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A preference for visual speed during smooth pursuit eye movement

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Abstract

Does the preference for visual speed extend to motion perception when the eye moves? Current evidence from psychophysics and neuroscience is limited to small patches of image motion and stationary fixation. Active observers, however, are more likely to use large patches of retinal flow and extra-retinal signals accompanying eye movement to judge motion. We therefore investigated whether speed remains a primary dimension during smooth pursuit using a 'discrimination-contour' technique. Our results showed that observers struggled most when trying to discriminate pursued stimuli that travelled at the same speed but moved over different distances and durations. This remained the case when retinal flow was added, and when we isolated trials in which extra-retinal signals were the only salient cue to motion. Our results suggest that preferential sensitivity for visual speed is quite general, supported by the many different types of motion mechanism used by active observers.

Public Significance statement

Speed is considered a primary dimension in vision science, sensed independently from distance and time. However, the evidence is limited to experiments that use small patches of image motion and restrict eye movements. This ignores the cues more likely to be used during normal active viewing, such as large patches of retinal flow and extra-retinal motor signals from the eye-movement system. With these cues in place, we found visual speed is still sensed independently from distance and time. The mechanisms serving motion perception in active observers are therefore built on speed.

Introduction

A good sense of visual speed is critical to performing everyday tasks like walking safely down a crowded street. Converging evidence suggests speed is analysed by specialized mechanisms that are distinct from those used to judge spatial and temporal dimensions. In monkey, single-cell recordings reveal subpopulations of neurons tuned to speed (DeAngelis & Uka, 2003; Maunsell & Van Essen, 1983; Nover, Anderson, & DeAngelis, 2005; Perrone & Thiele, 2001; Priebe, Cassanello, & Lisberger, 2003; Priebe, Lisberger, & Movshon, 2006). Analogous speed selectivity has also been shown in humans, using functional imaging of key motion processing areas (Lingnau, Ashida, Wall, & Smith, 2009). A preference for speed can also dictate perceptual behaviour. For example, observers struggle to differentiate between stimuli that travel at the same speed but nonetheless differ in their spatiotemporal parameters (Lappin, Bell, Harm, & Kottas, 1975; Reisbeck & Gegenfurtner, 1999).

Much of this evidence is based on experiments that use small patches of image motion and stationary fixation. In normal viewing, however, the eyes are rarely still and the scene is all around, so the cues to object movement can be very different. For instance, a pursued target is more or less stationary on the retina: the localized image motion signifying object movement no longer exists. In situations like this, observers rely on global retinal flow of the background (Eifuku & Wurtz, 1998; Layton & Fajen, 2016; Rushton & Warren, 2005; Warren & Rushton, 2007, 2009), extra-retinal information from the oculomotor system (von Holst, 1954) and retinal slip if the eye movement is inaccurate (O'Connor, Margrain, & Freeman, 2010; Welchman, Harris, & Brenner, 2009). It is therefore possible that the primary status of visual speed only applies to the processing of localised motion by specialized detectors.

The motion cues accompanying active viewing allow the observer to convert image motion into movement with respect to the scene and/or head (Freeman, 2001; Freeman & Banks, 1998; Freeman, Champion, & Warren, 2010; Furman & Gur, 2012; Haarmeier, Thier, Repnow, & Petersen, 1997; Nefs & Harris, 2007; Souman, Hooge, & Wertheim, 2006; Turano & Massof, 2001; Warren & Rushton, 2009; Wertheim, 1994). Compensation for eye movement is thought to occur in regions like the medial superior temporal (MST) area (Chukoskie & Movshon, 2009; Dunkley, Freeman, Muthukumaraswamy, & Singh, 2013; Inaba, Miura, & Kawano, 2011). The conversion is computationally expensive, requiring a number of steps (Perrone & Krauzlis, 2008; Van Den Berg & Beintema, 2000). This fact, coupled with the number of inputs that feed into the compensation process, begs the question of whether active observers remain preferentially sensitive to speed. If they did so, many fundamental issues could be resolved, such as whether extra-retinal signals resident within the visual system carry information about eye speed. As a number of neuroscientists have observed, vision science is largely silent on fundamental details like these (Cao, Mingolla, & Yazdanbakhsh, 2015; Newsome, Wurtz, & Komatsu, 1988; Ono & Mustari, 2006). A better understanding could also help illuminate the relationships that exist between extra-retinal signals and conditions like schizophrenia and infantile nystagmus (Bedell, 2000; Lindner, Thier, Kircher, Haarmeier, & Leube, 2005; Pynn & DeSouza, 2013; Thaker, Ross, Buchanan, Adami, & Medoff, 1999).

We therefore investigated whether speed remains an independent dimension during eye movement, and to what extent the motion cues accompanying active viewing affect motion sensitivity. We focused on one of the most important objects in the scene, namely the target being pursued. A 'discrimination contour' technique was used to reveal how dimensions like space and time are combined (Champion & Freeman, 2010; Cicchini, Anobile, & Burr, 2016; Reisbeck & Gegenfurtner, 1999; Wandell, 1985). At the heart of this technique lies the idea that preferential sensitivity to speed should make it difficult to detect subtle changes in distance and duration at threshold.

Figure 1A describes the 'discrimination contour' technique. Thresholds are based on an oddity task in which two identical 'standard' stimuli are presented, along with a different 'test' stimulus (in our experiments, the stimuli were shown sequentially and pursued by an eye movement). The standards move at a fixed speed, based on a specific pair of distance and duration values (central dot in Figure 1A). The test stimulus moves at a different distance and/or duration (e.g. somewhere along the blue line; note that distances and durations are normalized to the standard). The task for the observer is to identify which of three stimuli is the odd one out, based on whichever cue (or combination of cues) they choose to use. The exact values of test distance and duration are constrained by a direction (θ) in the distance-duration plane, along which the threshold is being measured. Two key pairs of directions are highlighted in the figure: a 'same-speed' line along which speeds are all the same and a 'max-speed' line along which speed changes most. A preference for speed will make discrimination along the same-speed line particularly difficult, while making discrimination along the 'max-speed' line relatively easy. Thresholds in other directions can also be measured, each uniquely weighting the salience of distance, duration and/or speed cues per unit of change.

If speed is a primary dimension, such that distance and duration become fused at threshold, the resulting discrimination contour will orient along the main diagonal (Figure 1B, top panel). This is the case for localised image motion, viewed with stationary fixation, albeit for speeds greater than about 1 deg/s (Reisbeck & Gegenfurtner, 1999). On the other hand, if speed is inferred more indirectly from distance and duration, the contour will lie parallel to the main axes (middle and bottom panels). The bottom panel describes the case for hearing (Freeman et al., 2014), emphasizing the fact that not all of the senses treat motion in the same way. Our aim was to investigate which is the case for active vision.

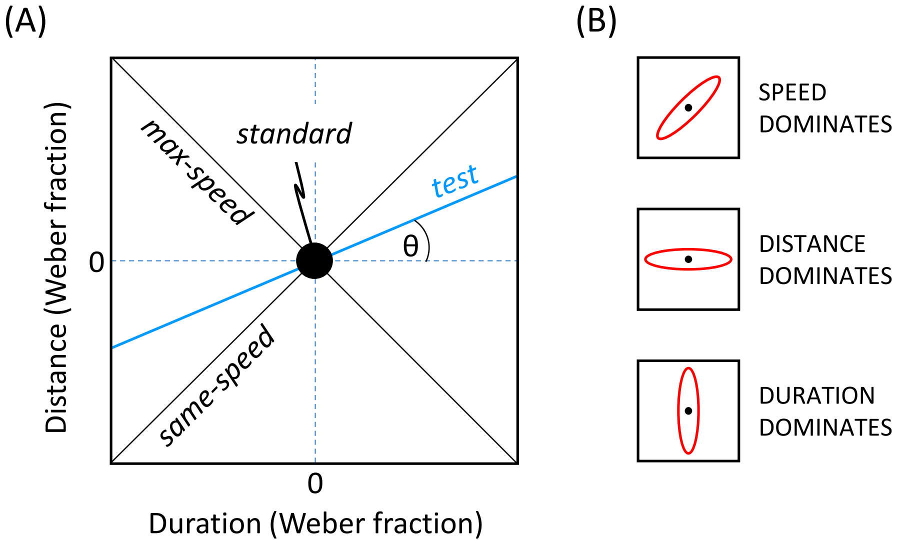

Figure 1: (A) Schematic of the ‘discrimination contour’ technique. Using a three interval ‘odd one out’ task, observers had to identify a test stimulus from two identical standard stimuli. The standards (S) travelled at the same speed, based on a fixed pair of distances and durations (central dot). The test (T) moved over a different distance and/or duration, depending on the direction θ along which the threshold was currently being measured. An example pair of θs shown in blue. Distance and time are expressed as Weber fractions (W), such that the test distance and duration become normalised to the standard (ie. $W_i=(T_i–S_i)/S_i$, where “i” is either distance or duration). Two important pairs of θ are highlighted: the ‘same-speed’ line (θ=45°,225°), where test and standards moved at the same speed but with different combinations of distance and duration; the ‘max-speed’ line (θ=135°,315°), where the difference in speed between test and standard changes most for a given unit of displacement in the distance-duration plane. (B) Three possible outcomes. The top panel shows the type of discrimination contour expected if speed is analysed separately from distance and duration. Observers find the discrimination hardest along the same-speed line, and easiest along the ‘max-speed’ line. The result is an ellipse oriented along the same-speed line. The middle and bottom panels show what happens if speed is inferred more directly, such that either distance or duration dominate, respectively. In these cases, the ellipse will be oriented

parallel to the axes of the space, stretched along the lines of same-distance or same-duration. Note that a circular contour (not shown) would indicate no particular discrimination cue was preferred.

Experiment 1: Preferential sensitivity to speed is supported by many different motion cues

Discrimination contours were measured in three conditions, each designed to determine the influence retinal flow, extra-retinal signals and retinal slip. In the 'no background' condition, a pursued target was viewed moving horizontally in complete darkness, eliminating retinal flow cues. The target's retinal slip, on the other hand, depends on the accuracy of the eye movement (its use was therefore investigated post data collection, using an analysis described below). In the 'vertical background' condition, global retinal flow was added to the display using static vertical lines. To control for luminance and texture, we also presented a 'horizontal background' condition, which contained a similar background pattern but no salient flow.

Methods

Observers: Thirteen observers participated in the experiment. Three were experienced and were used to collect discrimination contours at 16 evenly-spaced values of θ. One participant (obs.1) was naïve to the purposes of the experiment, and two were authors (obs.2 and 3). The remaining 10 observers were unpractised, and took part in a reduced set of testing conditions that sampled just four values of θ corresponding to the main diagonals in Figure 1A. The unpractised observers were undergraduates who participated for course credit. None of the observers knew the outcome of the experiment before they participated.

The use of a small number of experienced observers reflects the usual practice in psychophysics. For the most relevant papers cited above (Champion & Freeman, 2010; Cicchini et al., 2016; Reisbeck & Gegenfurtner, 1999; Wandell, 1985), the numbers of participants used in the first experiment reported were 5, 2, 3, 4, respectively. The use of low N reflects the fact that: (1) psychophysical experiments typically try and cover a fine-grained sampling of the parameter space in question; and (2) that dependent measures such as thresholds are robust and precise, being drawn from psychometric functions fit to responses across hundreds of trials.

We chose to enhance this practice by using a larger number of additional unpractised observers that made a coarser-grained sampling of the parameter space. We based the number partly on the results obtained for the practised observers, which showed large effects. Using Gpower, for effect sizes between 0.8-1 and power 0.7-0.8, the estimated numbers of participants needed when using paired t-tests range from 9-15. As will become evident in the Results sections, many of the effect sizes we obtained were over 1.

Stimuli: A ViewSonic P225f monitor was used to display stimuli at 100 Hz, via a Radeon 9800 Pro graphics card under computer control. Eye movements were sampled at 1000Hz using an Eyelink 1000 video eyetracker mounted on a chinrest. Viewing was at a distance of 70cm in a completely darkened room.

Each trial consisted of three intervals comprising a single pursuit target (small red dot, dia. 0.4°) moving horizontally at a constant speed. A random positional offset selected from the range ±2° was added to the target's start position to eliminate any fixed position cues at the beginning and end of movement. The target was displayed against the black background of screen, or a set of thin static vertical stripes or horizontal stripes (0.08° wide), depending on the condition. The stripes were spaced 4° apart and covered the full extent of the screen, producing a background texture measuring 32° x 26° (width x height). A horizontal corridor 4° high was left blank at the centre of the display, allowing the pursuit target to move unhindered (see schematics in leftmost column of Figure 2).

Procedure: For the experienced observers, the two standard intervals contained a pursuit target moving over a distance and duration of 8° and 2s, respectively; for the unpractised observers, values of 4° and 1s were used. This yielded a standard speed of 4°/s in both cases. (The duration was reduced for unpractised observers to allow enough time for testing to be completed in a single visit). The test interval moved at a distance and duration determined by the θ over which the current threshold was being measured (see Figure 1A for explanation). The distance and duration of the test along a given θ was controlled by a logarithmic 1-up 2-down staircase that terminated after 12 reversals. The staircase therefore determined the polar increment of the test with respect to the standard. Polar coordinates were then mapped onto Cartesian coordinates to determine the test's actual distance and duration for that trial.

The three intervals were shown in a random order. The observers task was choose the interval that appeared different, using a button press. Observers were informed that one of the intervals different either in the distance it travelled, the duration it was on and/or the speed it moved at, but were not told which dimension or combination of dimensions to use. No feedback was given.

Experimental design: For the experienced observers, each testing session consisted of two randomly-selected θs and their diametric pairs 180°. Each θ was assigned a single staircase, yielding four staircases per session, one of which was selected at random on each trial. Observers were blind to the θs being tested. Eight pairs of θ were investigated in total, ranging from 0 to 337.5° in 22.5° steps. For the unpractised observers, only thresholds along the main diagonals were measured. The two pairs of θ yielded four staircases, which could therefore be investigated within a single testing session.

All observers carried out two replications of each background condition. Conditions were presented in randomised blocks.

Psychophysical analysis: When performance is expressed as an error rate, the psychometric function for the 'odd one out' task is a Gaussian centred on the standard (Champion & Freeman, 2010; Ernst, 2007; Wardle & Alais, 2013). The positive and negative limbs of the Gaussian correspond to the increments of the test as they range across θ and its diametric pair (the blue line in Figure 1 describes an example). To construct the psychometric function, trials for a given θ and its pair were collapsed across the two replications, and then error rates collated across trials. Any associated increments that contained 3 or fewer trials were excluded from the analysis. We define the threshold as the standard deviation of the Gaussian that fit the data best, determined by a maximum likelihood technique. In theory, the amplitude of the Gaussian is equal to the 1-guess rate ie. 0.66. In practice, we allowed a lapse rate parameter to also vary in the fit, under the constraint that the amplitude of the Gaussian lay between peak error rates of 0.60 to 0.66.

Eye movement analysis: The sampled position traces were first low-pass filtered using a Gaussian (SD=8Hz) and then converting into eye speed using a time derivative. The first 0.25s and last 0.2s were discarded, as were any samples containing eye blinks. Saccades were detected using 'jerk' analysis (Wyatt, 1981), based on thresholding the eye speeds wherever the 3rd derivative (the 'jerk') exceeded 10,000°/s^3. These samples were also discarded before eye movement accuracy was calculated for each interval over the remainder. This was defined as the mean speed / pursuit target speed x 100%. For each observer, a mean accuracy was then obtained by averaging across all intervals.

Results and Conclusions

The results in Figure 2 show that the sensing of speed was independent of distance and duration in all conditions. For the three experienced observers (columns 1 to 3), discrimination contours were oriented along the same-speed line, as can be seen from the orientation of the main diagonals of the ellipses fit to the data. Likewise, for the unpractised observers (column 4), thresholds along the same-speed line were significantly larger than the max-speed line, although this was borderline for the third horizontal-stripe condition (two-tailed t_9=4.34,4.73,2.03, p=.002,.001,.073, Cohen's d=1.37,1.50,0.64). Our findings therefore provide good support for the primacy of speed in active vision.

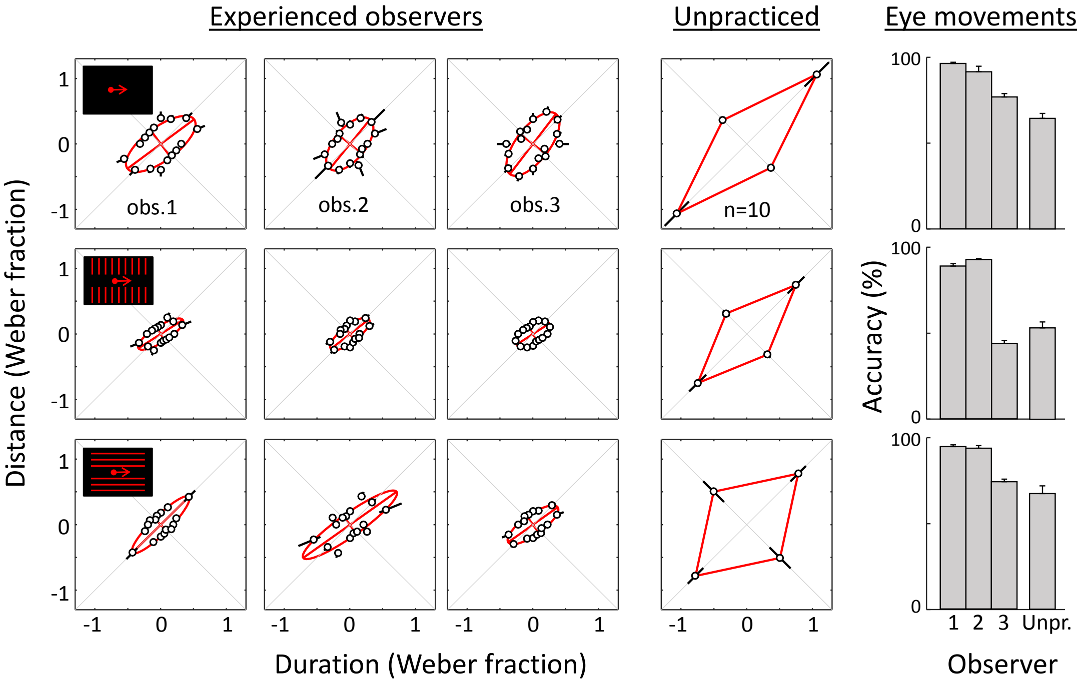

Figure 2. Results of Experiment 1. Reading from top to bottom, the rows correspond to the 'no background' condition, 'vertical background condition and the 'horizontal background' condition, respectively. The graphical insets to column 1 show schematics of the stimuli used in each condition, not drawn to scale. The first three columns correspond to the individual discrimination contours for the three experienced observers. The standard travelled over a distance of 8° for a duration of 2s (yielding a speed of 4°/s; a small delay of 0.25s was added before the start of the movement to allow observers to acquire the target). The error bars correspond to the 68%

confidence intervals, obtained by a non-parametric bootstrapping technique. The fourth column corresponds to the mean thresholds for the 10 unpractised observers (error bars are ±1SE). The same standard speed as for the experienced observers was used, but distance and duration were halved. In all cases, the discrimination contours are stretched along the same speed line on the main diagonal. Reasons why the contours become less stretched when the background texture was visible (rows 2 and 3) are taken up in the main text. The final column indicates the average pursuit accuracy (measured eye speed / stimulus speed x 100%). The first three bars correspond to the experienced observers, and the final bar the mean across the unpractised observers. Error bars are +1SE.

Analysis of the eye movement data indicated that pursuit accuracy varied across observers (rightmost column of Figure 2). Potentially, therefore, retinal slip was a more salient cue for some observers than others. To investigate whether extra-retinal cues support the preferential sensing of speed, the data of the experienced observers was re-analysed in the no-background condition. Any trials in which one or more of the three stimulus intervals contained an inaccurate eye movement were discarded, and thresholds recalculated. Of course, the probability of finding even a single interval containing perfect eye movement is vanishingly small. So we set individualised ranges, with the constraint that enough trials remained to fit a reasonable psychometric function. For the observer with the smallest range (obs.1), we were able to eliminate all trials accept those containing eye movements within ±10% of perfect pursuit and still obtain good psychometric functions. Hence the max. retinal slip speed in the trials that remained for this observer was 0.1x4=0.4°/s (note we did not analyse the distribution of slip speeds in these remaining trials; hence many trials would have had slip speeds less than 0.4°/s). For the observer with the largest range of ±30% (obs.3), the remaining trials were still heavily weighted in favour of extra-retinal cues (max. slip speed = 0.3x4=1.2°/s). Figure 3 shows the result. Despite the removal of trials with substantial retinal slip, discrimination contours remained oriented along the same-speed line. Hence distance and duration cues are fused at threshold even when the motion information originates from the motor system. This suggests that the extra-retinal eye-velocity mechanisms resident in the visual system are tuned to speed, a point taken up in more detail in the Discussion.

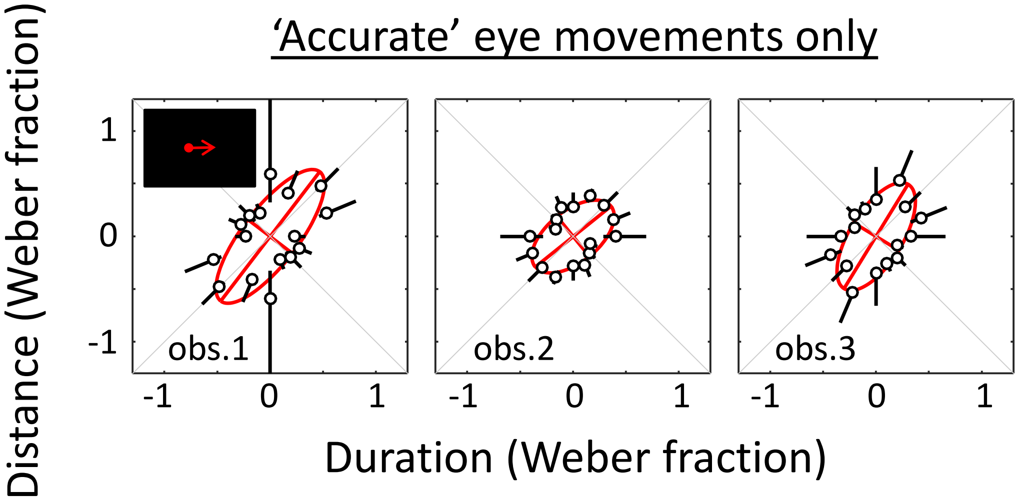

Figure 3. Discrimination contours for the no-background condition, re-analysed to include trials with 'accurate' eye movements only. For obs. 1, thresholds were re-computed for trials where eye movements in all three intervals were within ±10% of perfect pursuit. For obs.2 and obs.3, the range was relaxed to ±20% and ±30%, respectively, in order to allow reasonable psychometric functions to be fit to the remaining trials. The error bars correspond to the 68% confidence intervals, obtained by a non-parametric bootstrapping technique.

To our surprise, the addition of retinal flow in the vertical-stripe condition (middle row of Figure 2) did not enhance the domination of speed. If anything, the preference for speed shown in the no-background condition seemed somewhat reduced, with the ellipses of the experienced observers becoming less stretched along the same-speed line. The same was true for the horizontal-stripe condition. These unexpected findings were echoed by the unpractised observers, where the difference in the threshold between same-speed and max-speed lines (Δ) either decreased significantly with respect to the no-background condition, or exhibited a non-significant trend in that direction ($\Delta_{\text{no-background}}$ vs Δ_{vertical}: t_9=2.41, p=.039, d=0.76; $\Delta_{\text{no-background}}$ vs $\Delta_{\text{horizontal}}$, t_9=2.19, p=.056, d=0.69). It is unlikely that changes to duration cues were responsible for inhibiting the effect of the added flow, because these were carried by the onset and offset of the pursuit target, identical in all conditions. More likely is the idea that the static texture enhanced available distance cues, for instance by providing spatial markers for the distance covered by the pursued target. Our observers seemed to be quite sensitive to this type of information, because it remained influential in the horizontal-stripe condition, where the enhanced cue was only carried by the endpoints of the stripes, in the near periphery. Of course, the endpoints also provided a weakened flow cue; but whether weak or strong, retinal flow was unable to increase the preference for speed when a textured background was visible.

Experiment 2: Downgrading positional information enhances the preferential sensitivity to speed elicited by global retinal flow

To explore this counterintuitive finding, we ran a second experiment to remove any overt spatial information in the background, while preserving cues to speed. This was achieved in two ways. First, we made the background stimulus much larger by using a big projector screen. Secondly, we replaced the stripes with scintillating dots, a type of stimulus well known to eliminate spatial cues while preserving motion cues (Newsome & Pare, 1988). We emphasise that the dots did not move on the screen; the speed of flow was dependent on the eye movement, just like the striped backgrounds of Experiment 1.

Methods

Observers: Eleven undergraduate observers participated for course credit. One failed to complete the experiment and two produced erratic sets of responses that could not be fit with a Gaussian psychometric function. This left 8 observers.

Stimuli and design: Stimuli were rear-projected at 72Hz onto a large screen using a Sony Multiscan projector (VPH 1272QM) and a Radeon 9800 Pro graphics card. All stimuli were displayed using the green gun of the projector only. Viewing was at a distance of 140cm in a completely darkened room. When visible, the background textures measured 73° x 58°, with a 4° high blank corridor for the pursuit target, as in Experiment 1. The condition with vertical stripes also used the same texture element spacing as Experiment 1. The scintillating background condition comprised 1065 randomly positioned dots (0.5 dots/°, dia. 0.1°), each of which remained visible for 0.25s before being relocated to a new random position. Note that the appearance and disappearance of each dot was asynchronous with the others.

The standard distance and duration were the same as used for the unpractised observers in Experiment 1. The procedure was also identical, apart from the termination rule for individual staircases, which was reduced to 10 reversals. The analyses were the same as well.

Results and Conclusions

Figure 4 shows the results for a group of unpractised observers, together with replications of the no-background and vertical-stripe conditions. As in Experiment 1, discrimination was more difficult along the same-speed line compared to the max-speed line, regardless of whether the background was visible or not (t_7=3.51,9.74,6.99; p=.010,<.001,<.001, d=1.24,3.44,2.47, respectively). Likewise, adding vertical stripes did not increase preferential sensitivity to speed, as indexed by the difference in thresholds along the same-speed and max-speed lines ($\Delta_{\text{no-background}}$ vs. Δ_{vertical}: t_7=0.57, p=.585, d=0.20). This time, however, adding retinal flow via a scintillating background achieved the predicted increase in speed sensitivity ($\Delta_{\text{no-background}}$ vs. $\Delta_{\text{scintillating}}$: t_7=2.39, p=.048, d=0.85; Δ_{vertical} vs. $\Delta_{\text{scintillating}}$: t_7=2.96, p=.021, d=1.05). Thus, when all three motion cues are present, and the salience of spatial information reduced, the preferential sensitivity to speed is enhanced.

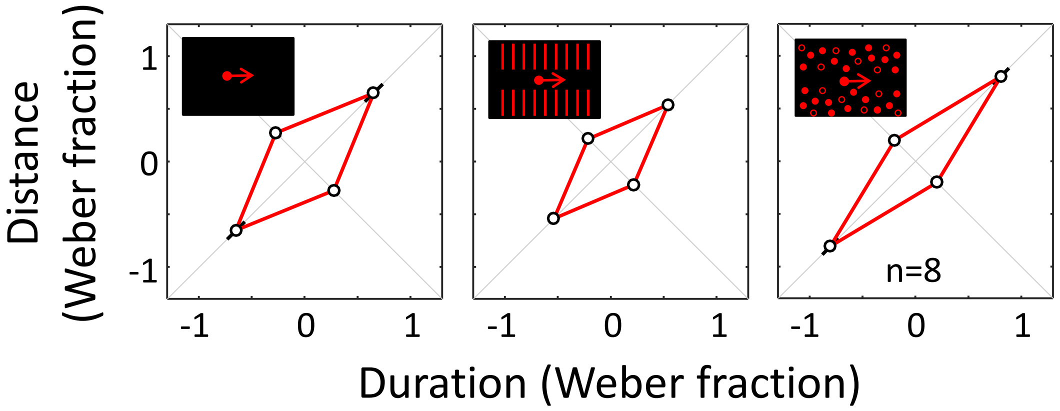

Figure 4. Mean thresholds across 8 unpractised observers for no-background, vertical stripe and scintillating-dots conditions. Error bars are ±1SE.

Discussion

Our data reveal two fundamentally important properties of motion processing in the visual system. First, the independent sensing of speed extends to the motion cues used in active vision. Our findings therefore build on the idea that the preference for visual speed is based on specialized motion detectors, analysing local motion in the image (Gekas, Meso, Masson, & Mamassian, 2017; Reisbeck & Gegenfurtner, 1999). It appears that the preference for speed is also based on cues that are more global, such as retinal flow, or come from a very different source, such as the motor system. Hence there are many different types of neural mechanism responsible for the primary status of speed.

Secondly, our findings indicate that extra-retinal eye-velocity signals resident in the visual system are tuned to speed. Although we weren't able to isolate these signals by completely eliminating all the retinal slip in our re-analysis of the no-background condition in Experiment 1, the speed of slip that remained in our 'accurate' trials was slow and more likely to support distance discrimination: previous work has showed that in the absence of any visible references, the processing of retinal motion at speeds 1°/s or less is unlikely to be carried out by specialized motion detectors (Smeets & Brenner, 1994). Hence there is good reason to conclude that the preferential sensitivity to speed in these 'accurate' trials was mediated by the extra-retinal signals resident in the visual system. On this basis, our finding sets new and important constraints on their source, suggesting that motor-system components that directly encode the speed of the eye are key, such as the Purkinje-cells found in the ventral paraflocculus (Krauzlis, 2004).

Our experiments were not designed to distinguish between extra-retinal information provided by proprioception or motor commands (inflow vs outflow: Bridgeman, 2007). However, it is tempting to suggest that finding speed-tuned extra-retinal signals might favour the latter, given that likely function of proprioception is to calibrate the sense of eye position (Wang, Zhang, Cohen, & Goldberg, 2007). Nevertheless, the literature on the perception of motion during pursuit is surprisingly silent on the cortical regions that deliver extra-retinal signals to the visual system, as is the literature on the visuomotor control of smooth pursuit. Area MST has been identified an important hub, a place where extra-retinal and image-motion signals interact. We also know that some neurons in MST receive extra-retinal information, such as 'visual-tracking neurons' that continue to fire when the pursuit target is momentarily extinguished (Ilg, Schumann, & Thier, 2004; Newsome et al., 1988; Thier & Erickson, 1992). Moreover, other neurons in MST integrate extra-retinal information with incoming image motion signals from area MT, as shown by their selectivity for screen motion, as opposed to image motion, during pursuit (Inaba et al., 2011). However, as Ono & Mustari (2006) conclude, 'None of these studies have defined the exact nature or source of extraretinal signals in smooth pursuit–related neurons.' (pp.2823). It is perhaps comes of little surprise that there is only one study, as far as we are aware, aimed at investigating how eye speed is encoded by visual-tracking neurons (Churchland & Lisberger, 2005).

The operation of extra-retinal eye-velocity mechanisms resident in the visual system remains largely unexplored, despite the frequency with which smooth pursuit eye movements are made. Much of the neuroscience associated with these types of signals provides evidence of their presence within the visual system, but not how they work. This contrasts with research on saccadic vision, where the information carried by associated extra-retinal signals, and the underlying circuity, is reasonably well understood (Sommer & Wurtz, 2008). Our study depicts one type of approach to understanding the mechanisms contributing to motion perception in active observers, one that allows a more detailed analysis of the types of cues involved, and the parameters and operations that support them.

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References

Bedell, H. E. (2000). Perception of a clear and stable visual world with congenital nystagmus. *Optometry & Vision Science, 77*(11), 573-581.

Bridgeman, B. (2007). Efference copy and its limitations. *Computers in biology and medicine, 37*(7), 924-929.

Cao, B., Mingolla, E., & Yazdanbakhsh, A. (2015). Tuning Properties of MT and MSTd and Divisive Interactions for Eye-Movement Compensation. *PloS one, 10*(11), e0142964.

Carlile, S., & Best, V. (2002). Discrimination of sound source velocity in human listeners. *The Journal of the Acoustical Society of America, 111*, 1026-1035. doi:10.1121/1.1436067

Carlile, S., & Leung, J. (2016). The perception of auditory motion. *Trends in hearing, 20*, 2331216516644254.

Champion, R. A., & Freeman, T. C. A. (2010). Discrimination contours for the perception of head-centred velocity. *Journal of Vision, 10(6):14*, 1-9. doi:doi:10.1167/10.6.14

Chukoskie, L., & Movshon, J. A. (2009). Modulation of visual signals in macaque MT and MST neurons during pursuit eye movement. *Journal of Neurophysiology, 102*(6), 3225-3233.

Churchland, A. K., & Lisberger, S. G. (2005). Relationship between extraretinal component of firing rate and eye speed in area MST of macaque monkeys. *Journal of Neurophysiology, 94*(4), 2416-2426.

Cicchini, G. M., Anobile, G., & Burr, D. C. (2016). Spontaneous perception of numerosity in humans. *Nature communications, 7*.

DeAngelis, G. C., & Uka, T. (2003). Coding of horizontal disparity and velocity by MT neurons in the alert macaque. *Journal of Neurophysiology, 89*(2), 1094-1111.

Dunkley, B. T., Freeman, T. C., Muthukumaraswamy, S. D., & Singh, K. D. (2013). Cortical oscillatory changes in human middle temporal cortex underlying smooth pursuit eye movements. *Human Brain Mapping, 34*(4), 837-851.

Eifuku, S., & Wurtz, R. H. (1998). Reponse to motion in extrastriate area MSTl: Center-surround interactions. *Journal of Neurophysiology, 80*, 282-296.

Ernst, M. O. (2007). Learning to integrate arbitrary signals from vision and touch. *Journal of Vision, 7(5):7*, 1-14.

Freeman, T. C. A. (2001). Transducer models of head-centred motion perception. *Vision Research, 41*, 2741-2755.

Freeman, T. C. A., & Banks, M. S. (1998). Perceived head-centric speed is affected by both extra-retinal and retinal errors. *Vision Research, 38*(7), 941-945.

Freeman, T. C. A., Champion, R. A., & Warren, P. A. (2010). A Bayesian model of perceived head-centred velocity during smooth pursuit eye movement. *Current Biology, 20*, 757-762.

Freeman, T. C. A., Leung, J., Wufong, E., Orchard-Mills, E., Carlile, S., & Alais, D. (2014). Discrimination contours for moving sounds reveal duration and distance cues dominate auditory speed perception. *PloS one, 9*(7), e102864.

Furman, M., & Gur, M. (2012). And yet it moves: Perceptual illusions and neural mechanisms of pursuit compensation during smooth pursuit eye movements. *Neuroscience and Biobehavioral Reviews, 36*, 143-151.

Gekas, N., Meso, A. I., Masson, G. S., & Mamassian, P. (2017). A Normalization Mechanism for Estimating Visual Motion across Speeds and Scales. *Current Biology, 27*(10), 1514-1520. e1513.

Haarmeier, T., Thier, P., Repnow, M., & Petersen, D. (1997). False perception of motion in a patient who cannot compensate for eye movements. *Nature, 389*, 849-852.

Ilg, U. J., Schumann, S., & Thier, P. (2004). Posterior parietal cortex neurons encode target motion in world-centred coordinates. *Neuron, 43*, 145-151.

Inaba, N., Miura, K., & Kawano, K. (2011). Direction and speed tuning to visual motion in cortical areas MT and MSTd during smooth pursuit eye movements. *Journal of Neurophysiology, 105*, 1531-1545.

Krauzlis, R. J. (2004). Recasting the smooth pursuit eye movement system. *Journal of Neurophysiology, 91*, 591-603.

Lappin, J. S., Bell, H. H., Harm, O. J., & Kottas, B. (1975). On the relation between time and space in the visual discrimination of velocity. *Journal of Experimental Psychology: Human Perception and Performance, 1*(4), 383-394.

Layton, O. W., & Fajen, B. R. (2016). A neural model of MST and MT explains perceived object motion during self-motion. *Journal of Neuroscience, 36*(31), 8093-8102.

Lindner, A., Thier, P., Kircher, T. T., Haarmeier, T., & Leube, D. T. (2005). Disorders of agency in schizophrenia correlate with an inability to compensate for the sensory consequences of actions. *Current Biology, 15*(12), 1119-1124.

Lingnau, A., Ashida, H., Wall, M. B., & Smith, A. T. (2009). Speed encoding in human visual cortex revealed by fMRI adaptation. *Journal of Vision, 9*(13), 3-3.

Maunsell, J. H., & Van Essen, D. C. (1983). Functional properties of neurons in middle temporal visual area of the macaque monkey. I. Selectivity for stimulus direction, speed, and orientation. *Journal of Neurophysiology, 49*(5), 1127-1147.

Nefs, H. T., & Harris, J. M. (2007). Vergence effects on the perception of motion-in-depth. *Experimental Brain Research, 183*, 313-322.

Newsome, W. T., & Pare, E. B. (1988). A selective impairment of motion perception following lesions of the middle temporal visual area (MT). *Journal of Neuroscience, 8*(6), 2201-2211.

Newsome, W. T., Wurtz, R. H., & Komatsu, H. (1988). Relation of cortical areas MT and MST to pursuit eye movements. II. Differentiation of retinal from extra-retinal inputs. *Journal of Neurophysiology, 60*(2), 604-620.

Nover, H., Anderson, C. H., & DeAngelis, G. C. (2005). A logarithmic, scale-invariant representation of speed in macaque middle temporal area accounts for speed discrimination performance. *Journal of Neuroscience, 25*(43), 10049-10060.

O'Connor, E., Margrain, T. H., & Freeman, T. C. A. (2010). Age and direction discrimination with and without smooth pursuit eye movement. *Vision Research, 50*, 2588-2599.

Ono, S., & Mustari, M. J. (2006). Extraretinal signals in MSTd neurons related to volitional smooth pursuit. *Journal of Neurophysiology, 96*(5), 2819-2825.

Perrone, J. A., & Krauzlis, R. J. (2008). Vector subtraction using visual and extraretinal motion signals: A new look at efference copy and corollary discharge theories. *Journal of Vision, 8*(14), 24-24.

Perrone, J. A., & Thiele, A. (2001). Speed skills: measuring the visual speed analyzing properties of primate MT neurons. *Nature Neuroscience, 4*(5), 526.

Priebe, N. J., Cassanello, C. R., & Lisberger, S. G. (2003). The neural representation of speed in macaque area MT/V5. *Journal of Neuroscience, 23*(13), 5650-5661.

Priebe, N. J., Lisberger, S. G., & Movshon, J. A. (2006). Tuning for spatiotemporal frequency and speed in directionally selective neurons of macaque striate cortex. *Journal of Neuroscience, 26*(11), 2941-2950.

Pynn, L. K., & DeSouza, J. F. (2013). The function of efference copy signals: implications for symptoms of schizophrenia. *Vision Research, 76*, 124-133.

Reisbeck, T. E., & Gegenfurtner, K. R. (1999). Velocity tuned mechanisms in human motion processing. *Vision Research, 39*, 3267-3285.

Rushton, S. K., & Warren, P. A. (2005). Moving observers, relative retinal motion and the detection of object movement. *Current Biology, 15*(14), R542-R543.

Smeets, J. B. J., & Brenner, E. (1994). The difference between the perception of absolute and relative motion: a reaction time study. *Vision Research, 34*(2), 191-195.

Sommer, M. A., & Wurtz, R. H. (2008). Brain circuits for the internal monitoring of movements. *Annu. Rev. Neurosci., 31*, 317-338.

Souman, J. L., Hooge, I. T. C., & Wertheim, A. H. (2006). Frame of reference transformations in motion perception during smooth pursuit eye movement. *Journal of Computational Neuroscience, 20*(1), 61-76.

Thaker, G. K., Ross, D. E., Buchanan, R. W., Adami, H. M., & Medoff, D. R. (1999). Smooth pursuit eye movements to extra-retinal motion signals: deficits in patients with schizophrenia. *Psychiatry research, 88*(3), 209-219.

Thier, P., & Erickson, R. G. (1992). Responses of visual-tracking neurons from cortical area MST-l to visual, eye and head motion. *European Journal of Neuroscience, 4*, 539-553.

Turano, K. A., & Massof, R. W. (2001). Nonlinear contribution of eye velocity to motion perception. *Vision Research, 41*, 385-395.

Van Den Berg, A. V., & Beintema, J. A. (2000). The mechanism of interaction between visual flow and eye velocity signals for heading perception. *Neuron, 26*(3), 747-752.

von Holst, E. (1954). Relations Between the Central Nervous System and the Peripheral Organs. *British Journal of Animal Behaviour, 2*, 89-94.

Wandell, B. A. (1985). Colour measurement and discrimination. *Journal of Optical Society of America A, 2*(1), 62-71.

Wang, X., Zhang, M., Cohen, I. S., & Goldberg, M. E. (2007). The proprioceptive representation of eye position in monkey primary somatosensory cortex. *Nature Neuroscience, 10*(5), 640.

Wardle, S. G., & Alais, D. (2013). Evidence for speed sensitivity to motion in depth from binocular cues. *Journal of Vision, 13*(1), 17-17.

Warren, P. A., & Rushton, S. K. (2007). Perception of object trajectory: parsing retinal motion into self and object movement components. *Journal of Vision, 7*(11), 2-2.

Warren, P. A., & Rushton, S. K. (2009). Optic flow processing for the assessment of object movement during ego movement. *Current Biology, 19*, 1-6.

Welchman, A. E., Harris, J. M., & Brenner, E. (2009). Extra-retinal signals support the estimation of 3D motion. *Vision Research, 49*, 782-789.

Wertheim, A. H. (1994). Motion perception during self-motion - the direct versus inferential controversy revisited. *Behavioral and Brain Sciences, 17*(2), 293-311.