, self-motion in a direction orthogonal to the global motion vector increased the relative dominance of the component percept.

In order to investigate whether this effect was due to an effect of vestibular input on an early motion-integration stage, or due instead to a later decision making stage at which the bi-stability of the stimulus is resolved, we carried out a second experiment. In this experiment, observers indicated the perceived direction of a moving texture in different self-motion conditions. The results



**Fig. 8.** Mean gaze position across all available time-points as a function of stimulus motion direction for three individual observers in Experiment 1 (top) and five individual observers in Experiment 2 (bottom). Error bars indicate standard deviations across all time-points and trials within each motion condition. Only observer S3 in Experiment 1 shows any evidence of a systematic effect of stimulus motion direction on mean gaze position. The absence of such an effect in the majority of observers across both experiments supports the interpretation that OKR did not play a significant role.



**Fig. 9.** Mean gaze position across all available time-points as a function of self-motion direction for three individual observers in Experiment 1 (top) and five individual observers in Experiment 2 (bottom). Error bars indicate standard deviations across all time-points and trials within each motion condition. None of the observers show a systematic effect of self-motion direction on mean gaze position, making an important contribution of VOR to our behavioral results unlikely.

showed that self-motion systematically biased the perceived direction of visual motion in the direction of the self-motion vector. This indicates that the results of Experiment 1 should be interpreted as an effect of vestibular input on relatively low-level motion processing, rather than an effect on a later ambiguity resolution stage.

It has long been recognized that the neural processes underlying visual motion processing and the vestibular system interact (Fetsch et al., 2013). However, this has largely been studied from the perspective of self-motion perception: perceiving how the body itself is moving through space (DeAngelis & Angelaki, 2012). Such studies have identified interactions between visual areas sensitive to optic flow patterns (such as primate area MST) and neural populations carrying vestibular input. When the task is to identify the heading, orientation, acceleration or rotation of one's own body, it makes sense that visual and vestibular inputs are integrated, presumably weighted according to the relative reliability of their information (Gu, Angelaki, & Deangelis, 2008). Additionally, when judging the movement of external objects whilst moving oneself, the self-motion signal (extracted from both visual and vestibular input) can be subtracted from the object's visual motion signal to obtain an accurate estimate of the object's movement in the world.

However, in the present tasks, vestibular input is task-irrelevant, and any integration with vestibular input is therefore in principle undesirable. In both experiments, stimuli were presented within an enclosed motion simulator which provided a stable visual reference frame with respect to the observer (i.e., when the observer moved, the stimulus and visible surrounding region moved consistently with the observer's motion). This ensured that the spatial envelope within which the plaid stimulus was presented remained stable in retinal coordinates, and thus in principle no correction for self-motion needed to be made. Nevertheless, both experiments revealed strong effects of self-motion on visual motion processing. The pattern of results in both experiments reveals a direction-dependent effect of self-motion on visual

motion perception, consistent with a vector addition of (part of) the vestibular self-motion vector to the retinal motion vector(s).

In Experiment 1, self-motion in the direction opposite to the direction of motion of the global plaid increased the dominance of the global percept and reduced the rate with which percepts alternated. This can be understood as resulting from an addition of the vestibular self-motion vector to the visual motion vector, because the addition of a self-motion signal in the opposite direction would reduce the plaid's perceived velocity. Reducing the velocity of a plaid stimulus has been found to increase the likelihood of the global percept, both empirically (Hupé & Rubin, 2003) and in modeling work (Hedges, Stocker, & Simoncelli, 2011). Note that in our data, when self-motion and global stimulus motion are in the same direction and so combine to increase perceived speed, no concomitant decrease in global percept dominance is observed. This is consistent with previous studies showing that the effect of speed on bistability is most pronounced at low speeds, rapidly reaching asymptote at speeds as low as  $3^\circ/\text{s}$  (Hupé & Rubin, 2003). In Experiment 1, stimulus speed was  $5.6^\circ/\text{s}$ , and self-motion speed an average of  $12^\circ/\text{s}$ . Although the relative weights of the vector sum are unknown (and unlikely to be equal), the addition of any self-motion vector in the same direction as the stimulus can only increase the perceived speed of the stimulus, and therefore cannot be expected to have great impact on dominance durations. Finally, when self-motion was in a direction orthogonal to global stimulus motion, addition of the self-motion vector to the motion vectors of the two components introduced an asymmetry in the velocities of the two components: one increased and one decreased. Asymmetries in component properties (including speed) are known to reduce the dominance of the bound percept (Adelson & Movshon, 1982; Movshon et al., 1985).

Although the present data do not allow us to disentangle the differential effects of different velocities over the course of the trial from a non-specific time-dependence, we did observe a striking match over time between orthogonal self-motion velocity and



the bias for the component interpretation (Fig. 5). This is consistent with what would be expected if the asymmetry in component speeds introduced by the orthogonal self-motion vector increased and subsequently decreased over the course of the trial. Altogether then, the pattern of results in Experiment 1 is consistent with an addition of the self-motion vector to the visual motion vectors in the plaid.

In Experiment 2, self-motion was found to bias the perceived direction of a stimulus moving in an orthogonal direction, drawing the perceived direction *towards* the direction of self-motion. This is also consistent with a vector addition (Verstraten, Fredericksen, & van de Grind, 1994) of the vestibular self-motion signal with the visual motion signal. In this way, the results of both Experiment 1 and 2 both support the interpretation that visual motion perception is biased by vestibular motion signals in a direction-dependent way. Furthermore, although this addition would serve to compensate for self-motion when judging motion whilst moving with respect to an external reference frame, in the present experiments some residual compensation remained even though observers judged motion in a reference frame that was fixed relative to their own body.

Importantly, this interpretation makes a very specific prediction concerning the integration of vestibular input on the perception of bistable plaids. This is because it hinges on an account in terms of perceived speed. It therefore predicts, and even requires, that the perceived speed of a stimulus moving in the direction opposite to the self-motion vector is reduced compared to the perceived speed of a stimulus moving in the same direction. This prediction however remains to be tested. Furthermore, due to the limits imposed by the intersection of constraints that define a plaid's global motion, this account predicts that vestibular motion should bias the perceived motion directions of the individual components, without necessarily affecting their orientations. This is possible because of the direction ambiguity introduced by the aperture problem for the individual components. Interestingly, several observers in Experiment 1 reported informally that they occasionally perceived the component bars as moving directly away from each other in opposite directions (i.e., a directional difference of 180°), despite the orientation difference of only 141°. That is, direction and orientation were decoupled and they perceived the bars as moving in a direction that was not perpendicular to their orientation. It is tempting to conclude that vestibular signals biased the resolution of the ambiguity resulting from the aperture problem. Formal empirical evidence will be needed to test this interpretation.

In sum, we show in two experiments that the perception of visual motion direction can be systematically affected by concurrent but uninformative and task-irrelevant vestibular input caused by self-motion. The direction of these effects is consistent with the interpretation that a motion vector calculated from vestibular input is added to local motion vectors extracted from the visual stimulus, in a similar manner to how saccadic remapping corrects for shifts in the retinal positions of stationary objects across eye movements.

## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.visres.2016.11.002>.

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