Velocity perception in a moving observer

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A B S T R A C T

Previous research has shown that when a moving stimulus is presented to a moving observer, the perceived speed of the stimulus is affected by vestibular self-motion signals (Hogendoorn, Verstraten, MacDougall, & Alais, 2017. *Vision Research 130*, 22–30.). This interaction was interpreted as a weighted sum of visual and vestibular motion signals. This interpretation also predicts effects of vestibular self-motion signals on perceived speed. Here, we test this prediction in two experiments. In Experiment 1, moving observers carried out a visual speed discrimination task in order to establish points of subjective equality (PSE) between stimuli presented in the same or opposite direction of self-motion. We observed robust effects of self-motion on perceived speed, with self-motion in the same direction as visual motion resulting in increases in perceived speed and *vice versa*. These effects were well-described by a limited-width integration window. In Experiment 2, the same observers carried out another speed discrimination task in order to establish discrimination thresholds. According to the Weber-Fechner law, these thresholds are expected to increase or decrease along with perceived speed. However, no effect of self-motion on discrimination thresholds was observed. This pattern of results suggests a limit on speed discrimination performance early in the visual system, with visuo-vestibular integration in later downstream areas. These results are consistent with previous work on heading perception.

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1. Introduction

There is considerable experimental evidence indicating that visual and vestibular motion signals are integrated in motion-sensitive visual areas (Chen, DeAngelis, & Angelaki, 2011; DeAngelis & Angelaki, 2012; Gu, Watkins, Angelaki, & DeAngelis, 2006). Amongst other things, these signals are informative about different aspects of self-motion, such as heading direction. In addition to contributing to the extraction of such relatively higher-order percepts, we previously investigated the direct effect of vestibular self-motion signals on low-level motion perception (Hogendoorn, Verstraten, MacDougall, & Alais, 2017). To do so, we used a bi-stable plaid stimulus which can be interpreted as either a single moving texture or two gratings transparently translating in different directions (Adelson & Movshon, 1982). We observed that the relative dominance of the two competing interpretations was affected by the movement of the observer: self-motion in the direction of one of the component directions

(roughly orthogonal to the global direction) increased the relative dominance of the transparent interpretation, and self-motion in the direction opposite to the global direction increased the relative dominance of the global duration.

The effects of moving the observer during presentation of the plaids was consistent with an interpretation in which the vestibular self-motion vector was added to the visual motion vector in a weighted vector sum. In a subsequent experiment, we tested this interpretation by moving observers in a direction approximately orthogonal to the direction of visual motion, and asking observers to report visual motion direction. Reports on this direction judgment task were systematically biased in the direction of self-motion, consistent with an interpretation of (weighted) vector summation of the vestibular and visual motion vectors.

This interpretation makes an explicit prediction regarding the perceived speed of moving stimuli observed by a moving observer. Namely, a stimulus moving in the same direction as the observer should be perceived as faster than the same stimulus presented when the observer is moving in the opposite direction, even though the retinal signal is identical in both conditions.

We test this hypothesis in two experiments using a 6-degree-of-freedom motion simulator in which we can move the observer during stimulus presentation. In Experiment 1, observers carried

out a speed judgment task, and we estimated the point of subjective equality (PSE) between stimuli presented with and against the direction of self-motion, for a range of stimulus speeds and self-motion speeds. In Experiment 2, we measured speed discrimination thresholds as a function of relative self-motion, to evaluate whether speed discrimination thresholds are contingent on real or perceived speed.

2. Experiment 1

2.1. Methods

2.1.1. Observers

Five observers (2 females) with normal or corrected-to-normal vision participated in the experiment, including one of the authors (HH). The remaining four observers were undergraduates recruited from The University of Sydney undergraduate subject pool. All observers 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 (V7, CKAS Mechatronics, Australia) that was used to rotate the observer around a vertical axis (Fig. 1). Observers were buckled into a racing-style driving seat with head and body support to ensure stability throughout the movement. No forehead support or chinrest was used. Maximum angular displacement was 24° either clockwise or counter-clockwise away from the central position (level, facing straight ahead). A large opaque cabin was rigidly mounted on the motion platform so that there were no optic flow signals when the observer was rotated. The room in which the motion system was located was darkened during the experiment to prevent outside illumination providing any cues to the observer's motion. The only visual motion came from a widescreen (60 degrees of horizontal visual angle) video monitor displaying the stimulus. The inside of the cabin was not otherwise lit, but scattered light allowed the observer to see the inside of the cabin, including the frame of the projection screen (all of which was static relative to the observer).

2.1.3. Stimuli

Visual presentation within the motion simulator was achieved by means of a DLP projector (BENQ MX618ST 1024 × 768, 60 Hz refresh rate) projecting the stimulus on a screen directly in front of the observer inside (and therefore moving along with) the cabin. The screen was placed at a distance of 130 cm from the observer and subtended 60 degrees of horizontal visual angle.

The stimuli consisted of two rectangular noise patches presented above and below a central fixation dot. The noise patches were spatially filtered to obtain a 1/f spatial frequency profile. The two patches were 28° wide and 9.4° high, presented at a center-to-center distance of 11.7° above and below fixation at 39% of maximum contrast. During the experiment, the textures within the two patches translated within the windows, in opposite directions. The directions of the patches were constant within observers (for a given observer, the top patch would always move leftward and the bottom always rightward, for example), but counterbalanced between observers.

2.1.4. Procedure

Observers performed a two-alternative forced-choice (2AFC) speed discrimination task on the two motion patches, indicating which of the two patches moved at a higher speed by means of a button press. Observers were specifically instructed to compare the visual speed as presented on the screen. Stimuli were presented for 500 ms in each of 21 experimental conditions, being the factorial combination of 3 stimulus-speed conditions (6°/s, 12°/s and 24°/s) and 7 self-motion velocity conditions (−48°/s, −24°/s, −12°/s, 0°/s, 12°/s, 24°/s and 48°/s). The relative speeds of the top and bottom patch were adjusted using a minimum expected entropy staircase procedure (Saunders & Backus, 2006) to find the point of subjective equality (PSE) for each combination of conditions. In adjusting the relative speeds, the geometric mean speed of the two patches was kept constant. For example, a ratio of 2 would be achieved by multiplying the speed of one patch by $\sqrt{2}$ and dividing the speed of the other by $\sqrt{2}$.

Trial duration was 1000 ms in the 0°/s and ±48°/s self-motion conditions, 2000 ms in the ±24°/s self-motion conditions, and 4000 ms in the ±12°/s self-motion conditions. Except in the 0°/s condition, over the course of the trial the motion simulator rotated from one extreme rotation angle to the other over a total angle of 48° (±24°) according to a sinusoidal velocity profile. The stimulus was always presented in the central 500 ms period of the rotation. As this was the peak of the sinusoidal velocity profile, velocity was maximal and approximately constant during the stimulus presentation. The condition labels indicate the mean velocity over the
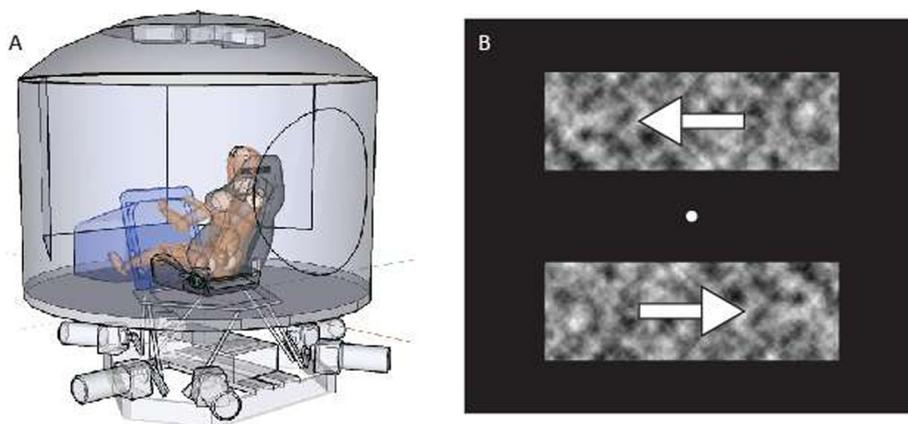

Fig. 1. (a) Apparatus. Observers were seated in a CKAS 6-degree-of-freedom motion platform. The platform was fully enclosed by a cabin so that no optic flow was perceived during rotation. Stimuli were presented inside the apparatus on a projection screen mounted directly in front of the observer. (b) Stimulus. The stimulus consisted of two noise patches, spatially filtered to have a 1/f spatial frequency profile. The noise patches were presented for 500 ms simultaneously above and below fixation, moving in opposite directions. Observers reported which of the two patches moved at a higher speed.

whole rotation. Due to the nature of the sinusoidal velocity profile, peak velocity was a factor of pi/4 higher than mean velocity.

Trials were presented in blocks, with 12 trials of each combination of 3 stimulus speed conditions and 7 self-motion conditions presented per block (a total of 252 trials per block). Observers completed 3 blocks each.

2.2. Results

Cumulative Gaussian psychometric functions were fitted to the data for each combination of stimulus and self-motion speed using the PSIGNIFIT MATLAB toolbox (Fründ, Haenel, & Wichmann, 2011), and the mean of the cumulative Gaussian was taken as the PSE. Psychometric functions for a representative observer are shown in Fig. 2.

Points of subjective equality for each combination of conditions and each observer were entered into a 7×3 repeated-measures analysis of variance. This revealed a significant main effect of self-motion velocity (F = 30.32, df = 6, p < 0.001). There was no main effect of stimulus speed (F = 0.16, df = 2, p = 0.856), but there was a clear interaction (F = 3.34, df = 12, p = 0.001). Mean PSEs across observers are shown in Fig. 3.

There was a clear effect of self-motion on perceived speed, whereby stimuli moving in the same direction as the observer were perceived as moving faster than stimuli moving in the direction opposite to the observer. The direction of this effect was as if observers consistently erred in the direction of reporting the speed of the patch in world coordinates, rather than in screen coordinates – although they were explicitly instructed to respond to visual speed on the screen. Although this effect was observed for all self-motion velocities tested, it did not scale monotonically with velocity. Rather, the integration appeared to have a limited bandwidth, with the greatest effect of self-motion being observed at low or intermediate self-motion speed. To model this tuning width, we fitted derivative-of-Gaussian functions to the PSEs (shown as black curves in Fig. 3). The parameters of these fitted functions reveal that both sensitivity (or 'gain', the amplitude of the turning points) and selectivity (the Gaussian bandwidth, σ) of the effect of self-motion on perceived speed depend on the velocity of the stimulus (6°/s: $\sigma = 0.342 \log_2°/s$, gain = 0.39; 12°/s: $\sigma = 0.226 \log_2°/s$, gain = 0.59; 24°/s: $\sigma = 0.188 \log_2°/s$, gain = 0.51). At low stimulus velocity (6°/s), sensitivity is relatively low, and tuning is broad. Tuning width becomes narrower as stimulus velocity increases. Of the three stimulus speeds tested here, maximum sensitivity is observed at an intermediate stimulus speed (12°/s). Reconstructed

Gaussian tuning functions, based on the gains and bandwidths from Fig. 3, are plotted in Fig. 4.

3. Experiment 2

Experiment 1 confirmed the hypothesis that the perceived speed of a visual stimulus can be affected by self-motion in the same or opposite direction consistent with a weighted combination of vestibular and visual motion vectors. In Experiment 2, we test a further hypothesis: that self-motion might affect not just perceived speed and direction, but also affect perceptual thresholds that depend on stimulus speed. Specifically, speed discrimination thresholds are known to be subject to the Weber-Fechner law (Zanker, 1995), whereby the just-noticeable difference (JND) in perceived speed scales linearly with the speed of the stimulus. If self-motion acts to increase or decrease the speed of a visual stimulus, then it might be expected to similarly increase or decrease the JND for perceived visual speed. We test this hypothesis in Experiment 2.

3.1. Methods

3.1.1. Observers

Four observers (2 male) that were part of Experiment 1 participated in this experiment as well, including one of the authors (HH).

3.1.2. Apparatus

Experiment 2 was carried out using the identical experimental setup as for Experiment 1.

3.1.3. Stimuli

The stimuli were identical to those used in Experiment 1, with the exception that they were presented sequentially rather than simultaneously, and that both patches moved in the same direction. The top patch was always presented first. The direction of the patches was constant for a given observer but randomized across observers.

3.1.4. Procedure

As in Experiment 1, observers performed a 2AFC speed discrimination task on the two motion patches, indicating by means of a button press which of the two patches moved at a higher speed. Stimuli were presented sequentially for 500 ms each in
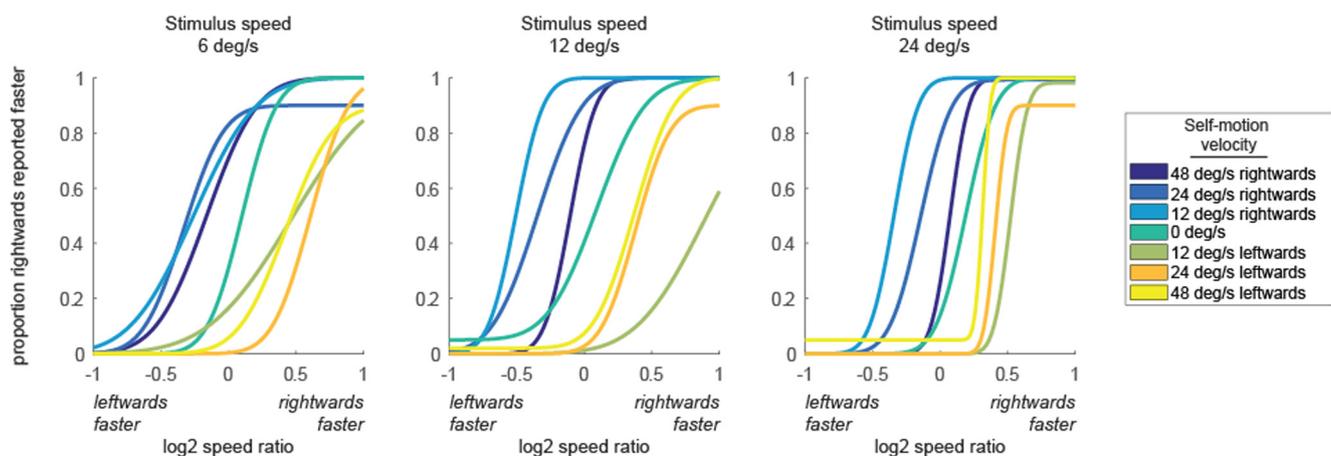

Fig. 2. Cumulative Gaussian psychometric functions for a representative individual observer on a 2AFC speed discrimination task, as a function of stimulus speed and self-motion velocity. Observers viewed two simultaneously presented motion patches moving in opposite horizontal directions and reported which one moved faster. Self-motion velocity shifted psychometric functions at each of the three stimulus speeds. The mean of each cumulative Gaussian was taken as the PSE.
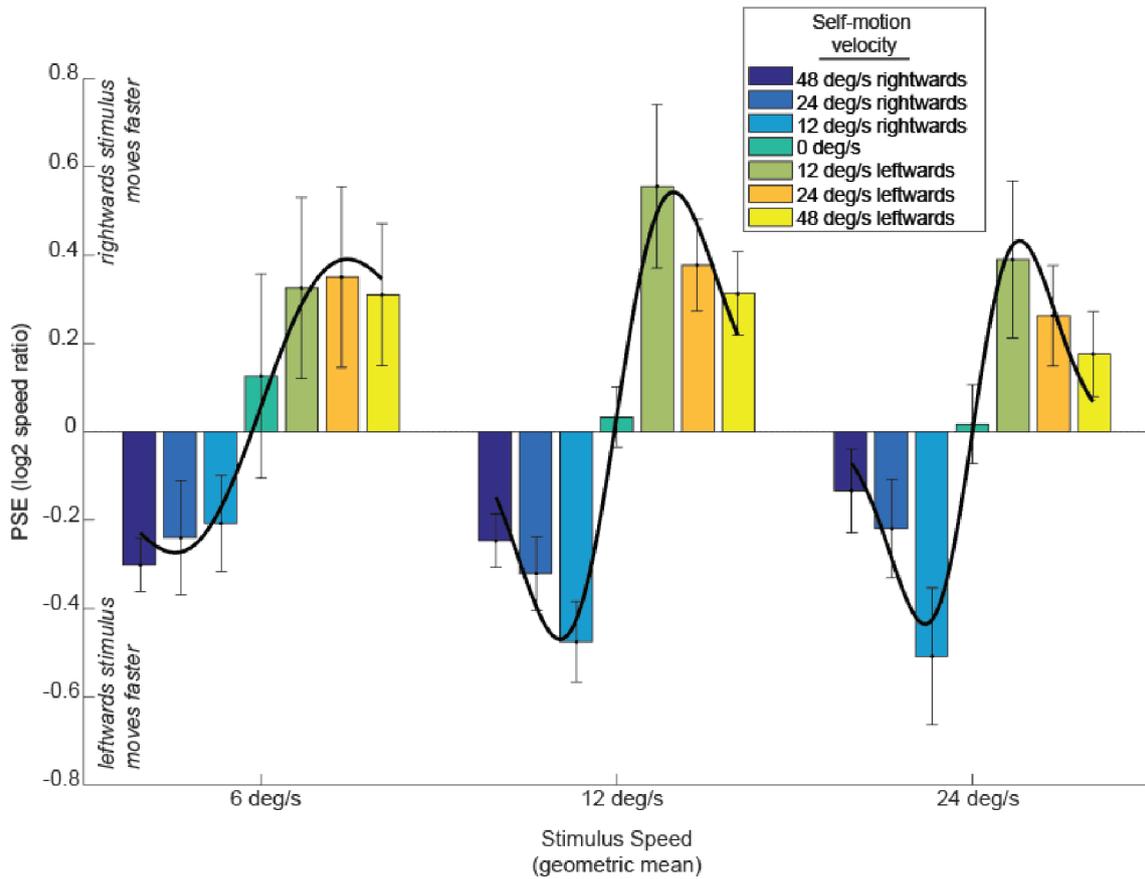
Fig. 3. PSE for the perceived speed of two motion patches moving in opposite directions, as a function of stimulus speed and self-motion velocity. Bars denote mean PSE across five observers, and error bars indicate ±1 standard error of the mean. Across stimulus speed, at PSE the relative speed of the patch in the direction of the observer's motion was lower than the other patch. Lines indicate a fitted first-derivative-of-Gaussian function, indicating the tuning width of the influence of self-motion of perceived speed. R^2 for these fits are 0.96, 0.95, and 0.95 for the 6°/s, 12°/s, and 24°/s conditions, respectively.
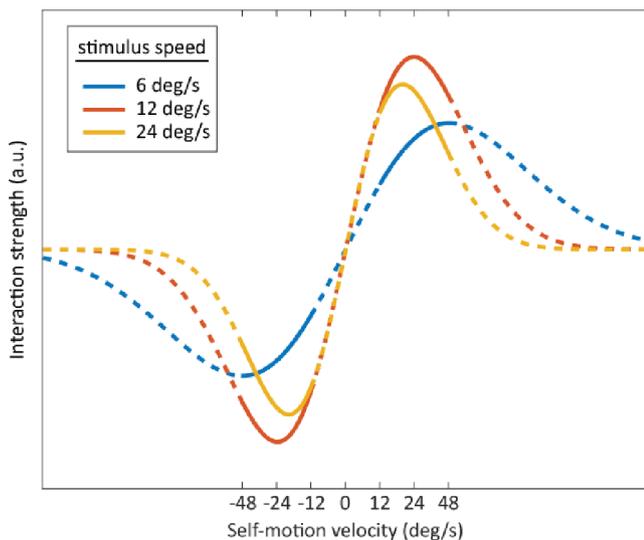

Fig. 4. Reconstructed Gaussian tuning profiles (based on fit parameters from Fig. 3) of the effect of self-motion velocity on perceived speed, plotted for three different stimulus speeds. The solid parts of the lines indicate the range of measured velocities, the dashed parts are based on extrapolation. Selectivity increases with increasing stimulus speed, and sensitivity is greatest for the intermediate stimulus speed.

one of 4 stimulus-speed conditions (3°/s, 6°/s, 12°/s, and 24°/s) and one of 5 self-motion conditions (−24°/s, −12°/s, 0°/s, 12°/s, 24°/s). An additional slower stimulus speed condition was

included to collect more datapoints to estimate the Weber Fraction for each self-motion condition. The fastest self-motion conditions were dropped as Experiment 1 showed that the effect of self-motion was attenuated at the highest speed. The relative speed difference between the top and bottom patch was adjusted using a minimum expected entropy staircase procedure (Saunders & Backus, 2006) to find the point of 75% discrimination performance for each combination of conditions. In adjusting the relative speeds, the geometric mean speed of the two patches was kept constant.

Trial duration was 1000 ms in the 0°/s self-motion condition, 2000 ms in the ±24°/s self-motion conditions, and 4000 ms in the ±12°/s self-motion conditions. Except in the 0°/s condition, over the course of the trial the motion simulator rotated from one horizontal extreme to the other over a total angle of 48° using a sinusoidal velocity profile. The two stimuli were always presented in the central 1000 ms period of the rotation.

Trials were presented in blocks, with 12 trials of each combination of 4 stimulus speed conditions and 5 self-motion conditions presented per block (a total 240 trials per block). Observers completed 9 blocks each. Cumulative Gaussian psychometric functions were fitted to the data for each combination of stimulus and self-motion speed using the PSIGNIFIT MATLAB toolbox (Fründ et al., 2011) in each combination of conditions, and the 75% point was taken as the discrimination threshold. Discrimination thresholds were then plotted as a function of stimulus speed, and the slope of the best-fit line taken as the Weber Fraction. Note that in Experiment 2, each data point reflects 3 times as many trials as in Experiment 1.

3.2. Results

Discrimination thresholds as a function of stimulus speed and self-motion velocity are shown in Fig. 5A. Discrimination thresholds were entered into a 4 × 5 repeated-measures analysis of variance with factors Stimulus Speed (3, 6, 12, 24°/s) and Self-Motion Velocity (−24, −12, 0, 12, 24°/s). This revealed a significant main effect of Stimulus Speed (F = 22.19, df = 3, p < 0.001) but no main effect of Self-Motion Velocity (F = 2.45, df = 4, p = 0.10) and no interaction (F = 1.7, df = 12, p = 0.11). Fig. 5B shows the expected magnitude of the shift in discrimination thresholds that would be expected based on the magnitude of the shift in perceived speed observed in Experiment 1 on the same observers. The shifts in discrimination thresholds predicted based on the changes in perceived speed due to self-motion in Experiment 1 are not evident in the discrimination data in Experiment 2.

Finally, we used JASP (version 0.8.1.1) to carry out a Bayesian repeated-measures analysis of variance to directly compare the null hypothesis (no effect of vestibular modulation of perceived speed on discrimination thresholds) with the alternative hypothesis that vestibular modulation of perceived speed does affect discrimination thresholds. This yielded a Bayes Factor of 4.02, constituting 'strong evidence' (Robert, Chopin, & Rousseau, 2009) for the model in which vestibular input has no effect.

4. Discussion

In two experiments, we investigated the effect of self-motion on visual speed perception. In Experiment 1, we showed that the perceived speed of a moving texture is increased by concurrent motion of the observer in the same direction, and decreased for self-motion in the opposite direction. This is consistent with a model of visual-vestibular motion integration in terms of weighted vector averaging that we previously proposed (Hogendoorn et al., 2017). Interestingly, it shows that even though observers were instructed to respond to stimulus speed on the screen (i.e., in retinal coordinates), they were unable to prevent vestibular self-motion signals from affecting their judgments. This is consistent with previous work using smooth pursuit (Freeman, Champion, Sumnall, & Snowden, 2009), which also found that observers do not have direct access to retinal motion signals (Wertheim, 1994). Finally, we showed that the visual-vestibular integration window has a limited width, with selectivity increasing with increasing stimulus speed. For the range of stimulus speeds tested,

maximum sensitivity (gain) was observed at intermediate speeds (12°/s).

Surprisingly, in Experiment 2, we found that self-motion did not affect visual speed discrimination thresholds, contrary to what would have been expected on the basis of the Weber/Fechner law if visual speed discrimination thresholds were contingent on perceived speed. In general, visual speed discrimination is believed to obey the Weber/Fechner law (Zanker, 1995), and this is also evident in our data. However, our data show that discrimination thresholds were unaffected by the effects of self-motion on perceived speed. This suggests that discrimination thresholds in this task were dependent on a visual speed signal that had not yet been integrated with vestibular motion signals.

Alternatively, the noise introduced by vestibular input might not increase with self-motion speed. There is some indication that as opposed to all other sensory modalities, vestibular discrimination thresholds do not scale linearly with vestibular input (Mallery, Olomu, Uchanski, Militchin, & Hullar, 2010). However, this non-dependence was found at rotational peak velocities well above those used in the current experiments (>60 deg/s). In contrast, at lower peak velocities in the range of rotational velocities used in the current experiments, discrimination thresholds were approximately linearly related to velocity, as would be expected on the basis of the Weber/Fechner law.

Speed-discrimination performance has previously been shown to be approximately an order of magnitude better for visual motion (Snowden & Braddick, 1991; Zanker, 1995) than for vestibular motion (Mallery et al., 2010). In this context, the present findings suggest that even though perceived speed is affected by vestibular input, the limiting process for speed discrimination is to be found in earlier unimodal visual areas. The putative locus would likely be in relatively early motion-sensitive visual areas, as particularly the later motion area MST receives considerable input from the vestibular system (Chen et al., 2011; DeAngelis & Angelaki, 2012; Gu, Angelaki, & Deangelis, 2008; Gu et al., 2006).

The interpretation that perceived speed is dissociable from performance on speed discrimination is also consistent with the observation in Experiment 1 that the magnitude of the effect of self-motion on perceived visual speed is non-monotonically dependent on visual speed. Whereas performance on visual speed discrimination has been shown to increase monotonically with stimulus speed (Fredericksen & Hess, 1998; Fredericksen, Verstraten, & van de Grind, 1994; Snowden & Braddick, 1991), here we observed maximum sensitivity to vestibular self-motion signals at an inter-
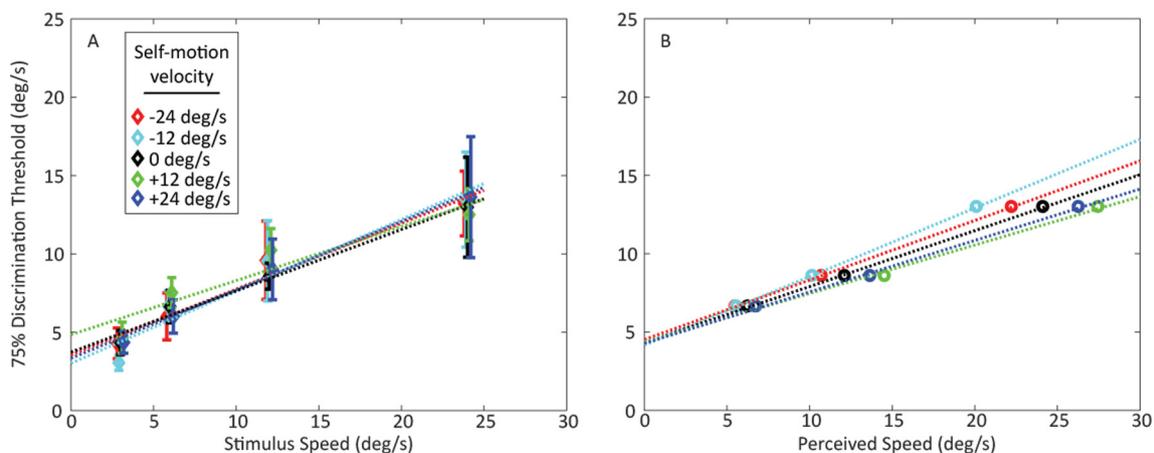

Fig. 5. A. Observed discrimination threshold as a function of stimulus speed, for four observers. Different lines denote different self-motion velocities relative to the stimulus. Error bars indicate ±1 SEM across observers. B. Expected discrimination thresholds if the effects on perceived speed observed in Experiment 1 in these same observers would have equivalent effects for the purposes of discrimination thresholds. The results do not match this prediction.

mediate speed. This further supports the idea that speed discrimination and speed perception do not share the same limiting mechanisms.

Interestingly, this interpretation contradicts a number of studies that have investigated limits on motion discrimination during smooth pursuit. On the one hand, it is well-established that pursuit eye movements can affect the perceived speed of moving objects, consistent with our Experiment 1 (e.g. Aubert (1886) and Fleischl (1882) cited in Krukowski, Pirog, Beutter, Brooks, & Stone, 2003; Turano & Heidenreich, 1999). However, Turano and Heidenreich (1996) reported that also retinal speed discrimination thresholds were affected by smooth pursuit, which is inconsistent with our Experiment 2 (albeit for lower retinal speeds than used here; <5 deg/s).

Our results from Experiment 2 are also at odds with a study investigating retinal speed discrimination whilst walking on a treadmill (Souman, Freeman, Eikmeier, & Ernst, 2010). In that study, the authors found that speed discrimination thresholds did depend on changes in walking speed, suggesting an early locus of interaction between vestibular (or possibly efference copy) and visual motion signals. One caveat in comparing that study with the present experiments is that the use of a treadmill meant that although observers walked, they did not actually receive vestibular input of forward motion, whereas in our experiments they did.

One interpretation of this contradiction is that vestibular signals and efference copy signals do not interact with visual motion signals in the same way. Given the current findings, we could postulate that where vestibular self-motion cues do not prevent the observer from accessing retinal motion before integration, the same is not true for efference copy signals. However, this dissociation is not entirely consistent with an influential model of motion perception during self-motion (Wertheim, 1994), which posits that vestibular and efference copy signals combine to form a "reference signal" before being integrated with retinal motion cues. Altogether, this study supports the hypothesis we previously proposed (Hogendoorn et al., 2017) that vestibular self-motion signals contribute to visual velocity perception through weighted vector summation, although the complete picture of visuo-vestibular motion integration remains complex. It points to a locus of visual-vestibular integration downstream from the process constraining visual speed discrimination performance. Future studies could further characterize how the tuning width of the visuo-vestibular integration depends on stimulus speed.

Acknowledgments

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