Motion versus position in the perception of head-centred movement

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Abstract. Observers can recover motion with respect to the head during an eye movement by comparing signals encoding retinal motion and the velocity of pursuit. Evidently there is a mismatch between these signals because perceived head-centred motion is not always veridical. One example is the Filehne illusion, in which a stationary object appears to move in the opposite direction to pursuit. Like the motion aftereffect, the phenomenal experience of the Filehne illusion is one in which the stimulus moves but does not seem to go anywhere. This raises problems when measuring the illusion by motion nulling because the more traditional technique confounds perceived motion with changes in perceived position. We devised a new nulling technique using global-motion stimuli that degraded familiar position cues but preserved cues to motion. Stimuli consisted of random-dot patterns comprising signal and noise dots that moved at the same retinal 'base' speed. Noise moved in random directions. In an eye-stationary speed-matching experiment we found noise slowed perceived retinal speed as 'coherence strength' (ie percentage of signal) was reduced. The effect occurred over the two-octave range of base speeds studied and well above direction threshold. When the same stimuli were combined with pursuit, observers were able to null the Filehne illusion by adjusting coherence. A power law relating coherence to retinal base speed fit the data well with a negative exponent. Eye-movement recordings showed that pursuit was quite accurate. We then tested the hypothesis that the stimuli found at the null-points appeared to move at the same retinal speed. Two observers supported the hypothesis, a third partially, and a fourth showed a small linear trend. In addition, the retinal speed found by the traditional Filehne technique was similar to the matches obtained with the global-motion stimuli. The results provide support for the idea that speed is the critical cue in head-centred motion perception.

1 Introduction

Global-motion stimuli have become an important tool for exploring the processing of retinal motion (Anstis et al 1998; Gros et al 1998; Hiris and Blake 1992; Newsome and Pare 1988; Scase et al 1996; Snowden and Braddick 1990; Williams and Sekuler 1984; Zanker and Braddick 1999). In a commonly used type of display, a certain proportion of picture elements (eg dots) are defined as a signal and the remainder as noise. The defining characteristic of noise is that it provides no coherent motion signal. One way to achieve this is to assign randomly chosen directions to each noise element. Conversely, signal is constrained to move in a coherent manner with a directional structure defined by the experiment in hand. The simplest and most common directional structure is motion in one particular direction. By adjusting the percentage of signal, the degree of coherence can be manipulated.

There are a number of advantageous properties of global-motion stimuli. Foremost is the ability to finely control the strength of motion signals independently of contrast and speed (Newsome and Pare 1988). This allows sensitivity measures to be made at motion levels well above threshold. Global-motion stimuli also allow position cues to be disentangled from motion cues, especially if the signal or noise status for each display element is determined at random on each frame. They are therefore well suited for use in areas where it may be important to minimise the intrusion of familiar position cues (Newsome and Pare 1988). A good example is the motion aftereffect.

As noted by many authors, adaptation gives rise to stationary objects that appear to move but do not seem to go anywhere (Anstis et al 1998; Hiris and Blake 1992; Nakayama 1985) [though see Nishida and Johnston (1999) and Snowden (1998) for evidence of positional aftereffects following motion adaptation]. Here we offer another example, namely the Filehne illusion, a term that describes the illusory motion of a stationary object in a direction opposite to a smooth-pursuit eye movement (Filehne 1922). As Stoper (1973, page 203) noted in his investigation of this illusion, most of his observers "... agree that the background moves but that it doesn't appear to change position". This is our impression as well. To measure the Filehne illusion, it would therefore seem important to isolate the phenomenal experience of motion from the apparent lack of change in perceived position.

Most previous studies of the Filehne illusion have used some form of motion nulling in which the observer controls stimulus velocity until the object appears stationary with respect to the head (Freeman 1999, 2001; Freeman and Banks 1998; Freeman et al 2000, 2002; de Graaf and Wertheim 1988; Haarmeier and Thier 1996; Mack and Herman 1973, 1978; Wertheim 1987, 1994; Wertheim and Bekkering 1992). Hence our knowledge of the Filehne illusion is built almost entirely on a technique that introduces changes in position where arguably none are experienced. This is an important issue because our understanding of the Filehne illusion is fundamental to our understanding of the perception of movement with respect to the head. To recover this head-centred movement, the visual system needs to compare a retinal motion signal with a comparison signal that encodes the motion of the eye in its orbit. By nulling the Filehne illusion we determine the point at which retinal and comparison signals are equal. The nulling technique is therefore a useful way to test various claims concerning the nature of the comparison signal, in particular whether it consists of an extraretinal signal dependent on pursuit speed alone (Freeman 2001; Freeman and Banks 1998; Mack and Herman 1973, 1978), an extraretinal signal that depends on both pursuit speed and the 'effort' required to maintain fixation (Heckmann and Post 1988; Heckmann et al 1991; Post and Leibowitz 1985; Raymond 1988), or an extraretinal signal supplemented by retinal estimates of eye velocity (Brenner and van den Berg 1994; Crowell and Andersen 2001; Haarmeier and Thier 1996; Turano and Massof 2001; Wertheim 1994).

Our experiments therefore had two goals. First, we were interested to see whether manipulating the noise in a global-motion stimulus could null the Filehne illusion. Second, we wished to determine the extent to which retinal position information influences head-centred motion perception.

In order to do so, some important methodological issues needed to be addressed. While there are various ways in which noise and signal can be constructed (eg Scase et al 1996), each is based on comparing the retinal properties of the two groups of elements. In our experiments, position cues were minimised by assigning dots to signal and noise groups at random on each frame of the display. Importantly, we intended noise and signal to differ only in their directional structure. This was achieved by moving both sets of dots at the same retinal speed and selecting the direction of each noise element at random from a rectangular distribution. This presented a problem because some of the experiments reported here involved a pursuit eye movement. To solve this, we added a constant velocity to the whole display when a pursuit eye movement was called for (see figure 1). The speed and direction of this constant was equal to the velocity of the moving fixation point. If it is assumed that the observer was able to track the fixation point accurately, then the signal and noise in eye-stationary (experiments 1 and 3) and pursuit conditions (experiment 2) was comparable. We measured pursuit eye movements in experiment 2 and found that they were reasonably accurate.

The second methodological issue concerned the retinal speed to assign to the dots. To study the motion aftereffect, one might sensibly set the base speed of the global-motion
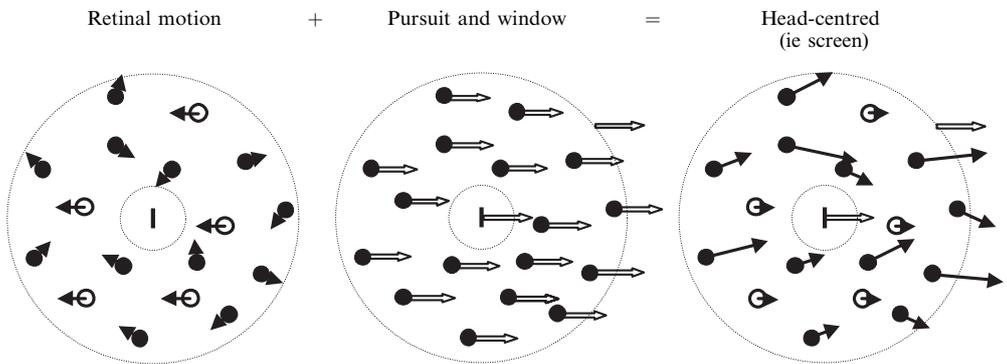
Figure 1. The global-motion stimuli used in our experiments. For clarity, signal dots are shown in white, noise dots in black, and the annulus window as dotted circles (in the actual experiments all dots were the same colour and the dotted lines were not visible). Each dot moved at a predefined base retinal speed. Noise was introduced by randomising the retinal direction of a fixed percentage of the dots (left-hand panel). During pursuit, therefore, a constant velocity was added to each dot in the display equal to that of the moving fixation point. This resulted in screen motions as shown on the right. If it is assumed that observers were able to track the stimuli accurately (see figure 4), eye-stationary and pursuit conditions contained stimuli that were retinally equivalent.

test equal to that experienced during adaptation. This ensures that the motion mechanisms stimulated during the adapt phase are the same as those probed by the test. Adjusting the percentage of noise in the test then nulls the aftereffect. In the case of the Filehne illusion, however, it is not obvious which base speed is preferable, because we are trying to balance signals that originate from quite different motion pathways. We therefore decided to investigate a range of base retinal speeds under the assumption that increasing the level of noise in a global-motion stimulus alters the size of the retinal motion signal.

According to this assumption, the null is achieved by adjusting the size of the retinal signal until it balances a comparison signal containing extraretinal (and possibly retinal) estimates of eye velocity. Presumably, retinal and extraretinal signals need a common language within which to converse and, as discussed above, it seems reasonable to suppose this is speed. On this logic, therefore, noise should affect the perceived speed of global-motion stimuli when the eyes are stationary. However, Zanker and Braddick (1999) failed to demonstrate any significant effect of noise on perceived speed in what is, as far as we are aware, the only investigation of this issue. Indeed, they found that noise affected perceived speed chiefly by affecting the visibility of coherent motion in the stimulus. As detailed later, the stimuli used here were substantially different from theirs. Nevertheless, if the effect of noise they report generalises to other types of global-motion display, the motivation for some of the ideas discussed above is called into question. For this reason, we used an eye-stationary speed-matching technique to establish whether noise affects perceived retinal speed at suprathreshold levels of coherence.

2 Experiment 1: Perceived retinal speed as a function of noise
2.1 *Method*
2.1.1 *Stimuli.* Sparse random-dot patterns (dot density $= 1.5$ dots deg^{-2}) were displayed on a computer monitor controlled by a VSG 2/3F graphics card housed in a PC. Dot position was updated at a refresh rate of 100 Hz and controlled by standard anti-aliasing techniques. Dots were defined as the centroid of a 2 by 2 pixel cluster that measured approximately 0.08 deg at the 57.3 cm viewing distance. They appeared as dim dots on a black background and were shown in a completely darkened room.

On any particular frame, the probability of a dot moving in a signal or noise direction was determined by the percentage of signal dots ('coherence strength') required. Noise direction was determined by random sampling of a rectangular distribution of all possible directions. Dot patterns were displayed through a software-generated annulus window (outer radius, 5 deg; inner radius, 1 deg). The motion of the window was yoked to the motion of the central fixation point. In the case of stationary fixation, therefore, the window did not move (experiments 1 and 3). In the pursuit conditions of experiment 2, however, the window moved with the fixation point. Under the assumption of accurate pursuit, this ensured the same region of retina was stimulated in all the experiments.

On each trial of experiments 1 and 3 a stationary fixation point was shown for 1500 ms. Within the central portion of this time period a global-motion stimulus appeared for 460 and 540 ms. The temporal jitter was selected at random from trial to trial and was used to encourage speed judgments.

2.1.2 *Procedure.* The effect of noise on perceived retinal speed was examined by a speed-matching technique. Standard and test intervals were presented sequentially in a random order and observers judged which appeared faster. The standard consisted of a global-motion stimulus with one of three base retinal speeds that covered a two-octave range (2.83, 5.66, and 11.31 deg s^{-1}) and one of five coherence strengths (20% to 100%, in 20% steps). The test interval consisted of 100% signal, the speed of which was determined by two randomly interleaved 1-up 1-down staircases. Each staircase converged on the test speed, yielding a perceived-speed match between test and standard. This was estimated from the mean speed at the last eight reversals. The 15 possible conditions were examined in separate experimental sessions. Data are based on the means of four separate speed matches.

To investigate the motion visibility issue, we also measured direction discrimination thresholds for each observer. To do this, a separate condition was run in which each trial depicted a single interval containing signal dots moving either left or right (but not both). The stimuli were identical to those just described and consisted of one of the three base speeds investigated. The direction of motion was chosen at random from trial to trial. Two randomly interleaved 1-up 2-down staircases controlled the coherence strength of subsequent trials. Direction discrimination thresholds were estimated from the mean of the last eight reversals. This yielded the coherence strength at 71% correct identification of direction. The three base retinal speeds were investigated in separate experimental sessions, each session providing two estimates of threshold.

2.1.3 *Observers.* The two authors (TCAF, JHS) and a naïve observer (SJMF) participated in the experiment.

2.2 *Results and conclusions*
In figure 2 test speed match is plotted against coherence strength for the three base speeds investigated. The three panels show the data of different observers. The results suggest an approximately linear relationship between speed match and coherence strength for all three observers. The lines show the regression of speed match on coherence strength. To a very close approximation, slopes are linearly related to base retinal speed (slopes for TCAF = 0.03, 0.064, 0.136; for JHS = 0.028, 0.057, and 0.117; and for SJMF = 0.035, 0.072, and 0.145).

The open symbols represent the direction discrimination thresholds at each of the three base speeds investigated. Threshold was well below the lowest coherence strength examined in the perceived-speed experiment and did not vary systematically with base speed. Closer inspection of raw data showed that by 5% – 10% coherence, direction discrimination was at ceiling for each observer. Hence the visibility of coherence does not seem to explain our results. This contrasts with the findings of Zanker and
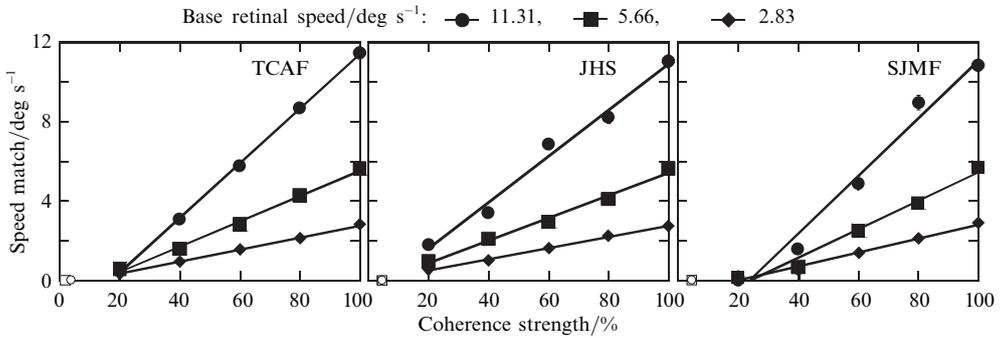
Figure 2. Effect of noise on perceived retinal speed. Each panel corresponds to a different observer. Lines indicate the regression of matched speed on coherence strength. Open symbols indicate direction discrimination threshold (71% correct detection) for each of the base speeds. Error bars are ±1 SE and are generally smaller than the symbol size.

Braddick (1999) who showed that their small effect of noise coincided with changes in the visibility of motion. Possible reasons for this discrepancy are considered in section 5.

It is tempting to suggest that these data are the result of a linear integrator that sums local velocity. In the limit, noise cancels within the integrator because it is distributed equally across all directions. Integrator output would then increase linearly with the number of signal dots and base retinal speed. This seems a reasonable first approximation to the data, though such a model fails to take into account any form of motion threshold. It also could not explain why the data of TCAF and SJMF intercept the x-axis at coherence strengths well above direction threshold.

The data of figure 2 support the claim that noise affects perceived retinal speed. Thus, global-motion stimuli could potentially be useful in nulling the Filehne illusion. More importantly, the noise effect also allows us to investigate whether the traditional method for measuring the Filehne illusion is confounded with information about retinal position. This issue can be approached in a slightly more sophisticated manner than simply presenting global-motion stimuli at some base speed and have observers adjust coherence until the target percept is nulled. We make use of the idea that altering the amount of noise in the display not only changes the 'speed' of the retinal signal but also the degree that positional cues intrude. As noise decreases, positional cues increase because signal dots are more likely to remain signal dots from frame to frame. A horizontal slice through the parameter space described in figure 2 therefore produces a set of stimuli that differ in positional content but are equal in the retinal motion signal they induce. Thus, if the Filehne illusion depends on speed alone, then any member of the set should null the illusion arising from a particular (ie fixed) pursuit speed. Alternatively, if position is important, then no single pursuit speed will exist. Each member of the set will need a different pursuit speed to achieve the null.

The most direct method for testing this idea is to take samples along a particular horizontal slice and find the pursuit speed that achieves the null. If pursuit speeds were similar over all samples then we have evidence that speed alone is the important factor. However, it is not easy to manipulate pursuit speed in this manner, because it requires psychometric functions to be probed with pursuit speed as the independent variable. The alternative is to hold pursuit speed fixed and determine the coherence that nulls a Filehne illusion over a range of retinal base speeds. One can then investigate whether the set of stimuli produced appear to move at the same retinal speed by replaying them in an eye-stationary speed-matching experiment. If they do, these stimuli define a particular horizontal slice through the space of figure 2. Under the assumption

that the set of stimuli vary in coherence, this would then allow one to conclude that positional content cannot be an important factor in the Filehne illusion.

3 Experiment 2: Nulling the Filehne illusion with noise

3.1 Methods

3.1.1 *Stimuli and procedure.* The stimuli were similar to those used in experiment 1. Each trial consisted of a single interval containing a fixation point (and window) moving at 4 deg s^{-1}. To cue the direction of pursuit, the fixation point appeared at the beginning of its sweep and remained stationary for 400 ms. It then moved for a total fixation sweep duration of 1500 ms. The global-motion stimulus appeared for between 460 and 540 ms in the central portion of the sweep. Initial and final periods of fixation-point motion occurred symmetrically in time about this and were used to encourage accurate eye movements when the dot pattern was viewed. Temporal jitter was randomly chosen from trial to trial.

Two randomly interleaved 1-up 1-down staircases controlled coherence strength. Each staircase was designed to home in on the point where the stimulus appeared stationary with respect to the head. Adjustments were made in linear steps of 4% coherence. Potentially, therefore, signal dots could all move against the eye movement (as shown on the left of figure 1) or with it. In practice, the null could only be achieved for signal dots moving against the eye, which makes sense because the null point occurs when retinal and comparison signals are opposite to one another.

The same two-octave range of retinal base speeds was investigated, this time sampled in half-octave steps. Each speed was investigated in a separate session with order of presentation determined by randomised blocks. Each experimental session yielded two estimates of the point of subjective 'stationarity'. Each observer completed at least two sessions per condition. Data reported are the mean of the final four estimates per observer.

3.1.2 *Eye-movement recording and analysis.* Eye movements were recorded for two observers (TCAF and JJN) with a video-based eye tracker (ASL Series 4000). Eye position was sampled at 50 Hz. To estimate mean eye speed across trials, each recording was low-pass filtered and differentiated with respect to time. The part of the recording coinciding with the global-motion stimuli was determined, and saccades within this located by using a velocity threshold of 40 deg s^{-1}. The routine was checked by inspecting individual velocity traces by eye. Any saccadic trials were discarded. Mean eye speed was determined over the remaining samples by first averaging within trials and then across trials. The standard errors reported in figure 4 are for the mean across trials.

3.1.3 *Observers.* The two authors (TCAF, JHS) and two naïve observers (JJN and SS) participated in the experiment.

3.2 Results and conclusions

A stimulus consisting of 0% signal appeared as an incoherent jumble that moved as a whole with fixation point and eye movement. A stimulus consisting of 100% signal appeared completely coherent, with all dots existing for an infinite lifetime. The perceived head-centred velocity of 100% signal is not so easy to describe as it depends on the relationship between retinal and comparison signals and the velocity of eye and stimulus movement (eg Freeman and Banks 1998). The traditional Filehne null point requires motion in the same head-centred direction as the eye movement but at a slower speed (eg Mack and Herman 1978). This corresponds to retinal motion against the eye, an example of which is given by the signal dots in figure 1. Our results showed that specific mixtures of signal and noise dots could null the Filehne illusion in all conditions so long as the signal dots moved in this fashion.

The actual mixtures required are shown in figure 3. Coherence strength at the point of subjective stationarity is plotted as a function of base retinal speed for the four observers studied. The data are shown on log–log axes. This emphasises the power-law relationship between base retinal speed and coherence strength. Power laws were fit by a least-squares technique. The lines depict the result. From top to bottom, the best-fitting exponents were −0.80, −0.57, −0.67, and −0.93, respectively. The only observer whose data did not fit this trend well is SS, although the discrepancy is not large. A more notable feature is the lack of data at the lowest retinal base speed for TCAF. This observer was unable to perform the task at the lowest base retinal speed. He appears to need more signal than is possible at 2.83 deg s^{-1}, as can be seen by extrapolating the curve fit back to the lower speed. Despite this, the power law describes the remaining four points extremely well.
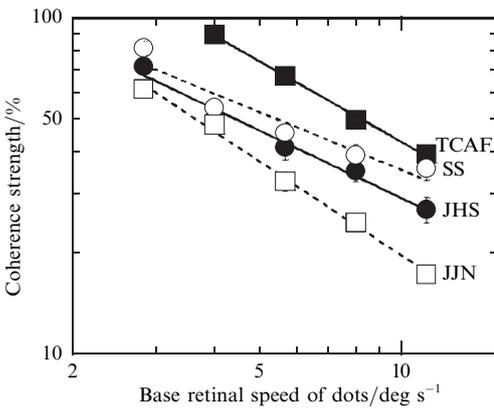
Figure 3. The percentage of signal dots ('coherence strength') needed to null the Filehne illusion for a range of base retinal speeds. Pursuit speed was 4 deg s^{-1}. Different symbols correspond to different observers. Lines are best-fitting power laws. Error bars are ±1 SE.

Eye movements were recorded for TCAF and JJN and these data are shown in figure 4. Despite the considerable psychophysical differences between these two observers there is very little difference to be found in terms of eye movement. Moreover, the eye movements are quite accurate: the thin horizontal line shows the actual speed of the pursuit target. This lends some support to our assertion that the stimuli used in our experiments were retinally equivalent whether the eyes moved (experiment 2) or not (experiments 1 and 3). The diamonds depict the eye movements made when assessing the Filehne illusion by the more traditional technique. Again the eye movements appear reasonably accurate. The reason for running this condition is discussed in experiment 3.
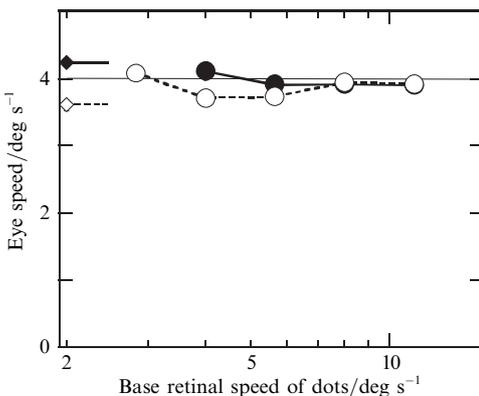
Figure 4. Eye movements for two observers nulling the global motion Filehne illusion (circles) or the more traditional Filehne illusion (diamonds)—closed symbols, TCAF; open symbols, JJN. Error bars are ±1 SE and are smaller than the symbol size.

Despite some individual differences, the data of figure 3 indicate that adjusting the coherence strength of a global-motion stimulus can null the Filehne illusion. At slow base speeds one needs a lot of signal to counteract the perceived head-centred motion, whereas at fast speeds one needs little. As suggested earlier, retinal position cues arguably decrease as coherence strength declines. At fast base speeds, therefore, stimuli at the null point are less likely to confound position and motion given the data of figure 3, whereas at lower speeds they are more likely to do so. The mere fact that one can null the illusion with low coherence levels at high base speeds does not in itself allow one to determine whether the 'traditional' Filehne illusion is influenced by position, although it does suggest that speed cues alone can be used to perform the task. What one needs to know is the perceived *retinal* speed of the stimuli defined by figure 3. To reiterate the logic described earlier, the data in experiment 2 were collected at one pursuit speed. On average, therefore, the data show the nulling coherence levels for a fixed comparison signal. If retinal and comparison signals are compared with the use of velocity codes untainted by positional information, then the stimuli defined by the curves of figure 3 should appear to move at the same retinal speed to the individual concerned. This issue was investigated in the final experiment by replaying the stimuli defined by the speed matches in figure 3 in an eye-stationary speed-matching procedure similar to that described for experiment 1.

We went one step further. In experiment 3 we used traditional motion-nulling to determine the retinal speed that made a 100% coherent stimulus appear stationary with respect to the head. To do this, we had observers null the Filehne illusion by adjusting the physical velocity of the stimulus. If speed is the major determinant of performance, the retinal speed found by the traditional technique should equal the retinal speed-match determined in the eye-stationary condition. The Appendix provides a mathematical proof of this assertion.

## 4 Experiment 3: Perceived retinal speed at the Filehne null point
4.1 *Methods*
Stimuli and procedure for the eye-stationary speed-matching condition were identical to those used in experiment 1. The standard interval consisted of a base speed and coherence strength determined by the data in figure 3.

To assess the similarities between the two measures of the Filehne illusion a more traditional nulling technique was implemented with a single stimulus interval consisting of 100% signal. The pursuit speed was the same as in experiment 2. After each trial, observers judged whether the stimulus appeared to move to the left or right of the head. Two interleaved staircases adjusted the speed of the stimulus, with a 1-up 1-down regime that converged on the speed at which the dot pattern appeared stationary.

The same four observers took part in this experiment.

4.2 *Results and conclusions*
In figure 5 speed match is plotted against base retinal speed for the coherence levels defined by figure 3. Each panel shows results for a different observer. For the two authors, there was no effect of base retinal speed on the perceived-speed match. Given that these observers knew the hypothesis of the experiment beforehand, one might argue that this is not a surprising result. The data could be interpreted as indicating observers who were able to match test stimuli to some internal standard other than those defined by results of experiment 2. However, this idea is not supported by the second condition, in which nulling the speed for the Filehne illusion was determined by the traditional technique. For both observers the nulling speed (horizontal arrows) is the same as the speed-matching data.
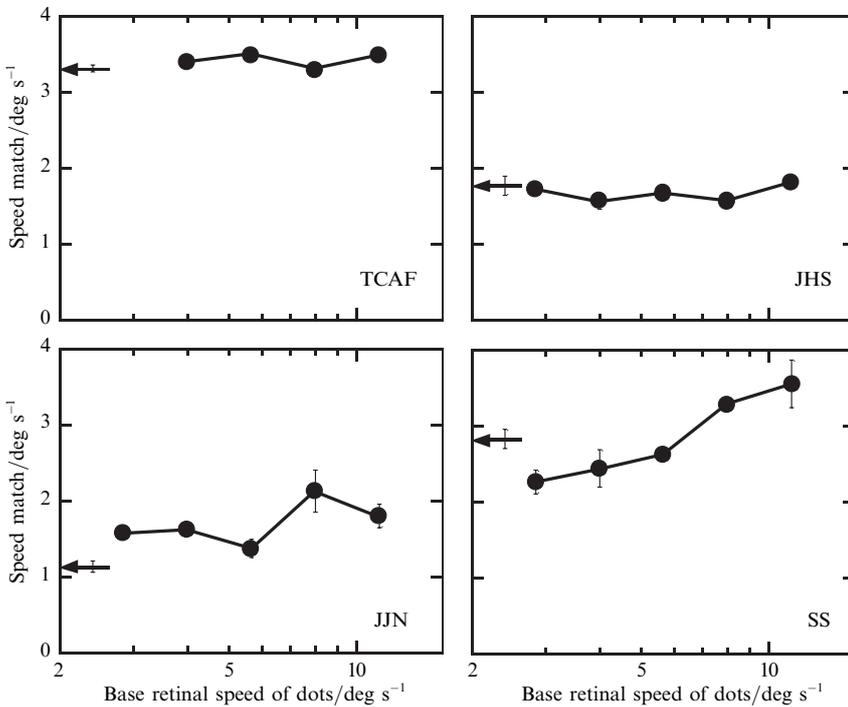
Figure 5. Matched retinal speed for the coherence strengths defined in figure 3. Each panel corresponds to a different observer. Arrows indicate the Filehne null point measured by the traditional nulling technique. Error bars are ± 1 SE.

For the observer JJN, the conclusion is a little less clear, although we would argue that her data are not substantially different from those of the authors. She shows little systematic change in speed matching across the set of stimuli. The fourth data point, however, is clearly different from the others, but it is not obvious why this should be. Certainly any inconsistencies in experiment 2 would carry over to this speed-matching condition because the stimuli are based on those data. However, JJN produced quite consistent settings in experiment 2 and the power law fit those data well. Another feature of her data is that her nulling speeds are lower than her speed matches. However, the difference is relatively small for all points apart from the fourth speed-matching condition.

Observer SS presents the bigger puzzle. There is a clear, almost linear increase in speed matches for this observer. It is worth pointing out that this trend is small in comparison to the two-octave range of base speeds investigated, but nevertheless her data do not support the idea that the stimuli nulling the Filehne illusion appear to move at the same retinal speed. One interpretation is that SS was influenced by positional information when nulling the Filehne illusion. This might also help explain why SS's settings show the greatest departure from the power-law relationship found in experiment 2. It is also worth noting that at higher base speeds there is considerably more 'activity' in a global-motion stimulus because noise dots move at faster speeds. Thus, an alternative interpretation is that SS had difficulty in ignoring the greater activity and responded accordingly when matching retinal speed in experiment 3. This may have influenced JJN's data as well, though in a less consistent manner.

Another peculiar feature of SS's data is that her nulling speed lies in the centre of the linear trend. We find this curious because the stimulus used to determine nulling speed contained 100% signal and so is most similar (in terms of coherence) to the

global-motion stimulus with the lowest base speed. It is therefore surprising to find so marked a difference.

In conclusion, the data of two of the observers provide extremely good evidence for the importance of speed when nulling the Filehne illusion. The data of one of the naïve observers provide partial support, whereas the data of the other naïve observer do not. Experiment 3 therefore provides some support for the idea that speed is the important commodity in head-centred motion perception.

5 General discussion

Our principal aim was to investigate the Filehne illusion with a technique that minimised the influence of familiar position cues. There were two reasons for this. Anecdotally, the illusory motion that results from eye pursuit over a stationary object is not accompanied by any powerful sense of changing position (eg Stoper 1973). It would therefore seem important to isolate perceived motion from changes in perceived position when measuring the Filehne illusion. Unfortunately, the nulling technique most commonly used confounds motion and position, echoing problems identified in attempts to null the motion aftereffect by adjusting the physical speed of a stimulus (Anstis et al 1998). Global-motion stimuli circumvent this problem by degrading the salience of familiar position cues while allowing the strength of the motion signal to be varied. The second reason is that the Filehne illusion is thought to result from a mismatch between retinal and comparison signal size. Whilst there is still some debate whether the latter is purely extraretinal, all current models of head-centred motion perception assume that it is retinal and comparison velocities that are compared. By using global-motion stimuli we were able to investigate this assumption directly. Noise affects perceived retinal speed (experiment 1) and can be used to null the Filehne illusion for a given retinal base speed (experiment 2). In experiment 3 we asked whether the stimuli found at the null point appeared to move at the same retinal speed. Because these stimuli differ in coherence and therefore the intrusion of positional cues, finding that they appeared to move at the same speed would suggest that speed is the primary factor in head-centred motion perception. We also compared speed matches to nulling speeds determined by the traditional motion-nulling technique because these too should be the same. The data from two observers supported the hypothesis, the data from one gave partial support, and the data from the fourth did not. Position cues do not seem to influence the perception of head-centred motion perception in some observers, whereas for others it is possible that they do. If the influence of positional cues varies from observer to observer, this might help explain why some studies report considerable individual differences in nulling speeds determined by the traditional technique (eg Haarmeier and Thier 1996).

The results of experiment 1 are at some odds with those reported by Zanker and Braddick (1999). We found large effects of noise on perceived speed that did not coincide with changes in visibility. Zanker and Braddick argued quite sensibly that their results might reflect a particular strategy adopted by observers, namely labelling less visible motion as slower in a forced-choice experiment. Though we do not disagree with the suggestion per se, we do find it wanting with respect to the results of their final experiment. There they used comparable stimuli to those used here, albeit dark dots on a light background, but introduced noise by altering the individual lifetime of dots. This is similar to the manipulation used by Treue et al (1993), who showed that altering temporal structure in this way produced changes in perceived speed at slow (4 deg s^{-1}) but not fast dot-pattern speeds (12 deg s^{-1}). They argued that, if perceived speed was determined by the relative activity between high- and low-temporal-frequency channels, then the lack of effect at high speeds could be explained by the activity that these speeds induce in the high-frequency channel. At slow speeds,

decreasing dot lifetime increases activity in a high-temporal-frequency channel and so acts to raise perceived speed. However, at high base speeds, that channel is already active and so adding more high-frequency noise should have less effect. It is possible, therefore, that Zanker and Braddick found little effect of temporal jitter because they used a relatively high speed of 9.2 deg s^{-1}. This suggestion is made more pertinent when one notes that Zanker and Braddick did not report discrimination data for this particular noise type. It is therefore unclear to what extent motion visibility impacted on the particular finding of theirs.

The discrepancy between the present results and Zanker and Braddick's first two experiments is not so easy to explain. In those experiments they used relatively brief stimuli consisting of densely packed 'Julesz' patterns containing a central region moving at 9.2 deg s^{-1} and surrounded by dynamic noise. One might therefore explain the discrepant findings in terms of the marked differences between the stimuli used in the two studies because, for instance, density (Watamaniuk et al 1993) and brightness levels (Gegenfurtner et al 2000) are known to affect perceived speed. However, this does not easily explain why noise has little effect above threshold in their experiments, but a considerable effect in ours. Stimulus duration might be an important factor. Differences in the type of noise might also contribute. Zanker and Braddick introduced noise into the central region by randomly switching pixels from light to dark (or vice versa) as the display refreshed. Noise level was determined by the probability that a given pixel would remain correlated in the next frame. This uncorrelated twinkle is therefore quite different from the incoherent motion used here. In particular, their decorrelating method imposes noise containing a wide range of speeds. Our method, on the other hand, confines signal and noise to move at the same speed. It is possible that we find greater effects of noise because it is concentrated within the same spatio-temporal pass band as the signal that the observer is asked to judge.

The experiments reported here show that noise can have a significant effect on the perceived speed of global-motion stimuli. They demonstrate that these stimuli are a viable tool for exploring the interaction between retinal and extraretinal signals. Finally, the experiments provide some evidence that, unlike studies of the motion aftereffect, the more traditional method of nulling the Filehne illusion does not fall foul of changes in perceived position.

References
Anstis A, Verstraten F A J, Mather G, 1998 "The motion aftereffect" *Trends in Cognitive Sciences* **2** 111 – 117
Brenner E, Berg A V van den, 1994 "Judging object velocity during smooth-pursuit eye-movements" *Experimental Brain Research* **99** 316 – 324
Crowell J A, Andersen R A, 2001 "Pursuit compensation during self-motion" *Perception* **30** 1465 – 1488
Filehne W, 1922 "Über das optische Wahrnehmen von Bewegungen" *Zeitschrift für Sinnesphysiologie* **53** 134 – 145
Freeman T C A, 1999 "Path perception and Filehne illusion compared: model and data" *Vision Research* **39** 2659 – 2667
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** 941 – 945
Freeman T C A, Banks M S, Crowell J A, 2000 "Extraretinal and retinal amplitude and phase errors during Filehne illusion and path perception" *Perception & Psychophysics* **62** 900 – 909
Freeman T C A, Naji J J, Margrain T H, 2002 "Head-centred motion perception in the ageing visual system" *Spatial Vision* (in press)

Gegenfurtner K R, Mayser H M, Sharpe L T, 2000 "Motion perception at scotopic light levels" *Journal of the Optical Society of America A* **17** 1505 – 1515

Graaf B de, Wertheim A H, 1988 "The perception of object motion during smooth pursuit eye-movements—adjacency is not a factor contributing to the Filehne illusion" *Vision Research* **28** 497 – 502

Gros B L, Blake R, Hiris E, 1998 "Anisotropies in visual motion perception: a fresh look" *Journal of the Optical Society of America A* **15** 2003 – 2011

Haarmeier T, Thier P, 1996 "Modification of the Filehne illusion by conditioning visual stimuli" *Vision Research* **36** 741 – 750

Heckmann T, Post R B, 1988 "Induced motion and optokinetic afternystagmus: parallel response dynamics with prolonged stimulation" *Vision Research* **28** 681 – 694

Heckmann T, Post R B, Deering L, 1991 "Induced motion of a fixated target—influence of voluntary eye deviation" *Perception & Psychophysics* **50** 230 – 236

Hiris E, Blake R, 1992 "Another perspective on the visual motion aftereffect" *Proceedings of the National Academy of Sciences of the USA* **89** 9025 – 9028

Mack A, Herman E, 1973 "Position constancy during pursuit eye movement: An investigation of the Filehne illusion" *Quarterly Journal of Experimental Psychology* **25** 71 – 84

Mack A, Herman E, 1978 "The loss of position constancy during pursuit eye movements" *Vision Research* **18** 55 – 62

Nakayama K, 1985 "Biological image motion processing: a review" *Vision Research* **25** 655 – 660

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** 2201 – 2211

Nishida S, Johnston A, 1999 "Influence of motion signals on the perceived position of spatial pattern" *Nature* **397** 610 – 612

Post R B, Leibowitz H W, 1985 "A revised analysis of the role of efference in motion perception" *Perception* **14** 631 – 643

Raymond J E, 1988 "The interaction of target size and background pattern on perceived velocity during visual tracking" *Perception & Psychophysics* **43** 425 – 430

Scase M O, Braddick O J, Raymond J E, 1996 "What is noise for the motion systems" *Vision Research* **36** 2579 – 2586

Snowden R J, 1998 "Shifts in perceived position following adaptation to visual motion" *Current Biology* **8** 1343 – 1345

Snowden R J, Braddick O J, 1990 "Differences in the processing of short-range apparent motion at small and large displacements" *Vision Research* **30** 1211 – 1222

Stoper A E, 1973 "Apparent motion of stimuli presented stroboscopically during pursuit movement of the eye" *Perception & Psychophysics* **13** 201 – 211

Treue S, Snowden R, Andersen R A, 1993 "The effect of transiency on perceived velocity of visual patterns: a case of 'temporal capture'" *Vision Research* **33** 791 – 798

Turano K A, Massof R W, 2001 "Nonlinear contribution of eye velocity to motion perception" *Vision Research* **41** 385 – 395

Watamaniuk S N J, Grzywacz N M, Yuille A L, 1993 "Dependence of speed and direction perception on cinematogram dot density" *Vision Research* **33** 849 – 859

Wertheim A H, 1987 "Retinal and extraretinal information in movement perception: how to invert the Filehne illusion" *Perception* **16** 299 – 308

Wertheim A H, 1994 "Motion perception during self-motion—the direct versus inferential controversy revisited" *Behavioral and Brain Sciences* **17** 293 – 311

Wertheim A H, Bekkering H, 1992 "Motion thresholds of briefly visible stimuli increase asymmetrically with age" *Vision Research* **32** 2379 – 2384

Williams D W, Sekuler R, 1984 "Coherent global motion percepts from stochastic local motions" *Vision Research* **24** 55 – 62

Zanker J M, Braddick O J, 1999 "How does noise influence the estimation of speed" *Vision Research* **39** 2411 – 2420

Appendix

We show here that the retinal velocity nulling the traditional Filehne illusion (R_{null}) must equal the test velocity (R_{match}) yielding a perceived speed match between a 100% coherent test stimulus and the global-motion stimuli found at the null points in experiment 2. Head-centred velocity (H) is the sum of retinal velocity (R) and pursuit velocity (P). Perceived head-centred velocity is therefore the sum of a retinal signal encoding R and a comparison signal encoding P:

$$H' = R' + P'. \tag{A1}$$

To null the Filehne illusion, observers adjust the retinal velocity of the stimulus until $H' = 0$, at which point, from (A1):

$$R' = -P'. \tag{A2}$$

The global Filehne (experiment 2) and the traditional Filehne (experiment 3) illusions gave rise to the same comparison signal because the same pursuit speed was used. From (A2):

$$R'_{\text{g}} = R'_{\text{t}} = -P', \tag{A3}$$

where R'_{g} is the retinal signal in the global Filehne illusion and R'_{t} is the retinal signal in the traditional Filehne illusion. The latter must be some function of retinal velocity R_{null}, so according to (A3):

$$R'_{\text{g}} = f(R_{\text{null}}). \tag{A4}$$

In experiment 3, speed matches were obtained between global-motion stimuli and a 100% coherent test. At the match point:

$$R'_{\text{g}} = R'_{\text{match}}, \tag{A5}$$

where R'_{match} is the retinal signal encoding the motion of the test.

Given that R'_{match} must be some function of retinal velocity, then according to (A5):

$$R'_{\text{g}} = f(R_{\text{match}}). \tag{A6}$$

The function f is the same in (A4) and (A6) because nulling and matching stimuli, R_{null} and R_{match}, were both 100% coherent. Thus, (A4) and (A6) can be combined to eliminate R'_{g}, in which case:

$$R_{\text{null}} = R_{\text{match}}, \tag{A7}$$

with f assumed to be a monotonic function.

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