VELOCITY AND SELF-ACCELERATION PERCEPTION

VELOCITY INFLUENCES THE RELATIVE CONTRIBUTIONS OF VISUAL AND

VESTIBULAR CUES TO SELF-ACCELERATION PERCEPTION

By DARREN KENNEY, B.Sc.

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ABSTRACT

During self-motion perception, the contribution of visual vs. vestibular sensory information may vary based on how useful the cue information is anticipated to be. The present study assessed whether initial velocity and acceleration magnitude influence the relative contribution of visual (optic flow) and vestibular (inertial) self-motion 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 initial velocities of 3, 9, or 15m/s, and accelerated to result in final velocities of 21, 27, or 33m/s. The vestibular cue was presented at corresponding magnitudes between 0.01g and 0.04g. Cues were presented at three stimulus onset asynchronies (SOAs): visual-first (by 100ms), in-sync, and vestibular-first (by 100ms). We found that presenting 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 3m/s, and vice versa for the fastest initial velocity of 15m/s. The fastest overall responses for visual-first and in sync were observed at 9m/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.

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LIST OF ABBREVIATIONS

SOA Stimulus onset asynchrony

MT/V5 Middle Temporal Visual Area (V5)

fMRI Functional Magnetic Resonance Imaging

EEG Electroencephalography

ERP Event-related potential. Average EEG activity over many trials in a given time window.

N2 A specific ERP component characterized by a negative amplitude approximately 200ms after stimulus onset

SPL Sound pressure level

dBA A-weighted decibels

gRMS Root mean square of the gravitational force equivalent (g-force)

IQR Interquartile range

SEM Standard error of the mean

ANOVA Analysis of variance

ANCOVA Analysis of covariance

Tukey's HSD Tukey's Honestly Significant Difference test

DECLARATION OF ACADEMIC ACHIEVEMENT

This thesis contributes valuable insight into the emerging literature on how visual and vestibular cues are integrated to result in reliable self-motion perception. Specifically, this thesis provides evidence that velocity of optic flow plays an important role in mediating the relative weighting of visual and vestibular cues during acceleration perception.

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 generally improves the accuracy of self-motion perception (Gu et al. 2008; Fetsch et al. 2009; 2011; Butler et al. 2010; 2015). 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 1999). Vestibular cues, in contrast, are from the net force acting on the observer during self-acceleration; translational accelerations are transduced by the otolith organs of the vestibular system, providing the observer with cues that gradually become more salient at greater acceleration magnitudes (Groen 1956; Gu et al. 2007; MacNeilage et al. 2010). 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 acceleration than to constant velocity (Gottsdanker 1956; McKee 1981; Watamaniuk et al. 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). In addition, vestibular perception is often very slow in the absence of visual cues (for a review see Barnett-Cowan, 2013). Extensive work has shown the contribution of the vestibular system (and in particular, the otolith organs) to the detection of passive linear translations (Israel and Berthoz 1989; Israel et al. 1993; Gu et al. 2007). Some work has found evidence that neck proprioceptors also project onto the vestibular nucleus in some monkeys (Gdowski and McCrea 2000; Sadeghi et al. 2009), however it is unclear whether these receptors play a role in the

normal detection of passive-self motion, or are used for the purpose of sensory substitution when the vestibular system fails (Sadeghi et al. 2012). To err on the side of caution, the present study used acceleration magnitudes that did not induce neck movements to avoid the activation of neck proprioceptors.

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 is often guided by optic flow cues from the visual system, demonstrating a high level of integration between the two senses (Townsend et al. 2019). The existing literature shows that visual-vestibular integration plays an important role in self-motion perception, however the circumstances at which the relative contributions from either system are most prominent remains unclear. The first goal of this study was to determine the relative contributions of visual and vestibular cues to self-acceleration across different velocities and acceleration magnitudes.

Previous literature has shown that the integration of visual and vestibular cues involves a dynamic reweighting process based on stimulus reliability (Fetsch et al. 2009; 2011; ter Horst et al. 2015). The relative weighting of vestibular cues tends to increase when the quality of visual cues are sufficiently degraded (Fetsch et al. 2009; 2011; Butler et al. 2010). Likewise, vestibular sensitivity decreases in the presence of congruent optic flow (Gallagher et al. 2020). Evidence of visual-vestibular reweighting has been found across different temporal frequencies: vestibular

cues tend to be more precise for sinusoidal motion occurring at frequencies above 2Hz, and

visual cues tend to be more precise for motion at frequencies below 2Hz (Berthoz et al. 1975;

Zacharias and Young 1981; Karmali et al. 2014). These results are consistent with findings that

the human visual system fails to detect sinusoidal acceleration occurring at very high frequencies

(Werkhoven et al. 1992; Nakayama and Motoyoshi 2017). Similar results have been reported in

visual psychophysics work; during angular velocity discrimination tasks, Weber-like fractions

tend to hold for most velocities, since it is easier to judge relative differences at slower velocities

(Schmerler 1976; Calderone and Kaiser 1989). However, discrimination thresholds begin to

violate Weber's law at extremely low (below 1 degrees/second) and extremely high (above 64

degrees/second) angular velocities, roughly following a U-shaped discrimination curve (McKee,

1981; Orban et al. 1984; de Bruyn and Orban 1988). This curve has also been demonstrated in

tasks measuring response times (Monen and Brenner 1994). Neuroscience work has corroborated

these observations, finding that most optic flow detecting neurons in the middle temporal area

(MT/V5) are tuned to velocities in the range of 7-30 degrees/second (Rodman and Albright

1987; Cheng et al. 1994; Chawla et al. 1999). The previous literature strongly implies that the

visual system is more sensitive to self-acceleration within a range of certain velocities, however

it remains an open question as to whether the visual and vestibular system adapt to such

limitations by adjusting their relative weighting based on the velocity of optic flow. It is possible

that cues from the vestibular system are capable of making up for the limitations of the visual

system at certain velocities. In the present experiment we used a simple response time task with

two target stimuli to determine the relative contributions of visual and vestibular cues to self-

acceleration.

METHODS

Participants

Thirty-five participants (20 females) between the ages of 18 to 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 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 x 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 Figure 1a) and the

accelerometer to ensure that the onset of visual and vestibular cues were precisely temporally

calibrated.

Experimental Design

    Participants were presented with an optic flow stimulus (Figure 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 (Figure 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 initial and

final velocity divided by Δt (0.333 s), resulting in five unique acceleration magnitudes (18, 36,

54, 72, or 90 m/s^2).

    The vestibular cue to self-acceleration was forward linear translation (surge) of the

simulator pod (Figure 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 0.01g for a duration that was dependent on the acceleration magnitude to return the

simulator to its starting position. These acceleration magnitudes were selected based on

preliminary testing in order to avoid compensatory movements of the head, neck, or upper body,

to ensure that the commanded motion was roughly consistent with utricle stimulation. We

presented motion vibration on the coronal plane at approximately 0.0035 g$_{RMS}$ to mask motion

jerk during acceleration onset. All acceleration magnitudes were well above the vestibular

detection threshold for surge, which ranges between 0.0025 g and 0.009 g based on the frequency of the motion profile (Heerspink et al. 2005). Figure 1e shows seven recorded motion profiles at 0.01 g (grey) as well as the ensemble average (black). For these recorded motion profiles, the mean over the first 166 ms was 0.010010 g, with a variance of 0.000027 g. Although at first glance these motion profiles may appear noisy, this was due to mechanical resonance (natural oscillations) of the motion simulator. We corrected for these natural oscillations using vibration analysis, characterizing the motion simulator's eigen-frequencies, delays, and step responses.

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 100ms), in-sync, or vestibular-first (by 100ms). Response times were defined as the time between the onset of the first cue and the button press. The present experiment had a 3x3x3 design: SOA by initial velocity by final velocity, with 27 conditions in total. Inter-trial intervals were randomized in an equal distribution between 1.66-2.66 seconds. For each of the 27 conditions, participants completed 30 trials (840 total trials). Participants 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 minutes between each block. The entire session lasted between 1 and 1.5h in duration.
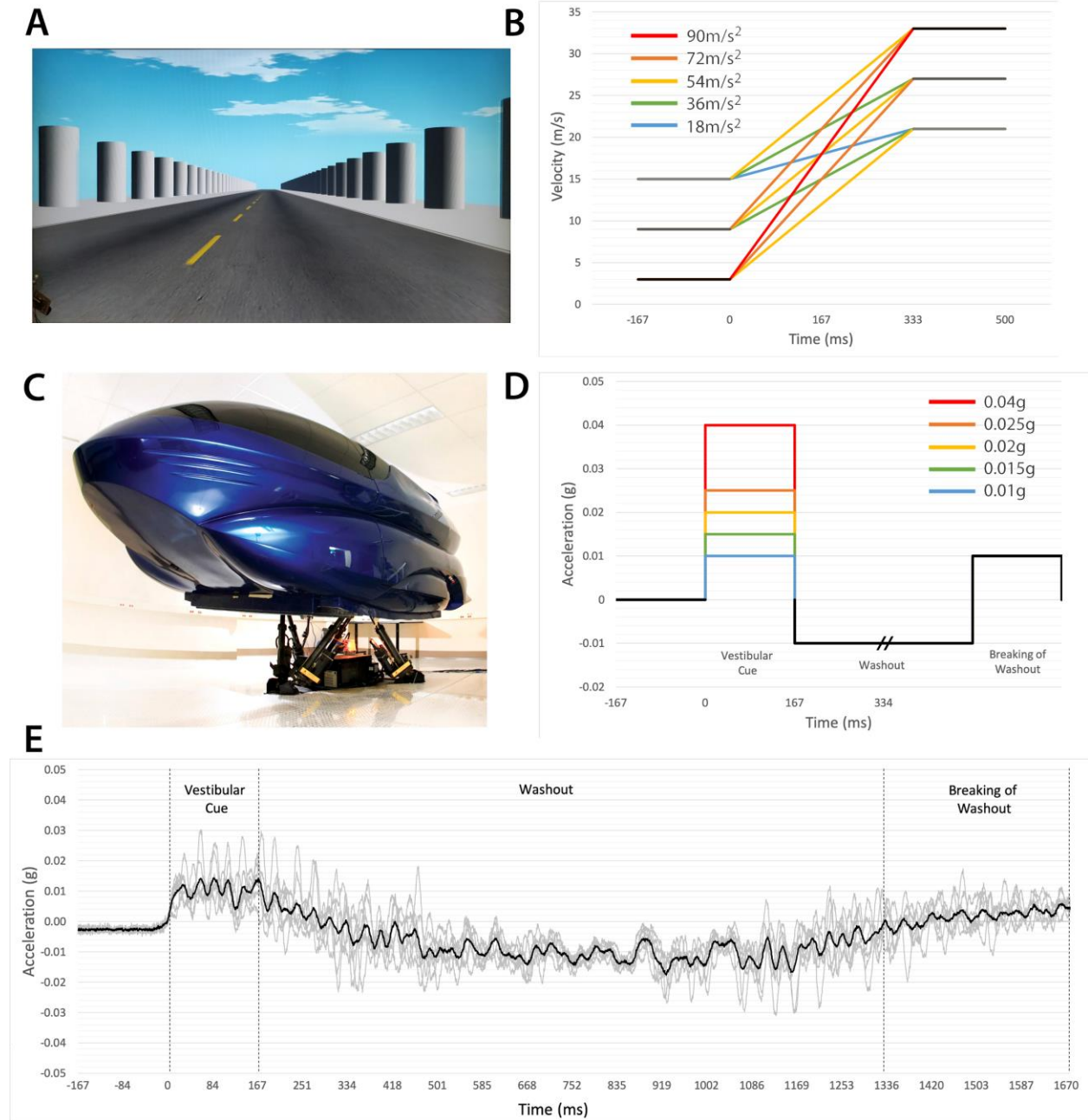
Figure 1 | (A) The optic flow stimulus used in the present experiment. (B) Time course

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).

Data Processing and Statistics

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 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 (Kassambara

2019), and R.matlab (Bengtsson 2018) packages. Raw data and code are available upon direct

request of the corresponding author.

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 (3x3). Since there appeared to be a crossover between

the visual- and vestibular-first SOAs across initial velocity (see Figure 2, compare SOAs

between panels A-C), we performed an 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

(3x3), 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 (3x3x4). All p-values were reported with

Huyhn-Feldt correction for sphericity whenever necessary. In total, 5 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 analyzed response times as a function of SOA and acceleration magnitude. Since there are a different set of acceleration magnitudes for each initial velocity, repeated measures ANOVAs were performed on each initial velocity separately (Figure 2).

For all three initial velocities, response times decreased at greater acceleration magnitudes (3m/s: $F_{(2, 68)} = 50.10$, $\epsilon = 0.868$, $p < .001$; 9m/s: $F_{(2, 68)} = 51.16$, $\epsilon = 0.898$, $p < .001$; 15m/s: $F_{(2, 68)} = 42.67$, $\epsilon = 0.769$, $p < .001$). 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 15m/s ($F_{(4,136)} = 5.573$, $\epsilon = 0.890$, $p < .001$).

Although SOA had a significant effect on response time for each of the initial velocities (3m/s: $F_{(2, 68)} = 137.72$, $\epsilon = 0.886$, $p < .001$; 9m/s: $F_{(2, 68)} = 117.00$, $\epsilon = 0.951$, $p < .001$; 15m/s: $F_{(2, 68)} = 85.54$, $\epsilon = 0.944$, $p < .001$), 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 (3m/s; shown in Figure 2a), compared to an advantage for the vestibular- over visual-first SOA at the highest initial velocity (15m/s; shown in Figure 2c). At the intermediate initial velocity of 9m/s (Figure 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.
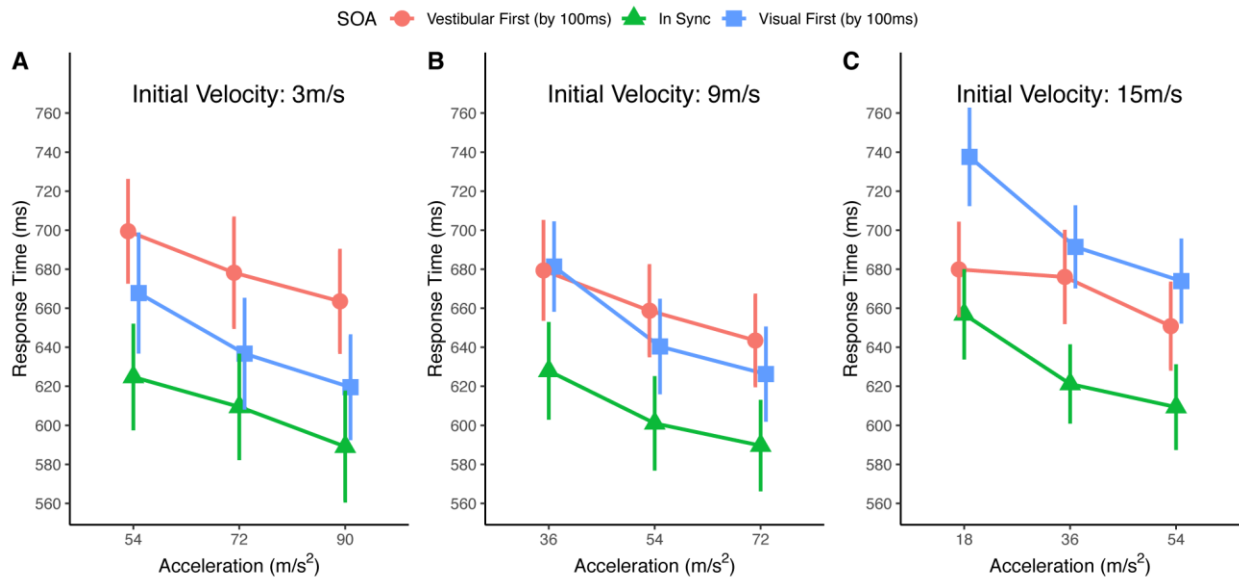
Figure 2 | Grand mean (+/- SEM) response times by SOA and acceleration magnitude at an initial velocity of (A) 3m/s, (B) 9m/s, and (C) 15m/s. SEM was calculated for each condition by taking the standard deviation of the means of all participants, divided by the square root of the number of participants (n=35).

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 (ANCOVA) with acceleration magnitude treated as a covariate across initial velocity (Figure 3). This was accomplished by modelling response times by both acceleration magnitude and SOA x initial velocity. To verify whether the homogeneity of slopes assumption was valid across the nine SOA x 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 Figure 3a, and the adjusted grand means are plotted in Figure 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 $(F(1,17) = 243.65, p < .001)$, SOA $(F(2,17) = 174.13, p < .001)$, initial velocity $(F(2,17) = 24.10, p < .001)$, and an interaction between SOA and initial velocity $(F(4,17) = 12.61, p < .001)$, validating the crossover discussed earlier.
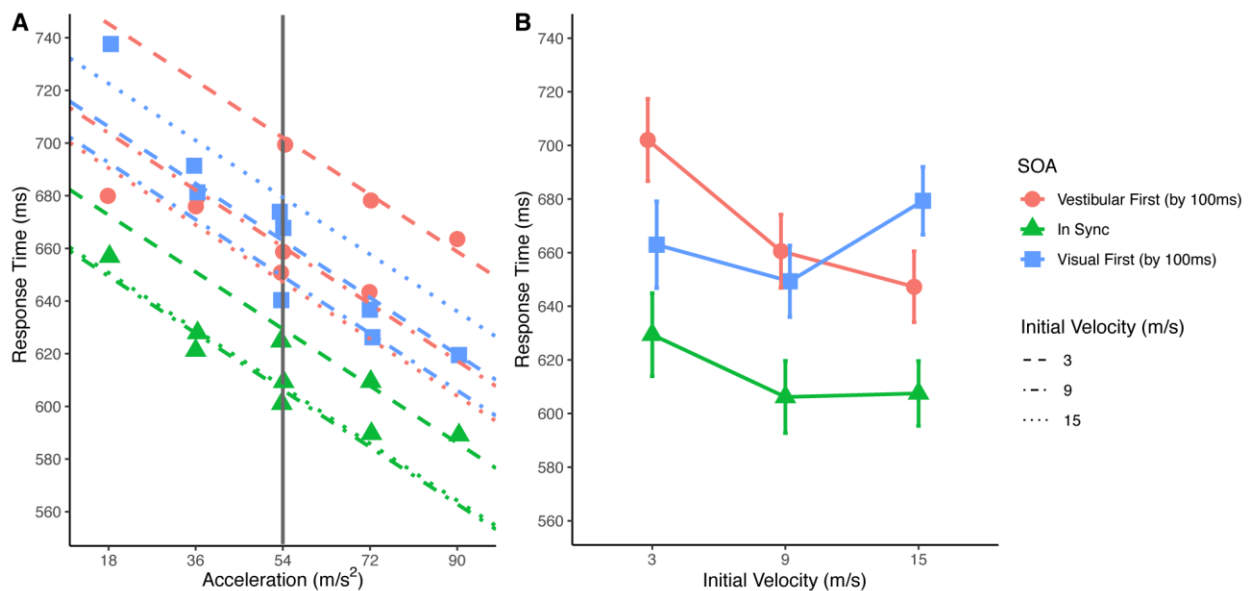
Figure 3 | (A) ANCOVA regression model for each SOA and initial velocity combination, with acceleration magnitude treated as the covariate. Adjusted grand means were taken where the regression line crossed the mean of the covariate, indicated by the vertical line. (B) Adjusted grand mean (+/- SEM) response times by SOA and initial velocity with acceleration magnitude

regressed out of the relationship. SEM was calculated for each condition by taking the standard deviation of the means of all participants, divided by the square root of the number of observations, which was the number of participants multiplied by the three final velocities in each condition (n=105).

For the in-sync SOA, although the fastest responses were found at the intermediate velocity of 9m/s, Tukey's HSD test for pairwise comparisons found that there were no significant differences for the in-sync SOA between 9m/s and 3m/s (p = 0.16), nor between 9m/s and 15m/s (p = 0.56). For the visual-first SOA, the fastest overall responses were also found at 9m/s, and responses were significantly faster at 9m/s compared to 15m/s (p < .001), but not significantly different between 9m/s and 3m/s (p = 0.89). For the vestibular-first SOA, the fastest responses were found at the fastest velocity of 15m/s, and responses became increasingly faster at higher initial velocities; responses were significantly faster at 9m/s compared to 3m/s (p < .001), and significantly faster at 15m/s compared to 3m/s (p < .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 from the visual-first SOA. This strongly suggests that the initial velocity of optic flow was influencing 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 completing more blocks (and hence trials) 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 ($F(3, 90) = 5.25$, $\epsilon = 0.725$, $p = .0063$), however there were no interactions between block and SOA, block and initial velocity, nor 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 could indicate learning and improved processing automaticity, whereas slower responses in the final block could 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. Grand mean response times across the four blocks are plotted below in Figure 4.
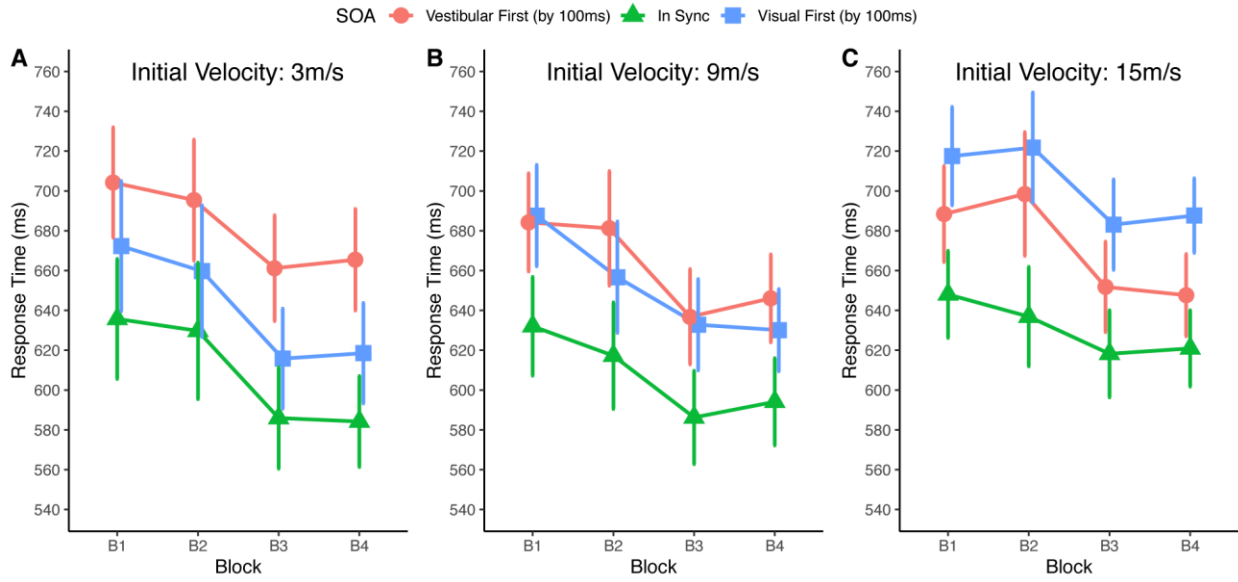
Figure 4 | Grand mean (+/- SEM) response times by SOA and block for an initial velocity of (A) 3m/s, an initial velocity of (B) 9m/s, and an initial velocity of (C) 15m/s. SEM was calculated for each block's condition by taking the standard deviation of the means of all participants, divided by the square root of the number of participants (n=35).

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 (Figure 2). For the lowest and intermediate initial velocities (3 and 9m/s), we found no interactions between SOA and acceleration magnitude. However, for the highest initial velocity (15m/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 (Figure 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 9m/s, and presenting the vestibular cue first resulted in relatively faster responses at the highest initial velocity of 15m/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 (and therefore the vestibular cue itself), 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 causes observers to reweight their dependence on visual versus vestibular cues when making speeded responses to self-acceleration detection. In the final analysis (Figure 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 participants developing a certain response strategy as they gathered statistical regularities across the trials.

Overall, our experiment demonstrated that there is 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 9m/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 7-30 degrees/second (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). 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. However, an earlier study using considerably lower velocities found opposing results, where very slow velocities found less activity in the MT/V5 region (Maruyama et al. 2002). Nonetheless, the N2 component has also been observed in the occipital lobe during the early stage of vection onset (Keshavarz and Berti 2014), potentially indicating that the N2 component reflects the visual contributions to self-motion perception. In fMRI studies, activity in MT/V5 has also been found to be associated with the experience of vection (Kovács et al. 2008; Uesaki and Ashida 2015). In future experiments, we believe that replicating the current study with EEG will help characterize the neural basis of visual-vestibular integration during self-motion perception. Future experiments may also be interested in assessing whether a greater field-of-view (and hence a stronger sensation of vection) results in greater visual contributions to self-motion perception.

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 lead to these novel results. Early work found that response times to vestibular cues tend to exponentially decrease as acceleration magnitude increases (Jones and Young 1978). In the present study, we found that our acceleration magnitudes had a relatively linear effect on response times, potentially due to the limited range of accelerations we presented. It is also important to note that the exact velocities and acceleration magnitudes used in the present study likely induced both visual and vestibular motion aftereffects that had an effect on response times to all trials (Harris et al. 1981; Crane 2012). In the present study, we chose to employ SOAs of 100ms to compare the relative contributions of visual versus vestibular cues to multisensory response times. This was analogous to presenting unimodal cues alone, however we chose this particular manipulation to minimize cue conflicts. For example, presenting the vestibular cue alone while the visual cue

remained at a constant velocity could have potentially provided conflicting evidence to the observer. Most past research on velocity discrimination has reported discrimination thresholds with 2-alternative forced choice tasks, whereas in the current study, we measured response times. Since vestibular response times have been directly linked to perceptual thresholds (Soyka et al. 2013), we believe they are an underutilized method for characterizing the basic principles of visual-vestibular integration. 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 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, existing evidence has shown that the visual system does not directly respond to the acceleration signal anyway, but rather is integrates changes in velocity over discrete time intervals (Werkhoven et al. 1992; Loose and Probst 2001, Schlack et al. 2008; Nakayama and Motoyoshi 2017).

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 (Jurgens and Becker 2006), and roll-tilt discrimination (de Vrijer et al. 2009; Clemens et al. 2011; Karmali et al. 2014). Although these studies have successfully demonstrated greater accuracy due to the integration of visual and vestibular cues, 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 anticipated reliability (Gu et al. 2008; Fetsch et al. 2009; 2011; Butler et al. 2010; ter Horst et al. 2015; Gallagher et al. 2020). Although reliability-based cue reweighting has been observed to

enhance visual-vestibular integration in a variety of tasks, many experiments have also observed over-weighting of vestibular cues which can sometimes lead to suboptimal integration (Fetsch et al. 2009; de Winkel et al. 2010; 2013). The present study contributes to this novel literature by providing evidence that velocity may also be reweighted during self-acceleration detection, however future experimentation is warranted. Since we chose to manipulate both velocity and acceleration in the present study, we are limited from having additional conditions that would have resulted in stronger conclusions about the causal mechanism underlying the differences in relative cue contributions.

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 changes in the contribution of visual versus vestibular cues with response times alone. In particular, responses to the visual cue were relatively faster when a lower initial velocity was presented, and relatively faster to the vestibular cue when a faster initial velocity was presented. The 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. Responses to the visual-first SOA were slowest at the fastest initial velocity, in a manner that is somewhat reminiscent of Weber's law. However, the fastest responses to the visual-first SOA were found at the intermediate velocity. This may be best explained by the tuning curves of velocity detecting neurons in MT/V5, which tend to be more responsive to intermediate velocities (Rodman and Albright 1987; Cheng et al. 1994; Chawla et al. 1999). Since there are more velocity detecting neurons that are responsive to intermediate velocities, self-acceleration is often reported to be

easier to detect in this range. Consistent with the literature, the fastest responses to the visual-first SOA were found at the intermediate velocity of 9m/s after regressing out acceleration magnitude. The most interesting finding of the present study was that initial velocity of the optic flow stimulus appeared to dynamically change response times when cues were presented at an SOA. This 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 therefore be independent from initial velocity. Instead, the present results found that responses to the vestibular-first SOA became faster at higher initial velocities. These results suggest that initial velocity of the optic flow stimulus was causing a shift in the relative perceptual contributions of visual and vestibular cues to self-acceleration.

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