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Judging object velocity during smooth pursuit eye movements

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Abstract Our tendency to constantly shift our gaze and to pursue moving objects with our eyes introduces obvious problems for judging objects' velocities. The present study examines how we deal with these problems. Specifically, we examined when information on rotations (such as eye movements) is obtained from retinal, and when from extra-retinal sources. Subjects were presented with a target moving across a textured background. Moving the background allowed us to manipulate the retinal information on rotation independently of the extra-retinal information. The subjects were instructed to pursue the target with their eyes. At some time during the presentation the target's velocity could change. We determined how various factors influence a subject's perception of such changes in velocity. Under more or less natural conditions, there was no change in perceived target velocity as long as the relative motion between target and background was maintained. However, experiments using conditions that are less likely to occur outside the laboratory reveal how extra-retinal signals are involved in velocity judgements.

Key words Motion perception · Eye movements Smooth pursuit · Velocity · Human

Introduction

We usually direct our gaze at the object we are interested in. If that object is moving, we pursue it with our eyes. The speed with which the object's image shifts across our retinas, therefore, does not provide direct information on its velocity. There are two principles by which we could nevertheless obtain such velocity judgements.

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Department of Physiology, Erasmus University, P.O. Box 1738, 3000 DR Rotterdam, The Netherlands A crucial difference between these methods is the source of information on one's own motion.

The first method uses the motion of the image of the surrounding on our retinas as a direct estimate of the rotation of the eyes relative to the surrounding. Rotations, the most conspicuous of which are the rotations of the eyes relative to the head (eye movements), shift the retinal images of both the object and its surrounding to the same extent. Judging an object's velocity on the basis of its motion relative to its surrounding would therefore prevent rotations from influencing the perceived velocity. Use of the surrounding as the frame of reference obviously implies that velocities must be misjudged (relative to the head, or to a real but invisible static surrounding) if the surrounding moves.

The second method uses extra-retinal signals to obtain information on our own motion. There are numerous potential sources of such extra-retinal information, including: "copies" of the signals that are used to drive the eye muscles, as the source of information on (changes in) the orientation of our eyes within our heads (Von Holst and Mittelstaedt 1950); cervico-somatosensory signals for motion of the head relative to the body (Probst et al. 1986); vestibular stimulation for motion of the head relative to the surrounding (Wertheim 1990). An advantage of this method is that one could obtain measures of motion relative to the head or body as well as relative to the surrounding. A disadvantage is that combining the signals to obtain judgements of velocity relative to the surrounding is complicated, because the axes of rotation are different.

Most electrophysiological studies on the cells responsible for motion perception have used anaesthetized and paralysed animals, implicitly assuming that a retinal frame of reference is used in motion perception. However, there is evidence that at least some motion-sensitive cells in the macaque visual cortex (area V3A) respond less vigorously to identical stimulation of their retinal receptive fields when the eye is moving (Galletti et al. 1990). Comparison between the influence of eye movements with and without textured back-

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grounds suggested that some cells use retinal image motion whereas others use extra-retinal input to determine whether the eye is moving. Unfortunately, Galletti et al. did not examine whether the optimal velocity changes when the eye is in motion, as it should if these cells responded to motion relative to the surrounding.

Motion-sensitive cells in the owl monkey's middle temporal cortex change their responses to a moving target when the background moves (Allman et al. 1985). Although some cells show specific inhibition when the background moves at the same velocity as the target, most show inhibition that increases with background velocity. As the target always moved at the optimal velocity, sensitivity to relative velocity would predict the latter pattern of inhibition by background motion. To determine whether these cells are specifically sensitive for certain relative motion, one would again have to show that the optimal target velocity changes when the background moves.

There are reports of cells in the monkey parietal cortex that have receptive fields that correspond with positions in space (relative to the monkey), rather than corresponding with certain parts of the retina. As these cells' receptive fields change in anticipation of eye movements (Duhamel et al. 1992), they must use extra-retinal information to account for changes in eye orientation. Responses of such cells could, in principle, be combined to specify motion relative to the head, but there is as yet no evidence that they are. Thus, the available electrophysiological studies cannot resolve the issue.

Psychophysical studies show without doubt that judgements of objects' velocities are led astray by moving the background (Brenner 1991; Duncker 1929; Mack 1986; Raymond et al. 1984; Rock et al. 1980; Wallach 1959). Stationary objects appear to move if the background moves, and moving objects' velocities are misjudged if the whole background is moving, or if the wrong part of the environment is considered to be stationary. However, the magnitude of the effect is often much smaller than would be expected from judgements using the surrounding as the frame of reference.

One explanation for the influence of background motion is that extra-retinal information is used to transform retinal slip into object motion, but that the extraretinal representation of the eye movements does not correspond with the actual eye movements (Heckmann et al. 1991; Raymond et al. 1984). Only "intentional" eye movements are accounted for. Eye movements caused by reflexes go by unnoticed. An alternative is that the lacking change in position, to accompany the perceived target motion that is induced by motion of the background, limits the influence of the background. The present study examines the extent to which retinal and extra-retinal information on eye movements are used for judging changes in an object's velocity. We chose conditions that we consider unfavourable for both optokinetic reflexes and precise localization.

Materials and methods

The stimulus used in the present study combines a dissociation between retinal and extra-retinal information on (ocular) rotation. with an emphasis on motion rather than position, and little room for an influence of ocular reflexes. The task was to report on changes in the velocity of a moving target. Retinal slip was dissociated from object motion by requiring that subjects pursue the target with their eyes. Retinal feedback on rotation of the eye was manipulated independently of extra-retinal information by moving the background. To emphasize motion rather than position, the target and background were filled with fine random texture and the duration of the motion was varied. The conflict between motion and position was limited by using a short duration of background motion. Besides minimizing the salience of changes in relative position, the random texture ensured that the target was only visible while moving. The fine texture and very limited duration of each presentation should limit ocular reflexes. We already knew that a moving background can influence perceived target velocity under such conditions (Brenner 1991).

The experiments were conducted using an Atari Mega ST 4 computer with an Atari SM 125 white monochrome screen (71 Hz; 640 by 400 pixels). Subjects looked at the 22 by $13^{1/2}$ cm (35 by 22°) image with one eye from a distance of 35 cm. They looked through a 15 mm diameter hole in a "box". Opposite this hole, the open side of the box fit tightly to the screen. The inside of the box was painted matt black. The experiments took place in a dark room.

The target was a $1^{1/4}$ by $1^{1/4}$ cm (2 by 2°) random pixel array (50% light; 50% dark) that moved from left to right. The background consisted of a similar random pixel array. New random pixel arrays were generated for each trial. The initial target velocity was 1.5 pixels per frame (alternating between steps of 1 and 2 pixels on consecutive frames), which is about 6°/s. A pilot study showed that at 71 Hz subjects could not distinguish between motion at a fixed number of pixels per frame, and various sequences resulting in the same average displacement, but with a much larger variability in the size of individual steps than those used in the present study. The luminance of the pixels was 3.0 and 0.015 cd/m² for light and dark pixels respectively.

Unless specified otherwise, the target appeared on the left half of the screen, and started moving to the right (at an initial velocity) across a static background. A tone warned the subjects of the onset of motion. The subjects had been instructed to follow the moving target with their eye. Between 500 and 800 ms later, a second tone indicated a possible change in the target's velocity. At the same time, the background could start moving. Target and background velocities changed gradually, taking 100 ms to reach their final values. The target and background continued moving at the final velocity for another 300–400 ms.

Subjects had to indicate whether the target moved faster, at the same speed, or more slowly during the final interval, than it had during the initial interval. We did not specify whether we meant motion relative to themselves or to the background, in order not to bias their responses. Subjects never had trouble with this potential ambiguity in the previous studies using the same task (Brenner 1991, 1993).

The target's final velocity depended on the subject's choices on previous presentations. Staircases were used to find two velocity settings for each experimental condition: the speed at which the target appeared to accelerate, and that at which a reduction in speed was observed (Fig. 1). We will refer to these settings as transitions, rather than thresholds, because the latter are associated with a certain methodology which assumes that there is a "correct" response. Between these two transition points lies the *range* of subjective equality between the initial and final perceived target velocities.

For finding the transition from no perceived change in velocity to a perceived increase in velocity (upper limit of the range of subjective equality), the staircase procedure was as follows. If the subject reported that the target accelerated, the target's final speed was set lower on the next presentation. If she either reported that

Order of presentation to subject

Responses and staircases



Fig. 1 Schematic representation of the method used to find the upper and lower limit of the range of subjective equality (final velocities at which the target appears to keep moving at its initial speed). Contributions to staircases for different conditions (and replications of these conditions) were presented in random order on consecutive trials. For each replication of each condition, separate staircases were used to search for the upper and lower limits. In both cases subjects had to indicate whether the target's final velocity was "faster", the "same" or "slower" than its initial velocity. For finding the upper limit, choosing "faster" resulted in a lower velocity. For finding the lower limit, choosing "faster" or "same" resulted in a lower velocity, whereas choosing "same" or "slower" resulted in a higher velocity.

it did not change its speed, or that its motion during the final interval was slower, its final speed was set higher on the next presentation. The magnitude of the increase or decrease was reduced (to 80% of the previous value) after each trial, until it reached a level that was negligible on the screen (less than one pixel during the whole final interval). The value onto which the staircase converged was taken as the transition point. The transition from no change to a decrease in velocity (lower limit of the range of subjective equality) was determined in the same manner, except that reports of no change in speed resulted in a lower (rather than a higher) velocity on the next presentation (for additional details see Brenner 1991).

The average of a subject's replications for each transition is referred to as the subject's settings. Within each experiment, all the staircases ran simultaneously, so that subjects could never predict the change in velocity. The number of staircases in an experiment was *two* (one for the upper and one for the lower limit) times the *number of replications* times the *number of conditions*.

In the first experiments the background was static during the initial part of the presentation, and moved during the final part. We examined the influences of target speed, target size, and duration of the background motion. For comparison, settings were also made in the complete absence of a background. In the experiments that followed, the background also moved during the initial part of the presentation. Identical changes in background motion could thus be obtained for various initial and final background velocities. Finally, the moving background was either presented during the initial or the final interval, with no visible background during the other interval. Apart from the first author (who took part in all the experiments), all the subjects were naive as to the purpose of the experiment they were performing. Two naive subjects performed most experiments, whereas others often only took part in one experiment. Some subjects had participated in earlier studies using the same task.

Results

Figure 2 shows the settings in the first experiment. The solid and open symbols show the upper and lower limits of the range of final velocities for which the target appears to continue to move at the initial velocity. Each symbol shows the mean and standard deviation of six subjects' settings for a certain final background velocity; each of which is the average of the outcome of three staircases. Positive values of velocity are for motion to the right (in the direction of the initial target motion). Negative values indicate motion to the left. The horizontal dashed line shows the initial target velocity. The vertical dotted line shows the initial background velocity (stationary). The slanted dashed line shows the final target velocity that would maintain the relative motion between target and background. The symbols on the extreme right (dark background) are for settings when the target moved across an empty, dark screen.

We did not instruct subjects on what frame of reference they should use, in order not to bias their responses. No subjects had any problem with this. Most subjects had no difficulties with the task; and some reported only occasionally noticing that the background moved. Several subjects did report occasionally having seen the target accelerate without undergoing the corresponding displacement (presumably because they judge position relative to their own body, whereas they judge velocity relative to the surrounding). This discrepancy occurs when the background moves fast in the opposite direction than the target. In that case, subjects all clearly judged the target's velocity relative to the background,



Final background velocity (pixels/frame)

Fig. 2 Target velocities at which the transitions occurred between a perceived increase in velocity and no change in perceived velocity (solid symbols), and between no change and a decrease in perceived velocity (open symbols), for various final background velocities. Each symbol shows the mean and standard deviation of six subjects' settings; each of which is the average of the outcome of three staircases. The horizontal dashed line shows the initial target velocity, i.e. the speed that subjects were required to match. The slanted dashed line indicates the final target speed at which the relative velocity would remain constant. The symbols in the right margin show settings when the target moved across a dark background. Positive values on the horizontal axis indicate background motion in the same direction as the target (to the right). Negative values indicate motion in the opposite direction. One pixel per frame corresponds with about $\hat{4}^{\circ}/s$. The initial target velocity is therefore approximately 6°/s

but they showed considerable variability in the highest final velocities for which they did not see the target accelerate (leftmost filled circles in Fig. 2). This variability may be caused by the perceived discrepancy between motion and change in position.

Although the standard deviations shown in Fig. 2 are quite reasonable, they suggest much more variability than was actually present. Subjects reproduced their own settings extremely well, both within a single session and between sessions (see also Fig. 7). The larger differences between subjects (see also Brenner 1991) are partly caused by some subjects answering "same velocity" when in doubt, whereas others choose between "faster" and "slower", unless they are sure that it is actually the same velocity. They were given no instructions as to which strategy to use. The justification for averaging across subjects is that the influences of the different conditions were very consistent amongst subjects. The standard deviations mainly reflect the variability in the strategy used by the subjects, and are therefore not shown in the following figures (in which variability between subjects was similar).

When the background moved in the opposite direction than the target, the target was judged to continue to move at the same velocity as long as its velocity relative to the background was maintained. The target was judged to increase its velocity when its velocity relative



Fig. 3a,b Target velocities at which the transitions occurred between a perceived increase in velocity and no change in perceived velocity (solid symbols), and between no change and a decrease in perceived velocity (open symbols), for various background velocities. Symbols show the mean of five **a** or six **b** subjects' settings (each of which is the average of two staircases). Neither target size nor the duration of motion at the final velocity influenced the settings. One pixel per frame corresponds with about 4°/s. For further details see text and legend of Fig. 2

to the background increased by more than about half a pixel per frame, and to decrease its velocity when the relative velocity decreased by a similar amount. Even *reversal* of the target's motion on the screen (negative final target velocity) went by unnoticed when accompanied by appropriate background motion.

When the background moved in the same direction as the target, the increase in target speed that maintained its perceived velocity was much smaller than the increase that would maintain the target's velocity relative to the background. However, this increase was not negligible. The range of velocities for which the target's speed did not appear to change (i.e. the distance between the two transition points) was very similar for all background velocities. It was also similar to the range when there was no visible background (dark background). Background motion in the same direction as the target shifted the range of velocities outside the range that was found in the absence of a background.

Figure 3 shows that the influence of background motion is independent of the target's size (a), and of the duration of the final interval (b). Figure 3a shows mean results for five subjects; Fig. 3b shows mean results for six subjects (two settings per subject in both cases). A subjective impression (reported by most subjects) that the task is more difficult when the target size is reduced beyond a certain level, and when the target is shown for a short time, is not evident in the settings. The ease with which one decides whether the target moved faster, more slowly, or at the same speed, is affected, but the decision apparently is not.

Figure 4 shows that the same pattern of responses could be obtained at twice the target velocity relative to the head. The figure shows the mean settings of six subjects (one staircase each) for two target velocities. Velocities are expressed in units of the initial speed of the



Fig. 4 Target velocities at which the transitions occur between a perceived increase in velocity and no change in perceived velocity (solid symbols), and between no change and a decrease in perceived velocity (open symbols), for various background velocities. Each symbol shows the mean of six subjects' settings; each of which is the outcome of a single staircase. The target initially either moved at 1.5 (circles) or at 3.0 (triangles) pixels per frame. One pixel per frame corresponds with about 4° /s. The dashed lines show the final target velocities that would keep the absolute and relative velocities constant. All velocities are presented in units of initial target velocity. Thus for the target initially moving at 3 pixels per frame, a scaled final background velocity of 1 means that the background moves at 3 pixels per frame during the final interval

target. The data for the two velocities are almost identical.

Figure 5 compares settings for an initially static background, with settings for initial background motion at 0.5 or 1 pixel per frame; both in the same direction as the target, and in the opposite direction. Symbols show the mean settings of seven subjects (three per subject). The final target velocity settings are presented as a function of the *change* in background velocity. There is a modest systematic influence of the initial background velocity: subjects rely on relative motion for a larger range of changes in background velocity when the background initially moves in the opposite direction than the target.

Figure 6 shows settings when the target initially moved in the dark, followed by motion across a (moving) background (a), or initially moved across a (moving) background, which then disappeared while the target continued on its path (b). The points are average settings of six subjects (three staircases per condition). The appearance or disappearance of a *stationary* background (final and initial background velocities of 0 pixels per frame in Figs. 6a and b, respectively) had little influence on the perceived velocity. Motion of the background had a much stronger influence during the final interval than during the initial interval.



Change in background velocity (pixels/frame)

Fig. 5 Target velocities at which the transitions occurred between a perceived increase in velocity and no change in perceived velocity (solid symbols), and between no change and a decrease in perceived velocity (open symbols). Each symbol shows the mean of seven subjects' settings; each of which is the average of the outcome of three staircases. The horizontal axis shows the change in background motion. Positive values indicate an increase in rightward or a decrease in leftward motion. Negative values signify an opposite change. The symbols show data for different initial velocities of the background. One pixel per frame corresponds with about $4^{\circ}/s$



Fig. 6a,b Target velocities at which the transitions occur between a perceived increase in velocity and no change in perceived velocity (*solid symbols*), and between no change and a decrease in perceived velocity (*open symbols*), for various background velocities. Each symbol shows the mean of six subjects' settings; each of which is the average of the outcome of three staircases. The moving background maintained its influence when it was only presented after the change (**a**), but had very little effect when only presented before the change (**b**). Note that the modest influence of background motion when the background suddenly disappeared does not necessarily mean that subjects initially saw the same velocity under all conditions. One pixel per frame corresponds with about $4^{\circ}/s$

Discussion

When judging an object's velocity during pursuit eye movements, its visual surrounding will usually be part of the static environment. Thus, the retinal image of the surrounding normally moves in the opposite direction than the eye movement. We found that as long as the retinal slip of the image of the surrounding is in the opposite direction than that in which the eyes are moving, subjects use the retinal slip of the surrounding as a measure of the rotation of their eyes (relative to the surrounding); they report that the target continues to move at the same speed when its velocity relative to the background remains constant. The results under other conditions are less straightforward, and reveal the role of extra-retinal signals in judging object motion.

If the velocity misjudgements with moving backgrounds were due to optokinetic reflexes that are not accounted for in the signals that provide us with information on our eye movements (Heckmann et al. 1991; Raymond et al. 1984; Wertheim 1990) the effect of background motion should depend on the extent to which the stimuli induce optokinetic responses. In that case, the influence of the background should have been very small in the present study, due to the short duration of the stimuli. Another objection to this proposal is that it does not predict the asymmetry that we found with respect to the direction of the retinal slip of the background. Moreover, contrary to our observations (Fig. 3), it predicts that the background's influence should diminish when the duration of background motion is decreased (Heckmann et al. 1991) and when target size is increased (decreasing the size of the surrounding).

As an alternative, we propose that we use an internal representation of the eye's rotation relative to the static environment (together with the target's retinal slip) for judging velocities. Both retinal (the motion of the background) and extra-retinal signals contribute to this internal representation. When the retinal signal specifies a faster rotation of the eye than the extra-retinal signal (in the same direction), the retinal motion of the surrounding determines the internal representation of the rotation of the eye. When the rotation specified by the retinal signal is slower than that specified by the extra-retinal signals, or in the opposite direction, the influence of the retinal signal is much smaller. Extra-retinal signals presumably specify the *direction* of the eye movement, as well as a minimal rotation in that direction, which even retinal information indicating very fast eye rotation in the opposite direction cannot overrule (extraretinal signals specifying that the eye is static could similarly limit the influence of background motion during fixation of a static target). We will proceed to discuss how our study supports this proposal.

Our results when a moving background suddenly appears demonstrate that extra-retinal information on eye movements can be very precise (Fig. 6a). A dark background during the initial part of the presentation is more or less equivalent to a static background. Figure 7 shows the settings of two of the subjects who participated in most of the experiments. The thin lines show data for an initially static background from three different experiments. The thick lines show the data for the target initially moving in the dark. The similarity between the



Fig. 7a,b Ranges of individual subjects' settings for the same background motion on three different occasions (*thin lines*; data included in Figs. 2, 3a, 5), and for the target initially moving in the dark (*thick lines*; data included in Fig. 6a). The absence of a background during the initial target motion had little effect. One pixel per frame corresponds with about 4°/s

settings when the target initially moved across a dark background, and those when it initially moved across a static textured background, demonstrates that the perceived target velocity during the initial interval was about the same when based on extra-retinal signals alone as when based on both extra-retinal and retinal information (although there are alternatives to the extra-retinal signal, such as the expected velocity, or the retinal velocity before the eye starts to move). The only finding reminiscent of an underestimated velocity during pursuit in the absence of a background (Dichgans et al. 1969; Dodge 1904; Festinger et al. 1976; Mack and Herman 1978; Mack 1986; Matin 1986; Stoper 1973) is the slightly lower final target velocity at which a decrease in velocity is seen (Fig. 7; lower thick lines). We conclude that veridical judgements of velocity do not require the presence of relative motion. Nevertheless, once a moving background appears, it influences our judgements in a manner that suggests that extra-retinal sources on eye rotation are overruled by retinal ones as soon as the latter become available. For example, when a target moving at 1.5 pixels per frame to the right (in the dark) was suddenly surrounded by a background moving at 1.5 pixels per frame to the left (Fig. 7: final background velocity of -1.5), it had to remain more or less static on the screen (a final target velocity of 0; so that the relative velocity was 1.5 pixels per frame) for Alex to report that it continued to move at the same speed.

It is evident from Figs. 2–5 that subjects abandon motion relative to the background for their judgements of object velocity when the background moves at a high velocity in the same direction as the target. In support of the suggestion that the *direction* of eye rotation that is specified by motion of the background's retinal image must correspond with the *direction* of the eye movement that is specified by extra-retinal sources, for the former (and thus relative motion) to determine the subject's judgements of object velocity, we replotted the data



Fig. 8a,b The data from Fig. 5 presented as a function of the final background velocity. The *dotted lines* indicate the velocity at which the background's image would temporarily be stationary on the retina if pursuit were perfect during the initial interval. The background was initially static (*circles*), moved at 1 (*squares*) or $1/_2$ (*diamonds*) a pixel per frame to the left, or at 1 (*triangles pointing upwards*) or $1/_2$ (*triangles pointing downwards*) a pixel per frame to the different symbols stop in creasing in proportion with the final background velocity (especially for the perceived increase in velocity; *arrow*) and start to converge about at the dotted lines. One pixel per frame corresponds with about $4^{\circ}/s$

from Fig. 5 as a function of the final background velocity (Fig. 8). If we look at the influence of the initial background velocity on the settings for each final background velocity (vertical distance between symbols), we see that the final target velocity settings change in proportion to the change in initial target velocity (i.e. the subjects' judgements maintain relative motion) until the final background velocity (to the right) approaches the initial target speed. For faster rightward background motion the settings stop increasing in proportion to background velocity and converge, indicating that target motion is no longer judged exclusively relative to the visual surrounding.

In the explanation of our data, we assume that the change in background motion does not change the eyes' pursuit of the target. We track targets with a combination of smooth pursuit and saccades. The gain of the smooth component of pursuit eye movements is lower than one, and saccades are used to keep the eyes on the target (Collewijn and Tamminga 1984). Subjects can follow targets almost perfectly with smooth pursuit alone at the low velocity we used (van den Berg and Collewijn 1986). Moreover, they can follow or fixate selected objects with their eyes, irrespective of motion of the background (Kowler et al. 1984; Mack et al. 1979; Matin 1986). To examine whether they still do so when having to judge the target's velocity, we measured the horizontal eye movements of one subject (the second author) while he performed the psychophysical task. Fluctuations in the gain of smooth ocular pursuit could be responsible for the gradual (rather than abrupt) departure from relying on relative motion, because such fluctuations will vary the velocity on the screen at which the background's image reverses its direction on the retina.



Fig. 9a,b Examples of eye movements when pursuing targets that did not change their velocities. The orientation of the eyes was recorded (at 250 Hz) from 1 s before to 1 s after the onset of background motion. The target actually only moved for 500–750 ms before to 250–500 ms after the onset. Target motion is always 0.21 m/s on the screen (about 6°/s). Only conditions in which the subject reported that the target had not changed velocity are shown. The *thin lines* in both parts of the figure are for a static background (n=3). The *thick lines* are for a background moving at the same velocity as the target (\mathbf{a} ; n=3) or at twice the target velocity (\mathbf{b} ; n=6) during the final interval. There are no systematic differences between the eye movements as a result of background motion. The *arrow* indicates the moment at which the background started moving



Fig. 10 Gains of ocular pursuit of the target at the onset of background motion. Occurrences of gains between 0.5 and 1.5 at the time at which the background started moving. The gain was determined from the eye orientations 100 ms before and after an abrupt change in background motion. There is a clear peak at gains between 0.9 and 0.95



Fig. 11 All values of the final target velocity for which the subject reported that the target appeared to continue to move at the same speed. The final target velocity is in metres per second $(0.21 \text{ m/s} \text{ corresponds with } 6^{\circ}\text{/s})$. The velocity of the background's image on the retina is given both in degrees per second and as an equivalent velocity on the screen in metres per second. The latter is the background velocity at which the same retinal slip would occur if the eye were stationary. The *dashed lines* show the final target velocities at which relative and absolute target velocities would remain constant

Horizontal eye movements were recorded with a scleral coil. A central target and two targets 9.7° to the left and right of this central target were used for calibration. The stimulus was back-projected onto a large screen at 2 m from the subject (Silicon Graphics workstation with resolution: 1280 by 1024 pixels covering 235 by 188 cm; 60 Hz). It consisted of a red square (6 by 6 cm) that moved at eye height across a background of 75 similar randomly coloured squares. The procedure was as in the main experiments, except that a constant step size was used in the staircase, and that the changes in velocity were abrupt rather than gradual.

Figure 9 shows the horizontal eye movement on individual presentations in which the target did not change its velocity and the subject reported not having seen a change in velocity. In Fig. 9a, the background either remained static (thin lines), or moved at the initial target velocity during the final interval (i.e. at the same velocity as the target; thick lines). Figure 9b shows the same traces for a static background (thin lines), together with traces for the background moving at twice the initial target velocity during the final interval (thick lines). The subject continues to follow the target despite considerable motion in the background.

Figure 10 shows the gains of ocular pursuit during a 200 ms interval centred on the moment that the target changed velocity (adjustments of the velocity of ocular pursuit to a change in target motion only start about 100 ms after unpredictable changes in target velocity; Carl and Gellman 1987). There is a clear peak in the frequency distribution for gains between 0.9 and 0.95.

The individual gains were used to determine the background's retinal slip at the moment that it started moving. The final target velocities at which the subject reported that the target did not change its velocity are plotted as a function of the background's retinal slip in Fig. 11. The data roughly support the hypothesis that the direction of the retinal slip of the background's image is important. However, the subject clearly starts relying on extra-retinal information to account for his eye movements when the retinal slip of the image of the background still specifies the same direction of rotation as does the extra-retinal signal. This supports our notion that the extra-retinal information sets a lower limit to the eye rotation that can be specified by the retinal information (as well as indicating its direction). On the basis of the present experiments, we cannot determine whether the lower limit depends on the magnitude of the extra-retinal signal.

The lower limit manifests itself in two ways in our data. The first is that it determines the final background velocity at which subjects abandon the use of relative motion for their judgements. The second is that it determines the final target velocity settings when relative motion is abandoned. Subjects with a lower minimal acceptable velocity of eye rotation (based on extra-retinal sources) will rely on retinal information to account for their eye movements down to lower retinal background velocities. In addition they will require higher final target velocities (to maintain the perceived velocity) when the background moves at a high velocity to the right, because the eye is presumed to be moving more slowly. This can be observed in the difference between Simone's and Alex's data in Fig. 7: Simone apparently has a lower minimal acceptable velocity of eye rotation, and therefore relies on relative motion up to faster rightward background motion, and more evidently underestimates the target's velocity when the background moves even faster to the right.

Our data show that subjects do not revert to extraretinal information when they abandon the use of relative motion to account for their eye movements during velocity judgements. The final target velocity settings are higher than the initial target velocity, whereas the eye velocity (and hence the extra-retinal signal) remains the same (Fig. 9). We believe that the lower limit to the acceptable visually specified eye rotation is used in that case (replacing both visual and extra-retinal sources of eye rotation information). Subjects do not even revert to using extra-retinal signals alone when the background suddenly disappears. In this respect, a suddenly appearing background is completely different from one that suddenly disappears. In the former case (Fig. 6a), a dark background is equivalent to a static one. In the latter (Fig. 6b), it is equivalent to one that continues to move at the same speed. In the latter case, the perceived velocity during the initial part of the presentation depends on the background velocity. For example, for an initial background velocity of -2 pixels per frame, the target is initially moving at 3.5 pixels per frame relative to the background. Thus, the subject will perceive a velocity of 3.5 pixels per frame. Nevertheless, the matched velocity when the background suddenly disappears is about 1.5 pixels per frame. We suggest that this is because the internal representation of the eye velocity does not change when the background disappears.

Our suggestion is that accurate extra-retinal eve movement signals are available, and set limits to the acceptable retinal signals, but that the retinal signals dominate whenever they specify a larger rotation of the eye in the same direction as that specified by the extraretinal signal (even when the retinal signal itself temporarily disappears). A possible reason for the internal representation being very rapidly adjusted to match retinal information is that the retinal information directly provides the combined effect of rotations of the eyes, head (neck), body (waist), legs and feet (locomotion) with respect to the environment (the assumption being that we perceive motion relative to the surrounding). Presumably the extra-retinal signals only account for some of these sources. As we normally turn our body, head and eyes in the same direction when pursuing a moving object, the absence of an extra-retinal signal to specify any contribution to the rotation of the eye relative to the surrounding implies that the extra-retinal signal will underestimate the rotation. To rely on visual information when it specifies a higher velocity is therefore not illogical. Moreover, the accuracy of velocity judgements (relative to the surrounding) based on extraretinal information would always be limited by the least precise extra-retinal signal.

The reason for not always relying on the retinal signal for information on ocular rotation may be indirect. A problem with relying on motion relative to the surrounding is that it is not always evident which structures on the retina are part of the static surrounding, rather than being moving objects. Moreover, if the observer's eye is translating as well as rotating, the images of different parts of the static surrounding will move at different velocities across the retina (motion parallax). The limits imposed by the extra-retinal signal may help to determine whether a part of the background could provide reliable information on the rotation of the eye. Moreover, using the latest value based on retinal information – when the surface of which the retinal slip was being used to specify ocular rotation suddenly disappears from view - prevents us from seeing objects suddenly change velocity when this happens.

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