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Velocity influences the relative contributions of visual and vestibular cues to self-acceleration

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Abstract

Self-motion perception is based on the integration of visual (optic flow) and vestibular (inertial) sensory information. Previous research has shown that the relative contribution of visual and vestibular cues can change in real time based on the reliability of that information. The present study assessed whether initial velocity and acceleration magnitude influence the relative contribution of these cues to the detection of self-acceleration. Participants performed a simple response time task with visual and vestibular self-acceleration cues as targets. Visual optic flow was presented at three possible initial velocities of 3, 9, or 15 m/s, and accelerated to result in three possible final velocities of 21, 27, or 33 m/s. Corresponding vestibular cues were presented at magnitudes between 0.01 and 0.04 g. The self-acceleration cues were presented at three possible stimulus onset asynchronies (SOAs): visual-first (by 100 ms), in-sync, and vestibular-first (by 100 ms). We found that presenting the cues in-sync resulted in the fastest responses across all velocities and acceleration magnitudes. Interestingly, presenting the visual cue first resulted in a relative advantage over vestibular-first at the slowest initial velocity of 3 m/s, and vice versa for the fastest initial velocity of 15 m/s. The fastest overall responses for visual-first and in-sync were observed at 9 m/s. The present results support the hypothesis that velocity of optic flow can alter the relative contribution of visual and vestibular cues to the detection of self-acceleration.

Keywords Self-motion · Optic flow · Vestibular system · Multisensory integration · Response times · Motion simulator · Velocity · Acceleration

Introduction

Self-motion perception is most often a result of integration of multiple sensory inputs that provide information such as velocity, acceleration, direction of heading, and rotations along an axis. In particular, the integration of visual (optic flow) and vestibular (inertial) motion cues improves the

precision of self-motion perception (Gu et al. 2008; Fetsch et al. 2009, 2011; Butler et al. 2010, 2015; de Winkel et al. 2013). Optic flow is the pattern of visual motion on the retina during self-motion, and provides the observer with velocity and acceleration cues that are critical for successful sensorimotor coordination and navigation (Gibson et al. 1955; McKee et al. 1986; Orban et al. 1984; Lappe et al. 1999). Vestibular cues, in contrast, are from the net force acting on the observer during self-acceleration; these cues become more salient as acceleration magnitudes increase (Groen 1956; Gu et al. 2007; MacNeilage et al. 2010). In the present study, we use the term “vestibular” to refer to both the detection of translational motion transduced by the otolith organs of the vestibular system (Israel and Berthoz 1989), as well as any possible contributions from the activation of proprioceptive receptors (Hlavačka et al. 1996). The integration of visual and vestibular cues is important, because the detection of self-motion based on either system alone is limited. The visual system is much less sensitive to

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Significance statement The present study contributes novel evidence to the emerging literature on how visual–vestibular integration can result in reliable self-motion perception.

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acceleration than to constant velocity (Gottsdanker 1956; McKee 1981; Watamaniuk and Heinen 2003), and the vestibular system can only transduce the net force acting on the observer during acceleration, and is therefore unable to detect constant velocity (Corey and Hudspeth 1979; Gillespie and Mueller 2009). Moreover, vestibular perception is relatively slow in the absence of visual cues (for a review see Barnett-Cowan 2013).

The contribution of optic flow to self-motion perception has been understood since Mach (1875), who found that optic flow can induce the illusion of self-motion (vection). Vection strength depends on both the field of view of the optic flow stimulus (Brandt et al. 1972; Mergner et al. 2000; Ash and Palmisano 2012), as well as the acceleration magnitude (Palmisano et al. 2008). Individual differences in vection strength are positively correlated with dependence on visual self-motion cues (Keshavarz et al. 2017), and negatively correlated with dependence on vestibular cues (Lepecq et al. 1999; Arshad et al. 2019). The interpretation of vestibular cues to heading has been found to be highly influenced by optic flow cues from the visual system (Townsend et al. 2019). Although it is clear that visual–vestibular integration plays an important role in self-motion perception, further research is required to explore the range of conditions under which the relative contributions from visual and vestibular systems changes.

Previous literature has shown that the integration of visual and vestibular cues is mediated by a dynamic reweighting process based on stimulus reliability (Fetsch et al. 2009, 2011; ter Horst et al. 2015). In particular, it has been found that the relative weighting of vestibular cues tends to increase when the quality of visual cues is sufficiently degraded (Fetsch et al. 2009, 2011; Butler et al. 2010; Gallagher et al. 2020). It has also been found that relative visual–vestibular reliability changes as a function of temporal frequency: vestibular cues tend to be more precise for sinusoidal motion occurring at frequencies above 2 Hz, whereas visual cues tend to be more precise for motion at frequencies below 2 Hz (Berthoz et al. 1975; Zacharias and Young 1981; Karmali et al. 2014). These results are consistent with the finding that the human visual system fails to detect sinusoidal acceleration occurring at very high frequencies (Werkhoven et al. 1992; Nakayama and Motoyoshi 2017).

There is also some evidence from visual psychophysics research that the reliability of visual self-motion perception changes as a function of velocity. In angular velocity discrimination tasks, Weber-like fractions tend to hold for velocities at which it is easy to judge relative differences (Schmerler 1976; Calderone and Kaiser 1989); however, discrimination thresholds tend to violate Weber's law at extremely low (below 1 degrees/s) and extremely high (above 64 degrees/s) angular velocities, resulting in a U-shaped discrimination curve (McKee 1981; Orban et al.

1984; de Bruyn and Orban 1988). This curve has been replicated in tasks measuring response times (Monen and Brenner 1994). Neuroscience work is consistent with these observations; most optic flow detecting neurons in the middle temporal area (MT/V5) are tuned to moderate velocities in the range of 7–30 degrees/s (Rodman and Albright 1987; Cheng et al. 1994; Chawla et al. 1999; Liu and Newsome 2005).

Taken together, the existing literature suggests that the visual and vestibular systems may be more sensitive within different comparative ranges of velocities. Given that self-motion perception is most often a result of integration of visual and vestibular information, we were interested in whether we could observe differences in the contribution of visual versus vestibular inputs in a simple self-acceleration detection task across a range of velocities and acceleration magnitudes. We tested the hypothesis that response time to detect a difference in self-motion would reflect different sensitivities of the visual and vestibular systems to acceleration at different velocities. We used a simple response time task in which participants detected the onset of self-acceleration cued by both visual (e.g. changes in optic flow) and vestibular (e.g. forward movement of the motion simulator) inputs. Critically, we biased the inputs by manipulating stimulus onset asynchrony (SOA), so that onset of visual and vestibular cues to acceleration were synchronous or offset by 100 ms (either visual first or vestibular first). Our prediction was that these small biases in temporal onset would reveal different patterns of integration of visual and vestibular information, reflecting visual and vestibular sensitivities across different velocities.

Methods

Participants

Thirty-five participants (20 females) between the ages of 18 and 26 ($M = 18.50$ years, $SD = 1.66$ years) were recruited from McMaster University's psychology participant pool and the McMaster community. Those recruited from the participant pool were compensated with course credit. All participants reported normal or corrected-to-normal vision and no problems with vertigo, motion sickness, or claustrophobia. The experiment was approved by the Hamilton Integrated Research Ethics Board and complied with the Canadian Tri-Council policy on ethics.

Experimental setup

The motion simulator pod was supported by a MOOG © platform with six degrees of freedom (MOOG series 6DOF2000E). Participants sat in a bucket-style car seat

with a button box placed on their lap. They wore earplugs while white noise was presented at 65 dBA to mask auditory noises from the simulator mechanics. Sound pressure levels remained at 65 dBA across all conditions (verified by Galaxy Audio CM-130 Check Mate SPL meter). Visual cues were presented on a single 43-inch LCD monitor, situated 51 inches from the participant, subtending a visual angle of 41.23 degrees, therefore recruiting a portion of their near peripheral visual field (Strasburger et al. 2011). The screen resolution was 1920×1080 (1080p) and the optic flow stimulus was presented at a refresh rate of 60 Hz. Acceleration magnitudes were calibrated with a piezoelectric

accelerometer located in the frame of the motion simulator (Endevco model number 752A13), with a 1 KHz sampling rate and 1 mV/g sensitivity. We used real-time data acquisition with a photocell sensor on the screen (visible at the bottom left of Fig. 1a) and the accelerometer to ensure that the onset of visual and vestibular cues were precisely temporally calibrated.

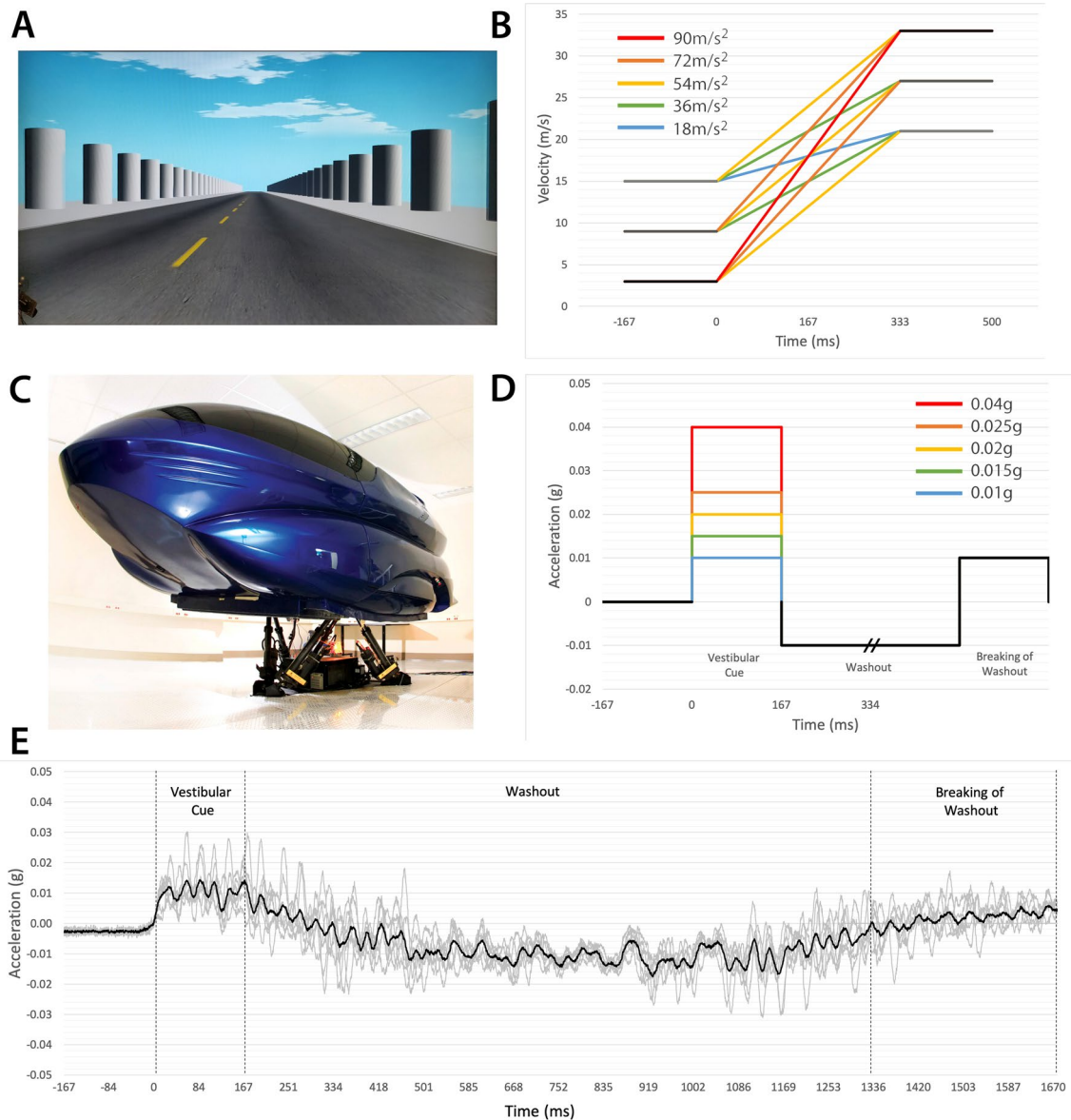


Fig. 1 **a** The optic flow stimulus used in the present experiment. **b** Time course displaying velocity of the visual cues. **c** Outside view of the motion simulator supported by a MOOG motion platform. **d**

Commanded magnitudes of the vestibular cues. **e** Seven recorded motion profiles of the vestibular cue at 0.01 g (grey), and the ensemble average (black)

Experimental design

Visual cues

Participants were presented with an optic flow stimulus (Fig. 1a) depicting passive forward movement along a road at one of three constant velocities (3, 9, or 15 m/s). The yellow lane markers, cylindrical posts, and texture of the road served as visual cues to velocity and acceleration.

The visual cue to self-acceleration was an increase in the rate of optic flow (Fig. 1a, b). Optic flow could be presented at one of three initial velocities (3, 9, or 15 m/s) and could result in one of three final velocities (21, 27, or 33 m/s), with an acceleration duration of 333 ms. Acceleration magnitude of the visual cue was determined by the difference between the initial and final velocity divided by Δt (0.333 s), resulting in five unique acceleration magnitudes (18, 36, 54, 72, or 90 m/s²).

Vestibular cues

The vestibular cue to self-acceleration was forward linear translation (surge) of the simulator pod (Fig. 1c–e). The five unique acceleration magnitudes corresponded to surge at 0.01, 0.015, 0.02, 0.025, or 0.04 g. Each vestibular cue was presented for 166 ms, followed by a washout at 0.01 g to return the simulator to its starting position. We presented motion vibration on the coronal plane to mask motion jerk during acceleration onset. All acceleration magnitudes were well above the vestibular detection threshold for surge, which ranges between 0.0025 and 0.009 g based on the frequency of the motion profile (Heerspink et al. 2005). These acceleration magnitudes were selected based on preliminary testing to achieve perception of forward motion within the spatial restrictions of the movement of the platform while minimizing compensatory movements of the head, neck, or upper body. This was done to target stimulation to the otolith organs; however, head movement was not quantified. The commercial Stewart platform provides excellent control response with minimal overshoot and low rise time; the variance in the motion profiles is due to mechanical resonance (natural oscillations) of the motion simulator pod itself. Full characterization of eigenfrequencies, delays, and step responses of the system allowed a close match between commanded and actual motion. Figure 1e illustrates seven recorded motion profiles at 0.01 g (grey) as well as the ensemble average (black). The mean over the first 166 ms was 0.01 g, with a variance of 0.000027.

Task

Participants completed a simple response task with two target stimuli, and were instructed to press a button upon

detection of either the visual or vestibular self-acceleration cue. Visual optic flow was presented at one of three initial velocities, resulted in one of three final velocities, and cues could be presented at one of three stimulus onset asynchronies (SOAs): visual-first (by 100 ms), in-sync, or vestibular-first (by 100 ms). We used these SOAs to compare the relative contributions of visual versus vestibular cues to multisensory response times. This approach manipulated the timing of the cue onset, where one cue was given a small temporal advantage towards the response process. This also minimized potential cue conflicts; for example, presenting the vestibular acceleration cue alone while the visual cue remained at a constant velocity could have resulted in a perceptual cue conflict. Response times were defined as the time between the onset of the first cue and the button press. The present experiment had a repeated measures $3 \times 3 \times 3$ design: SOA by initial velocity by final velocity, producing 27 conditions. Inter-trial intervals were drawn from a uniform distribution between 1.66 and 2.66 s. For each of the 27 conditions, participants completed 30 trials (840 total trials). Each participant completed four identical blocks in which trial presentation order was randomized (210 trials per block; 7–8 trials per condition per block). Participants were given a mandatory break of at least 5 min between each block. The entire session lasted between 1 and 1.5 h in duration.

Data trimming procedures

Since response times are known to follow a right-skewed distribution, outlier detection was performed on the log-transformed values. Response times were pooled into a grand distribution for each condition, and removed if their log-transformed values surpassed the criteria for extreme outliers: below $Q1 - 3.0(IQR)$ or above $Q3 + 3.0(IQR)$, where $Q1$ and $Q3$ indicate the first and third quartile of the log-transformed values, and IQR indicates the interquartile range between $Q1$ and $Q3$. After outlier removal, there were 714–815 response times in each condition. Figures were created in R with the `ggplot2` (Wickham 2017), `ggpubr` (Kasambara 2019), and `R.matlab` (Bengtsson 2018) packages. Raw data and code are available upon direct request of the corresponding author.

Statistical analyses

To disambiguate the effect of acceleration magnitude and initial velocity, we first split the data by initial velocity and performed three separate repeated measures ANOVAs with the design of SOA by acceleration magnitude (3×3). Since there appeared to be a crossover between the visual- and vestibular-first SOAs across initial velocity (see Fig. 2, compare SOAs between panels A–C), we performed an

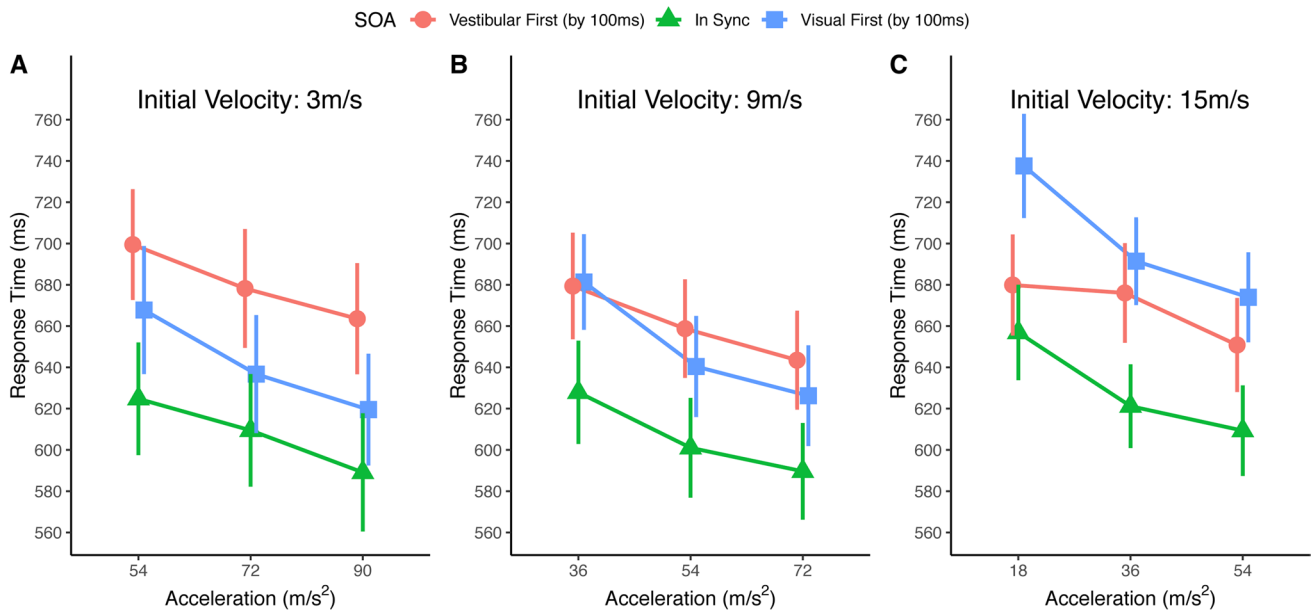


Fig. 2 Grand mean (\pm SEM) response times by SOA and acceleration magnitude at an initial velocity of (a) 3 m/s, (b) 9 m/s, and (c) 15 m/s. SEM represents the between and within subject variance

ANCOVA analysis with acceleration magnitude treated as a covariate. We verified that acceleration magnitude could appropriately be treated as a covariate by creating another linear model that allowed slope to vary between the SOA by initial velocity conditions. This model found no interactions between acceleration magnitude and SOA by initial velocity condition, validating the homogeneity of slopes assumption in the ANCOVA. We performed an independent measures ANCOVA with the design of SOA by initial velocity (3×3), and pairwise comparisons were evaluated with Tukey's HSD. The final goal of this experiment was to determine whether the effects of SOA and initial velocity varied over the course of the experiment. This was achieved by performing a final repeated measures ANOVA with the design of SOA by initial velocity by block ($3 \times 3 \times 4$). All p values were reported with Huyhn–Feldt correction for sphericity whenever necessary. In total, five parametric tests were performed. Statistics were performed in R with the car and effects packages (Fox and Weisburg 2019).

Results

Response times by SOA and acceleration magnitude

We first analysed response times as a function of SOA and acceleration magnitude. Since there were a different set of acceleration magnitudes for each initial velocity, repeated measures ANOVAs were performed on each initial velocity separately (Fig. 2).

For all three initial velocities, response times decreased at greater acceleration magnitudes (3 m/s: $F(2, 68) = 50.10$, $\epsilon = 0.868$, $p < 0.001$; 9 m/s: $F(2, 68) = 51.16$, $\epsilon = 0.898$, $p < 0.001$; 15 m/s: $F(2, 68) = 42.67$, $\epsilon = 0.769$, $p < 0.001$). This shows that greater acceleration magnitudes resulted in faster responses across all conditions. An interaction was found between SOA and acceleration magnitude, but only at the smallest acceleration magnitude for the fastest initial velocity of 15 m/s ($F(4, 136) = 5.573$, $\epsilon = 0.890$, $p < 0.001$).

Although SOA had a significant effect on response time for each of the initial velocities (3 m/s: $F(2, 68) = 137.72$, $\epsilon = 0.886$, $p < 0.001$; 9 m/s: $F(2, 68) = 117.00$, $\epsilon = 0.951$, $p < 0.001$; 15 m/s: $F(2, 68) = 85.54$, $\epsilon = 0.944$, $p < 0.001$), the ordered trend of SOA changed across initial velocity. This suggests an advantage for the visual- over vestibular-first SOA at the lowest initial velocity (3 m/s; shown in Fig. 2a), compared to an advantage for the vestibular- over visual-first SOA at the highest initial velocity (15 m/s; shown in Fig. 2c). At the intermediate initial velocity of 9 m/s (Fig. 2b), the relative advantage of the visual- over vestibular-first SOA was not as prominent. The fastest responses were found across all initial velocities and acceleration magnitudes when cues were presented in-sync.

Response times by SOA and initial velocity

The previous analysis found an ordered trend of SOA that crossed over across initial velocity, suggesting an interaction between SOA and initial velocity. We tested this observation statistically by performing an analysis of covariance

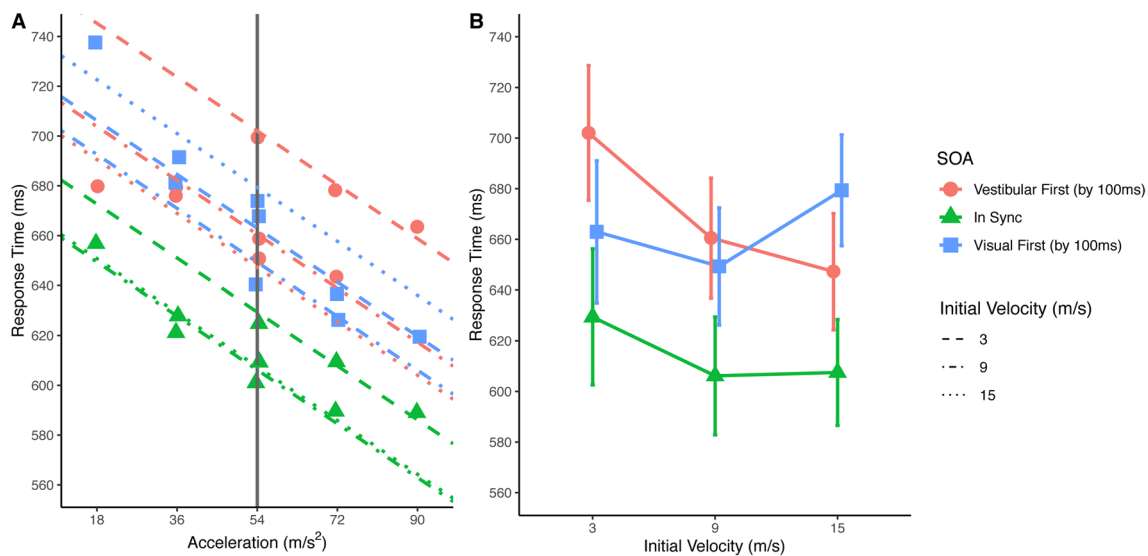


Fig. 3 **a** ANCOVA regression model for each SOA and initial velocity combination, with acceleration magnitude treated as the covariate. Adjusted grand means were taken where the regression line crossed the mean of the covariate, indicated by the vertical line. **b** Adjusted

grand mean (\pm SEM) response times by SOA and initial velocity with acceleration magnitude regressed out of the relationship. SEM represents the between and within-subject variance

(ANCOVA) with acceleration magnitude treated as a covariate across initial velocity (Fig. 3). This was accomplished by modelling response times by both acceleration magnitude and SOA \times initial velocity. To verify whether the homogeneity of slopes assumption was valid across the nine SOA \times initial velocity conditions, we performed another model that allowed slope to vary between the nine conditions. Since the second model did not find a significant three-way interaction between acceleration, SOA, and initial velocity ($F(8, 9) = 1.74, p = 0.21$), the homogeneity of slopes assumption was considered valid.

The ANCOVA model is plotted in Fig. 3a, and the adjusted grand means are plotted in Fig. 3b. The individual regression lines for each condition are indicated by colour (SOA) and linetype (initial velocity). Adjusted grand means were calculated by taking the value of the regression line as it crossed the mean of the covariate (54 m/s^2) to control for the linear association between acceleration magnitude and response time. We found a significant main effect of acceleration magnitude ($F(1,17) = 243.65, p < 0.001$), SOA ($F(2,17) = 174.13, p < 0.001$), initial velocity ($F(2,17) = 24.10, p < 0.001$), and an interaction between SOA and initial velocity ($F(4,17) = 12.61, p < 0.001$), validating the crossover discussed earlier.

For the in-sync SOA, although the fastest responses were found at the intermediate velocity of 9 m/s, Tukey's HSD test for pairwise comparisons found that there were no significant differences for the in-sync SOA between 9 m/s and 3 m/s ($p = 0.16$), or between 9 and 15 m/s ($p = 0.56$). For the visual-first SOA, the fastest overall responses were also

found at 9 m/s, and responses were significantly faster at 9 m/s compared to 15 m/s ($p < 0.001$), but not significantly different between 9 m/s and 3 m/s ($p = 0.89$). For the vestibular-first SOA, the fastest responses were found at the fastest velocity of 15 m/s, and responses became increasingly faster at higher initial velocities; responses were significantly faster at 9 m/s compared to 3 m/s ($p < 0.001$), and significantly faster at 15 m/s compared to 3 m/s ($p < 0.001$). By regressing out the main effect of acceleration, we are regressing out the effect of the vestibular cue itself, and leaving behind only the effect of initial velocity. Despite regressing out the vestibular cue itself, the slope of the vestibular-first SOA was opposite to that the visual-first SOA. This strongly suggests that the initial velocity of optic flow influenced the relative contributions of visual and vestibular cues to self-acceleration detection.

Response times by SOA, initial velocity, and block

Finally, we were interested in determining whether practice could influence the observed relationship between SOA and initial velocity. Hypothetically, participants could learn statistical regularities across the trials and adjust their response strategy accordingly. For example, participants could learn that low velocity will result in a more reliable visual cue to self-acceleration and consciously change their allocated attention towards vision. Any interactions between block and the various SOA and initial velocity conditions would therefore indicate that participants were learning statistical regularities across the trials as they completed more blocks.

We found a main effect of block ($F(3, 90) = 5.25, \epsilon = 0.725, p = 0.0063$); however, there were no interactions between block and SOA, block and initial velocity, or three-way interaction between block, SOA, and initial velocity. The main effect of block indicates that response times were influenced by block, regardless of condition. Faster responses over the first three blocks indicate learning and improved processing automaticity, whereas slower responses in the final block indicate the presence of fatigue. The lack of interactions between block and the various conditions suggests that differences between the conditions occurred at the beginning of the experiment and were likely not due to the development of a particular response strategy as participants learned more about the experiment. The grand mean response times across the four blocks are plotted below in Fig. 4.

Discussion

The present study assessed response times to visual and vestibular self-acceleration cues at three initial velocities. The relative contributions of visual and vestibular cues were measured by manipulating the SOA between the onset of the cues. In the first set of analyses, we found that as acceleration magnitude increased, response times decreased for all initial velocities and SOAs (Fig. 2). For the lowest and intermediate initial velocities (3 and 9 m/s), we found no interactions between SOA and acceleration magnitude. However, for the highest initial velocity (15 m/s), we found an interaction between SOA and acceleration magnitude. In all three

analyses, there was a significant effect of SOA on response time. The ordered trend of the visual and vestibular-first SOAs appeared to cross over across initial velocity. This observation was tested statistically by treating acceleration magnitude as a covariate across initial velocity, and directly comparing SOA and initial velocity (Fig. 3). This analysis found an interaction between SOA and initial velocity. In particular, presenting the visual cue first resulted in relatively faster responses at the lowest and intermediate initial velocities of 3 and 9 m/s, and presenting the vestibular cue first resulted in relatively faster responses at the highest initial velocity of 15 m/s. As anticipated, presenting the cues in-sync resulted in the fastest responses across all velocities and acceleration magnitudes. This analysis produced the most interesting finding of the present study; after regressing out the main effect of acceleration magnitude, initial velocity of optic flow still appeared to dynamically change response times to the vestibular-first SOA. These results are interesting because they are consistent with the hypothesis that velocity of optic flow resulted in a redistribution of the influence of visual versus vestibular cues when making speeded responses to self-acceleration detection. In the final analysis (Fig. 4), we were interested in determining whether the interaction between SOA and initial velocity could be attributed to the development of a particular response strategy as participants completed more trials, and hence learned more about the experiment. This analysis did not find any interactions between block, SOA, and initial velocity, suggesting that the interaction between SOA and initial velocity occurred during all blocks, and was not a result of

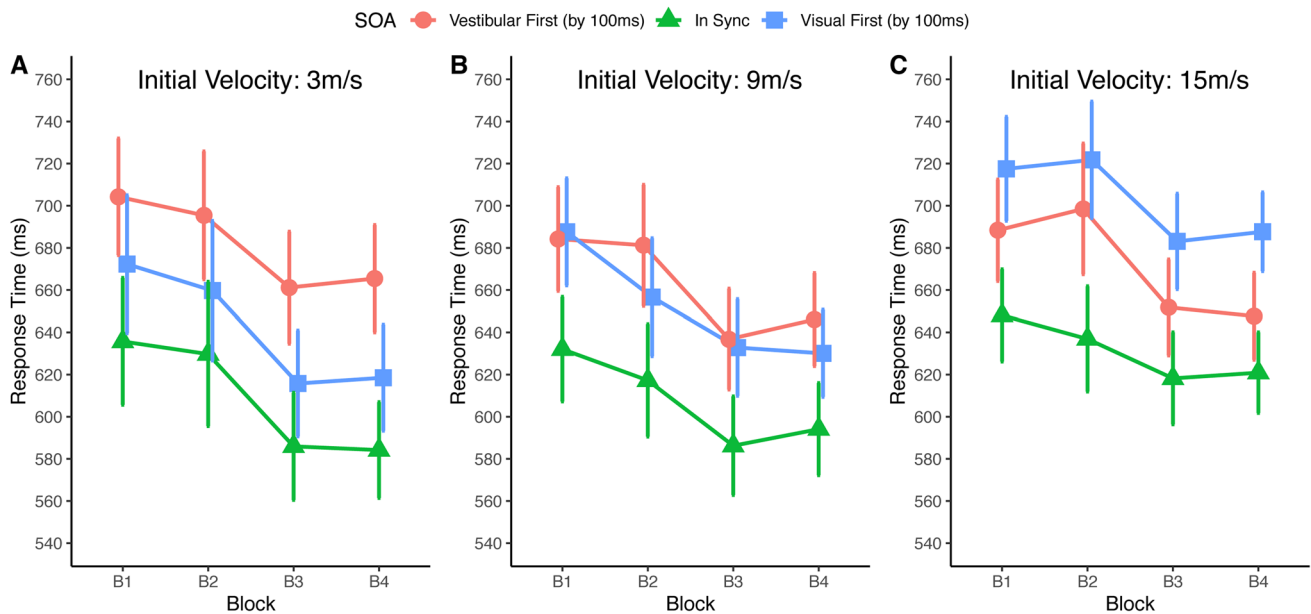


Fig. 4 Grand mean (\pm SEM) response times by SOA and block for an initial velocity of (a) 3 m/s, an initial velocity of (b) 9 m/s, and an initial velocity of (c) 15 m/s. SEM represents the between- and within-subject variance

participants developing a certain response strategy as they gathered statistical regularities across the trials.

Overall, our experiment demonstrated that there was a response time advantage for visual cues over vestibular cues at lower initial velocities. This is roughly consistent with Weber's law, where increases in velocity are relatively easier to detect when they are presented at lower initial velocities (Schmerler 1976; Calderone and Kaiser 1989). However, this simple relationship was complicated by findings that when the visual cue was presented first, the fastest overall responses were found at the intermediate initial velocity of 9 m/s. This finding reflected the tuning curves of velocity detecting neurons in the middle temporal area (MT/V5). Previous research has found an inverted U-shaped tuning curve for velocity, where the majority of velocity detecting neurons in MT/V5 seem to be responsive to angular velocities between 7 and 30 degrees/s (Rodman and Albright 1987; Cheng et al. 1994; Chawla et al. 1999; Liu and Newsome 2005). This has also been demonstrated in psychophysics research, where the best perceptual performance is generally found in the same range (Orban et al. 1984; de Bruyn and Orban 1988; Monen and Brenner 1994). Moreover, a recent study recorded EEG while participants were presented with passive optic flow at three possible velocities and found that velocity modulated the peak amplitude and latency of an N2 ERP component located over MT/V5 (Vilhelmsen et al. 2015). In their study, the lowest velocity was found to elicit the greatest peak amplitude and shortest peak latency. The authors argued that this amplitude reflects greater activity of the neural population and faster processing speed. An earlier study using considerably lower velocities found that very slow velocities resulted in less activity in the MT/V5 region (Maruyama et al. 2002). The N2 component has also been observed over the occipital lobe during the early stage of vection onset (Keshavarz and Berti 2014), potentially indicating that this component reflects the visual contributions to self-motion perception. In fMRI studies, neural activity in MT/V5 has also been found to be associated with the subjective experience of self-motion (Kovács et al. 2008; Uesaki and Ashida 2015). Together, these findings may reflect the visual system adjusting its relative contributions to self-motion based on velocity of optic flow.

The relative advantage of visual cues over vestibular cues at lower initial velocities is a novel finding. There are a few key differences in the design of our study that may have led to these results. Most past research on velocity discrimination has reported discrimination thresholds with two-alternative forced choice tasks, whereas in the current study, we measured response times. Response times have been directly linked to perceptual thresholds to self-motion (Soyka et al. 2013). One advantage to using response times is that they are typically less challenging and fatiguing for participants, allowing for more trials over the course of an experiment.

In a recent study that incorporated both perceptual thresholds and response times in a heading discrimination task, it was suggested that visual weighting could be dependent on the velocity profile of the stimulus (Drugowitsch et al. 2014). However, it is important to note that in their study, 'weighting based on velocity' means that a faster velocity corresponded to an increased rate of information per second about the target cue, whereas in our study, velocity did not correspond to an increased rate of information about the target since participants were responding to the onset of the acceleration stimulus. Although response times to vestibular cues tend to be much slower than visual cues when presented alone (Barnett-Cowan and Harris 2009; Barnett-Cowan 2013), it is interesting that there was not much of a difference between the visual-first and vestibular-first conditions in the present results. Psychophysics studies tend to report perceptual thresholds as the Weber fraction between initial and final velocity, which inherently accounts for percentage differences in velocity. Psychophysics studies also tend to use a sinusoidal acceleration stimulus where the final velocity is not held constant, unlike the present study. Although in our experiment it is unclear whether participants were responding to the acceleration signal or the absolute difference between initial and final velocity, there is existing evidence showing that the visual system does not respond to the acceleration signal directly, but rather integrates changes in velocity over discrete time intervals (Werkhoven et al. 1992; Loose and Probst 2001; Schlack et al. 2008; Nakayama and Motoyoshi 2017). Early work on vestibular perception found that response times to vestibular cues tend to decrease as acceleration magnitude increases (Jones and Young 1978). In the present study, we found that our acceleration magnitudes had a linear effect on response times, but this may have been due to the limited range of accelerations we presented. It is also possible that visual and vestibular motion aftereffects had an effect on trial-to-trial response times (Harris et al. 1981; Crane 2012).

Visual-vestibular integration has been found to facilitate heading estimation (Telford et al. 1995; Ohmi 1996), distance estimation (Harris et al. 2000; Bertin and Berthoz 2004), rotation perception (Jürgens & Becker 2006), and roll-tilt discrimination (de Vrijer et al. 2009; Clemens et al. 2011; Karmali et al. 2014). Although many studies have demonstrated that the integration of visual and vestibular signals leads to improved self-motion perception, the mechanism underlying visual-vestibular integration has remained somewhat elusive until recently. Recent studies have demonstrated that visual and vestibular cues are reweighted in real time based on their reliability (Gu et al. 2008; Fetsch et al. 2009, 2011; Butler et al. 2010; ter Horst et al. 2015; Gallagher et al. 2020). Although the present study does not test the reweighting hypothesis directly, the results contribute to this novel literature by suggesting that velocity may

influence the relative contributions of visual and vestibular cues during self-acceleration detection. Future experimentation is warranted to validate our hypothesis that these results were caused by a velocity-dependent reweighting process.

To summarize, the present experiment found evidence that the velocity of optic flow changes the relative contributions of visual and vestibular cues to self-acceleration in a simple response time task. To the best of our knowledge, this is one of the first studies to find evidence of such a phenomenon. In particular, we found that responses to the visual cue were relatively faster when a lower initial velocity was presented, and responses to the vestibular cue were relatively faster when a higher initial velocity was presented. This crossover suggests that relative sensitivity to visual and vestibular cues may be complementary across initial velocity. When the cues were presented simultaneously, the fastest responses were observed across all velocities and acceleration magnitudes. The fastest responses to the visual-first SOA were found at the intermediate velocity of 9 m/s, which is in agreement with existing neuroscience and psychophysics research. This crossover effect became more evident after acceleration magnitude was regressed out of the relationship. This was surprising, because vestibular cues were from forward surge of the motion simulator, which is directly proportional to the acceleration magnitude. After regressing out acceleration magnitude, the contribution of vestibular cues should be independent of the initial velocity. Instead, the present results found that responses to the vestibular-first SOA became faster at higher initial velocities. These results suggest that the initial velocity of the optic flow stimulus caused a shift in the relative perceptual contributions of visual and vestibular cues to self-acceleration.

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Compliance with ethical standards

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References

- Arshad Q, Ortega MC, Goga U, Lobo R, Siddiqui S, Mediratta S, Bednarczuk NF, Kaski D, Bronstein AM (2019) Interhemispheric control of sensory cue integration and self-motion perception. *Neuroscience* 408:378–387
- Ash A, Palmisano S (2012) Vection during conflicting multisensory information about the axis, magnitude, and direction of self-motion. *Perception* 41:253–267
- Barnett-Cowan M (2013) Vestibular perception is slow: a review. *Multisensory Res* 26(4):387–403
- Barnett-Cowan M, Harris LR (2009) Perceived timing of vestibular stimulation relative to touch, light and sound. *Exp Brain Res* 198(2–3):221–231
- Bengtsson H (2018). R.matlab: Read and Write MAT Files and Call MATLAB from Within R. R package version 3.6.2. <https://CRAN.R-project.org/package=R.matlab>
- Berthoz A, Pavard B, Young LR (1975) Perception of linear horizontal self-motion induced by peripheral vision (linear vection) basic characteristics and visual-vestibular interactions. *Exp Brain Res* 23:471–489
- Bertin RJ, Berthoz A (2004) Visuo-vestibular interaction in the reconstruction of travelled trajectories. *Exp Brain Res* 154:11–21
- Brandt T, Dichgans J, Koenig E (1972) Perception of self-rotation (circular vection) induced by optokinetic stimuli. *Pflugers Arch* 332:R398
- Butler JS, Smith ST, Campos JL, Bühlhoff HH (2010) Bayesian integration of visual and vestibular signals for heading. *J Vis* 10(11):1–13
- Butler JS, Campos JL, Bühlhoff HH (2015) Optimal visual-vestibular integration under conditions of conflicting intersensory motion profiles. *Exp Brain Res* 233(2):587–597
- Calderone JB, Kaiser MK (1989) Visual acceleration detection: effect of sign and motion orientation. *Percept Psychophys* 45(5):391–394
- Chawla D, Buechel C, Edwards R, Howseman A, Josephs O, Ashburner J, Friston KJ (1999) Speed-dependent responses in V5: a replication study. *NeuroImage* 9:508–515
- Cheng K, Hasegawa T, Saleem KS, Tanaka K (1994) Comparison of neuronal selectivity for stimulus speed, length, and contrast in the prestriate visual cortical areas V4, and MT of the macaque monkey. *J Neurosci* 14(6):2269–2280
- Clemens IA, de Vrijer M, Selen LP, van Gisbergen JA, Medendorp WP (2011) Multisensory processing in spatial orientation: an inverse probabilistic approach. *J Neurosci* 31:5365–5377
- Corey DP, Hudspeth AJ (1979) Response latency of vertebrate hair cells. *Biophys J* 26:499–506
- Crane T (2012) Fore-aft translation aftereffects. *Exp Brain Res* 219(4):477–487
- de Bruyn B, Orban GA (1988) Human velocity and direction discrimination measured with random dot patterns. *Vision Res* 28:1323–1335
- de Winkel KN, Soyka F, Barnett-Cowan M, Bühlhoff HH, Groen EL, Werkhoven PJ (2013) Integration of visual and inertial cues in the perception of angular self-motion. *Exp Brain Res* 231:209–218
- de Vrijer M, Medendorp WP, van Gisbergen JA (2009) Accuracy-perception trade-off in visual orientation constancy. *J Vis* 9:9–15
- Drugowitsch J, DeAngelis GC, Klier EM, Angelaki DE, Pouget A (2014) Optimal multisensory decision making in a reaction time task. *eLIFE* 3:e03005
- Fetsch CR, Turner AH, DeAngelis GC, Angelaki DE (2009) Dynamic reweighting of visual and vestibular cues during self-motion perception. *J Neurosci* 29(49):15601–15612
- Fetsch CR, Pouget A, DeAngelis GC, Angelaki DE (2011) Neural correlates of reliability-based cue weighting during multisensory integration. *Nat Neurosci* 15:146–154
- Fox J, Weisberg S (2019) An R companion to applied regression, 3rd Edition. Thousand Oaks, CA <https://tinyurl.com/carbook>
- Gallagher M, Choi M, Ferre ER (2020) Multisensory interactions in virtual reality: optic flow reduces vestibular sensitivity, but only for congruent planes of motion. *Multisens Res* 1:20. <https://doi.org/10.1163/22134808-20201487>

- Gibson JJ, Olum P, Rosenblatt F (1955) Parallax and perspective during aircraft landings. *Am J Psychol* 68:372–385
- Gottsdanker RM (1956) The ability of human operators to detect acceleration of target motion. *Psychol Bull* 53(6):477–487
- Groen JJ (1956) The semicircular canal system of the organs of equilibrium-I. *Phys in Med & Biol* 1(2):103
- Gu Y, Angelaki DE, DeAngelis GC (2007) A functional link between area MSTd and heading perception based on vestibular signals. *Nat Neurosci* 10(8):1038–1047
- Gu Y, Angelaki DE, DeAngelis GC (2008) Neural correlates of multisensory cue integration in macaque MSTd. *Nat Neurosci* 11(10):1201–1210
- Harris LR, Morgan MJ, Still AW (1981) Moving and the motion after-effect. *Nature* 293:139–141
- Harris LR, Jenkin M, Zikovitz DC (2000) Visual and non-visual cues in the perception of linear self-motion. *Exp Brain Res* 135:12–21
- Heerspink H, Berkouwer W, Stroosma O, van Paassen R, Mulder M, Mulder B (2005). Evaluation of vestibular thresholds for motion detection in the SIMONA research simulator. AIAA modeling and simulation technologies conference and exhibit, pp 6502.
- Hlavačka F, Mergner T, Schweigart G (1996) Human self-motion perception during translatory vestibular and proprioceptive stimulation. *Neurosci Lett* 210(2):83–86
- Israel I, Berthoz A (1989) Contribution of the otoliths to the calculation of linear displacement. *J Neurophysiol* 62:247–263
- Jürgens R, Becker W (2006) Perception of angular displacement without landmarks: evidence for Bayesian fusion of vestibular, optokinetic, podokinesesthetic, and cognitive information. *Exp Brain Res* 174:528–543
- Karmali F, Lim K, Merfeld DM (2014) Visual and vestibular perceptual thresholds each demonstrate better precision at specific frequencies and also exhibit optimal integration. *J Neurophysiol* 111:2393–2403
- Kassambara A (2019). ggpubr: 'ggplot2' Based Publication Ready Plots. R package version 0.2.3. <https://CRAN.R-project.org/package=ggpubr>
- Keshavarz B, Berti S (2014) Sensory integration precedes the perception ofvection as mirrored by the N2 component of the human event-related brain potential. *Can J of Exp Psychol* 68(4):283–284
- Keshavarz B, Speck M, Haycock B, Berti S (2017) Effect of different display types onvection and its interaction with motion direction and field dependence. *i-Perception*:1–18.
- Kovács G, Raabe M, Greenlee MW (2008) Neural correlates of visually induced self-motion illusion in depth. *Cereb Cortex* 18:1779–1787. <https://doi.org/10.1093/cercor/bhm203>
- Lappe M, Bremmer F, van den Berg AV (1999) Perception of self-motion from visual flow. *Trends Cogn Sci* 3:329–336
- Lepecq J-C, Giannopulu I, Mertz S, Baudonnière P-M (1999) Vestibular sensitivity andvection chronometry along the spinal axis in erect man. *Perception* 28:63–72
- Liu JL, Newsome WT (2005) Correlation between speed perception and neural activity in the middle temporal visual area. *J Neurosci* 25(3):711–722
- Loose R, Probst T (2001) Velocity not acceleration of self-motion mediates visual-vestibular interaction. *Perception* 30:511–518
- Mach E (1875) *Grundlinien der Lehre von den Bewegungsempfindungen*. Engelmann, Leipzig, Germany
- MacNeillage PR, Banks MS, DeAngelis GC, Angelaki DE (2010) Vestibular heading discrimination and sensitivity to linear acceleration in head and world coordinates. *J Neurosci* 30(27):9084–9094
- Maruyama K, Kaneoke Y, Watanabe K, Kakigi R (2002) Human cortical responses to coherent and incoherent motion as measured by magnetoencephalography. *Neurosci Res* 44:195–205. [https://doi.org/10.1016/S0168-0102\(02\)00129-3](https://doi.org/10.1016/S0168-0102(02)00129-3)
- McKee SP (1981) A local mechanism for differential velocity detection. *Vision Res* 21:491–500
- McKee SP, Silverman GH, Nakayama K (1986) Precise velocity discrimination despite random variations in temporal frequency and contrast. *Vision Res* 26:609–619
- Medline Jones GM, Young LR (1978) Subjective detection of vertical acceleration: a velocity-dependent response? *Acta Oto-Laryngol* 85(1-2):45-53
- Mergner T, Schweigart G, Müller M, Hlavacka F, Becker W (2000) Visual contributions to human self-motion perception during horizontal body rotation. *Arch Ital Biol* 138:139–166
- Monen J, Brenner E (1994) Detecting changes in one's own velocity from the optic flow. *Perception* 23:681–690
- Nakayama R, Motoyoshi I (2017) Sensitivity to Acceleration in the Human Early Visual System. *Front Psychol* 8:925
- Ohmi M (1996) Egocentric perception through interaction among many sensory systems. *Cogn Brain Res* 5:87–96
- Orban GA, DeWolf J, Maes H (1984) Factors influencing velocity encoding in the human visual system. *Vision Res* 24:33–39
- Palmisano S, Allison RS, Pekin F (2008) Accelerating self-motion displays produce more compellingvection in depth. *Perception* 37(1):22–33
- Rodman HR, Albright TD (1987) Coding of visual stimulus velocity in area MT of the macaque. *Vision Res* 27(12):2035–2048
- Schlack A, Kregelberg B, Albright TD (2008) Speed perception during acceleration and deceleration. *J Vis* 8(8):9–9
- Schmerler J (1976) The visual perception of accelerated motion. *Perception* 5(2):167–185
- Soyka F, Bulthoff HH, Barnett-Cowan M (2013) Temporal processing of self-motion: modeling reaction times for rotations and translations. *Exp Brain Res* 228(1):51–62
- Strasburger H, Rentschler I, Jüttner M (2011) Peripheral vision and pattern recognition: a review. *J Vis* 11(5):13
- Telford L, Howard IP, Ohmi M (1995) Heading judgments during active and passive self-motion. *Exp Brain Res* 104:502–510
- ter Horst AC, Koppen M, Selen LPI, Medendorp WP (2015) Reliability-based weighting of visual and vestibular cues in displacement estimation Ben Hamed S, ed. *PLoS ONE* 10:e0145015
- Townsend B, Legere JK, O'Malley S, von Mohrenschildt M, Shedden JM (2019) Attention modulates event-related spectral power in multisensory self-motion perception. *NeuroImage* 191:68–80
- Uesaki M, Ashida H (2015) Optic-flow selective cortical sensory regions associated with self-reported states ofvection. *Front Psychol* 6:775
- Vilhelmsen K, van der Weel FR, van der Meer ALH (2015) A high-density EEG study of differences between three high speeds of simulated forward motion from optic flow in adult participants. *Front Syst Neurosci* 9:146
- Watamaniuk SN, Heinen SJ (2003) Perceptual and oculomotor evidence of limitations on processing accelerating motion. *J Vis* 3:698–709. <https://doi.org/10.1167/3.11.5>
- Werkhoven P, Snippe HP, Toet A (1992) Visual Processing of Optic Acceleration. *Vision Res* 31(12):2313–2329
- Wickham H (2017). Tidyverse: Easily Install and Load the 'Tidyverse'. R package version 1.2.1. <https://CRAN.R-project.org/package=tidyverse>
- Zacharias GL, Young LR (1981) Influence of combined visual and vestibular cues on human perception and control of horizontal rotation. *Exp Brain Res* 41:159–171

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