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Evidence for flow-parsing in radial flow displays

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Abstract

Retinal motion of objects is not in itself enough to signal whether or how objects are moving in the world; the same pattern of retinal motion can result from movement of the object, the observer or both. Estimation of scene-relative movement of an object is vital for successful completion of many simple everyday tasks. Recent research has provided evidence for a neural *flow-parsing* mechanism which uses the brain's sensitivity to optic flow to separate retinal motion signals into those components due to observer movement and those due to the movement of objects in the scene. In this study we provide further evidence that flow-parsing is implicated in the assessment of object trajectory during observer movement. Furthermore, it is shown that flow-parsing involves a global analysis of retinal motion, as might be expected if optic flow processing underpinned this mechanism.

Keywords: Optic flow; Motion processing; Self movement; Object movement; Psychophysics

1. Introduction

When an observer moves through the world, images of objects in the visual scene drift across the retina. The resultant structured patterns of global image motion are commonly referred to as *optic flow*. Extensive psychophysical research has demonstrated the sensitivity of the primate brain to patterns of optic flow. Further neurophysiological and imaging research has identified area MT+, as a candidate neural substrate for this sensitivity (for a review of optic flow processing see Lappe, Bremmer, & van den Berg, 1999).

Due to the work of J.J. Gibson, sensitivity to optic flow is associated primarily with the visual guidance of locomotion (Gibson, 1950, 1958; but see Mollon, 1997 regarding a prior claim; and Rushton, Harris, Lloyd, & Wann, 1998 for a challenge to this association), although it has been shown to have other roles, for example in stabilisation of gaze (e.g. Bussetini, Masson, & Miles, 1997; Miles, 1997), updating perceived direction (e.g. Lepecq, Jouen, & Dubon, 1993) and maintenance of posture (e.g. Lee & Aronson, 1974). We have recently a proposed a new role for optic flow in the assessment of scene-relative object trajectory during self movement. Under the 'flow-parsing' hypothesis of Rushton and Warren (2005), the brain uses its sensitivity to patterns of optic flow to identify components of retinal motion that are due to self-movement; these components can then be separated out, isolating retinal motion arising from movement of objects within the scene and supporting the estimation of object trajectory (Rushton, Bradshaw, & Warren, 2007; Rushton & Warren, 2005; Warren & Rushton, 2007).

In our previous work we exploited distance-dependent geometric relations between self-movement and the resultant retinal flow to test for flow-parsing (Rushton & Warren, 2005; Rushton et al., 2007; Warren & Rushton, 2007. Here we manipulate the structure and symmetry of a radial flow field and assess the impact on a vertically moving probe object placed in the centre of the field.

In-line with previous work, the approach we have taken is to look for evidence of 'subtraction' of global flow components. We have deliberately placed subtraction in quotation marks because thinking of a literal subtraction process makes it easier to understand our predictions, we do not mean to suggest that the motion is literally subtracted

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out. The process we describe could be re-described as a pattern of activation within a complex motion filter (e.g. see McLeod, Driver, & Crisp, 1988; Perrone, 1992). We place a probe dot in the middle of a background dot flow display and assume that the probe's perceived trajectory will be influenced by the subtraction of global components of motion that the brain attributes to self-movement. We then change the structure of the background dot motion and test to see whether changes in perceived probe trajectory are commensurate with flow-parsing.

Stationary human observers *do* display behaviour consistent with flow-parsing when presented with 2D stimuli containing motion information signalling an eye rotation. However, the relevant data is not presented in terms of flow parsing. Consider a stationary observer viewing the pattern of retinal motion arising from a leftward eye rotation. In this situation, images of stationary objects within the scene move to the right across the retina with a common angular speed directly proportional to the speed of the simulated eye rotation. Under perfect flow-parsing, the resulting field of motion should be recognised as retinal flow arising from eye movement and a common motion vector subtracted across the whole field; a process which would leave zero resultant motion. If a probe dot is viewed together with this field of motion then it should also be subject to the same motion subtraction. If the dot is stationary on the retina, then the result of the subtraction should be a net perceived leftward motion of the probe against the background dots. This phenomenon has been described numerous times in the literature and is commonly referred to as induced motion (e.g. Duncker, 1929; see Reinhardt-Rutland, 1988 for a review).

For our flow-parsing proposal to be more than a relabelling of a previous described effect (induced motion), it is necessary to make and test a novel prediction: If the brain subtracts the global components of retinal motion that can be attributed to self-movement then it should do so during forward movement. Consider a scenario in which the observer is moving forwards and there is an object ('probe') directly ahead. If a component of motion due to self-movement is identified and parsed out then the subtraction motion field will have a radial structure and the subtraction field will be zero at the centre. Since the probe occupies this position it should be unaffected by the parsing process—its perceived trajectory should not be changed.

What would we expect if the radial flow pattern were not symmetric (e.g. if there were more objects in the left half of the field than the right)? Asymmetry should not influence the brain's ability to recognise that the flow field is radial. Therefore, there should be no influence on the parsing process, and in this scenario the perceived probe trajectory should still be unaffected by asymmetry. This is our first prediction.

Now, consider what would happen if we introduced some noise into a symmetric radial flow field (e.g. by perturbing the speed and direction of the dots making up the radial flow field and consequently decreasing its consistency with forwards movement). If the noisy radial flow field is symmetrical then a forward translation component should still be identified and extracted and due to symmetry the residual should have no net motion. So, in this scenario, we expect that the perceived probe trajectory should still be unaffected by the parsing process. This is our second prediction.

Consider now, however, the case in which the flow field is asymmetric and noise is introduced. For illustration, assume that there are more objects in the left of the field than the right, and that noise is introduced by 'shuffling' the location of a proportion of the velocity vectors (Fig. 1). As a consequence the same motion vectors are present but some of their locations in the visual field are not compatible with forwards translation. Therefore when the parsing process occurs, some of the retinal motion will no longer be identified as being due to forward translation. Because there are more objects on the left of the field than the right, and because the objects on the left are moving

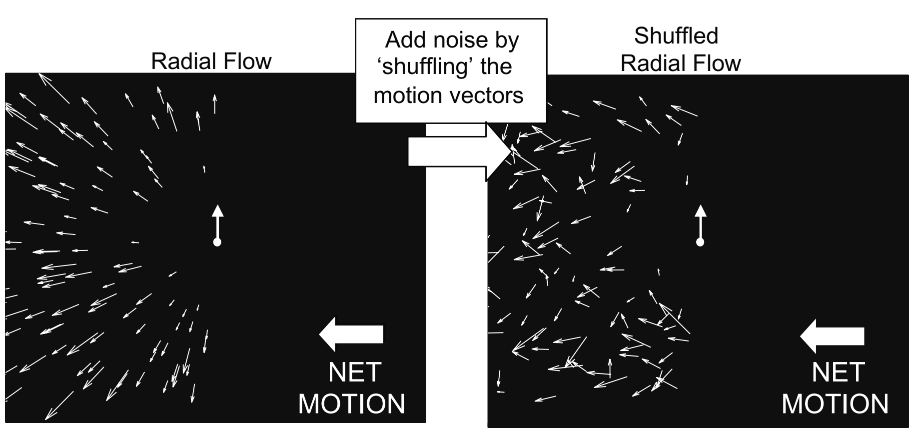

Fig. 1. Schematic illustration of the stimuli used in the two experiments undertaken. In the left hand panel an asymmetric (more dots on the left hand side than the right hand side) radial flow pattern is shown. Observers assessed the trajectory of a small probe object moving upwards along a short linear path. In the right hand panel noise has been added to the radial flow display: the 2D velocity vectors of the asymmetric flow pattern have been 'shuffled' (i.e. the on screen locations of the velocity vectors is swapped).

leftwards (after the introduction of motion noise, this will still be true on average), this remaining motion will have a net leftward motion. A net motion is compatible with a gaze rotation, in this case a rightward gaze rotation. Therefore, under the parsing account, leftward motion should be subtracted from the probe object (and every other object in the field) and so the probe should be perceived as moving rightwards—or in the direction opposite the highest concentration of objects. This is our third prediction.

To pull these three predictions together: under the flow-parsing hypothesis we predict that when a probe object is placed in a radial flow field there will be an interaction between the symmetry of the flow field and the amount of noise present.

For comparison, it is useful to generate an alternative set of predictions. Consider a classic induced motion account; under most of the common explanations of induced motion, provided that target and background (inducing) elements are confined to a plane, the strength of the effect depends upon the net motion of the background. If the radial flow field is symmetrical then there is no net motion across the visual field. Consequently, under this account the probe object should be unaffected by the motion of the other scene objects. This is the same as the prediction from the flow-parsing account. If, however, the radial flow field is not symmetric then there will be a net motion across the visual field (in both the shuffled and unshuffled scenarios). Therefore, in this situation the probe object should undergo an induced motion, opposite to the net motion, or in the direction opposite to the majority of the inducing background objects. This is the first difference in the predictions from the flow-parsing and induced motion accounts (counter prediction 1). Furthermore, the amount of noise in the flow field should have no influence on the perceived trajectory. This is the second difference in the predictions (counter prediction 2). Considering the predictions as a whole, the induced motion account contradicts the flow parsing account prediction of an interaction between noise and symmetry.

In our experiments we test the predictions described above explicitly by varying the proportion of dots on the left and right of the display (the symmetry factor) and ‘‘shuffling’’ the position of a percentage of the dots in the two hemi-fields (the noise factor).

2. Methods

2.1. Observers

Six observers participated in experiments 1 and 2. All were staff or students within the School of Psychology at Cardiff University. One of the observers in Experiment 1 was an author and two observers in Experiment 2 were authors, the remainder were naive about the purpose of the experiment. All observers had normal or corrected to normal vision. Observers' participation in the experimental studies was regulated by the Ethics Committee of the School of Psychology, Cardiff University.

2.2. Stimulus and display

In the experiments reported, we generated patterns of retinal motion through *simulation* of self-movement. At all times the observer remained stationary (with the head on a chin rest). Stimuli were viewed on a 22″ CRT with a 100 Hz refresh rate and at a viewing distance of 0.75 m. At this distance the horizontal extent of the screen subtended around 30 deg arc.

The stimuli consisted of a cloud of 300 limited lifetime (approximately 200 ms) moving dots. Each dot was first given a random 2D screen location (this led to a constant dot density over the screen). It was then assigned a random distance in the range 0.5–1.5 m from the observer. From the 2D screen coordinate and the distance the 3D position of the probe was calculated under perspective projection. The appropriate screen velocity of the dot was calculated based upon its 3D position and a forward translation speed of 10 cm/s. On asymmetric trials, the proportion of dots on the left and right hand side was manipulated. On shuffled trials the 2D onscreen locations of a proportion of the dots were switched so that the same motion components were present, however, the velocity vectors were now at inappropriate positions in the display to signal forwards translation (see Fig. 1).

A probe dot was presented simultaneously with the dot displays and moved in one of five linear directions, which varied by 0°, ±15° or ±30° about vertical in a fronto-parallel plane. Changing the direction of the probe from trial to trial made it very difficult for observers to tell which condition they were currently viewing since it was impossible to assess whether the perceived movement of the probe was real or illusory The probe moved at a constant (screen) speed of 1 cm/s (0.76 deg/s) for 1.2 s starting at the centre of the screen, which coincided with the focus of expansion of the radial flow field. The dots and the probe were drawn in red because it has the fastest phosphor and a red filter was placed in front of the screen to increase contrast.

2.3. Experiment 1 vs. Experiment 2

Experiment 2 was identical to Experiment 1 except for one difference in the stimuli. In the second experiment the probe was surrounded by a mask of diameter 8 cm (around 6.1 deg) which moved with the probe and occluded any adjacent background motion.

2.4. Procedure

In all experiments, at the beginning of each trial observers saw a small fixation cross in the centre of the screen for 0.75 s (75 frames). Subsequently, observers saw the dot display and the moving probe simultaneously for 1.2 s (120 frames) and the observers were instructed to track the moving probe dot.[1]

Using a modified version of the *tilt-test* (Heckmann & Howard, 1991; Howard & Childerson, 1994), observers were then asked to report the perceived 2D (in a fronto-parallel plane) trajectory of the probe. Immediately after presentation of the stimulus the observer saw onscreen axes (a cross defined by horizontal and vertical lines) with an adjustable 'paddle' passing through the origin (see Fig. 2). To change the angle of the paddle observers turned a knob linked to a linear potentiometer. The axes and the adjustable paddle were always presented in the plane of the screen.

[1] We did not record eye movements during the experiment; however, we have no reason to believe that observers chose to make the task more difficult for themselves by looking at objects other than the target. Furthermore, moving the eyes would have generated additional flow components in the image, however, these would have been be parsed out under the flow-parsing hypothesis. Perhaps most importantly, if observers did choose to look around the display, it is difficult to imagine a pattern of behaviour that might have led to the systematic results that were obtained.

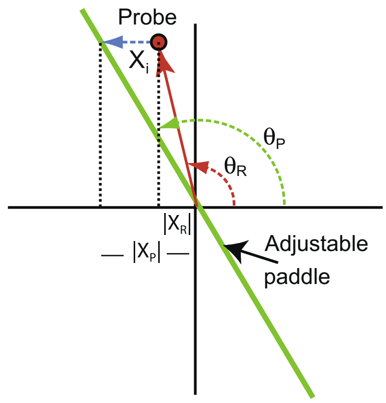

Fig. 2. Schematic example of adjustable paddle illustrating coordinate system and sign convention. Absolute angles are measured relative to the X-axis in a counter-clockwise direction. The quantity X_i which characterises the error in observer setting is also shown.

2.5. Analysis

Observer responses are coded as an angular measure θ_i. This quantity is derived from the illusory or "induced" horizontal motion seen by observers but is deliberately converted back to an angular quantity since, in this experiment, observers made angular adjustments (the results are similar when the horizontal motion is considered). The coordinate system and sign conventions used are shown in Fig. 2.

Angles describing 'real' physical probe trajectory, θ_R, and perceived trajectory, θ_P, are defined relative to the X-axis with counter-clockwise (CCW) taken as positive (+ve). It was assumed that the simulated horizontal observer movement did not interfere with the perceived vertical motion of the probe (i.e. the perceived and physical vertical motion were identical). Consequently, any difference between the perceived and physical angles was due to an additional perceived horizontal component of probe motion X_i. Using simple trigonometry, given the distance, r, travelled by the probe, this quantity can be calculated as:

$$X_i = X_R - X_P = r\sin(\theta_P - \theta_R)/\sin(\theta_P) \quad (1)$$

For the sake of consistency with angular measures (which increase in a CCW direction) X_i is defined as positive to the left. In order to make the measurement commensurate across the different probe direction conditions it was calculated as follows. The component X_i was transformed back to an angular quantity θ_i, as if it had been induced relative to a physical probe motion which was purely vertical:

$$\theta_i = \tan^{-1}(X_i/r) \quad (2)$$

This quantity also increases in a CCW direction but is now measured relative to the Y-axis. Note that for the condition in which the physical probe trajectory really is vertical ($\theta_R = \pi/2$), Eq. (1) and (2) reduce to $\theta_i = \theta_P - \pi/2$, as required. In the results that follow, θ_i is referred to as the induced tilt.[2]

3. Experiment 1 results and discussion: Evidence for flow-parsing using 2D radial flow displays

In Experiment 1, observers judged the perceived probe trajectory in the presence of 15 different background motion conditions. The asymmetry in the number of dots on the left and right hand side of the field was varied over five levels (10%, 30%, 50%, 70% and 90% of dots on the right hand side of the field). At each of these five levels the percentage of dots shuffled was varied over three levels (0%, 50% and 100% of dots shuffled). In the 0% condition, the stimulus was a standard radial flow field, in the 100% condition the stimulus contained the same motion vectors as a radial flow field but the locations of all the vectors were shuffled. Observers reported the perceived trajectory of a central probe object moving over a short linear path.

The results of Experiment 1 are shown in Fig. 3. Fig. 3a illustrates mean induced tilts obtained for a typical observer (RAC) together with linear fits to the perceived trajectory data in the three noise conditions (solid line—0% noise, dashed line—50% noise, dot-dash line—100% noise). Each induced tilt value is the average of 15 (no. probe angles x no. repetitions) data points. Group mean data for the composite observer are also shown (marked 'comp'). In Fig. 3b the data are shown for each of the physical probe directions separately. Note, in particular, that trends in the data are similar across probe directions within a noise condition. The slope parameters of the linear fits to the data are presented separately for each of the probe direction conditions (averaged over the 6 observers) in Table 1. Within a noise condition the slopes are similar across the different probe directions conditions. In the remainder of this paper results are averaged over probe direction conditions.

The results appear consistent with the predictions of the flow parsing hypothesis as discussed in the introduction. Specifically, the perceived probe trajectory is unaffected by symmetry (approximately flat solid lines in Fig. 3) in the 0% conditions (prediction 1). When the flow field is symmetric, there is no influence of the percentage of noise on the perceived trajectory of the probe (prediction 2). When the flow field is asymmetric and there is noise in the display, the probe is seen to move in the direction opposite the highest concentration of dots (prediction 3).

A two-way repeated measures ANOVA was conducted to formally test these results. In agreement with the predictions of the flow parsing hypothesis there was a significant interaction between the amount of noise present and level of symmetry ($F(8,40) = 34.14$, $p < 0.001$).

The results contradict the classic induced motion account predictions: there is no induced motion when the field is asymmetric but the noise is zero (contradicting counter prediction 1) and the induced motion varies with the percentage of noise in the asymmetric conditions (contradicting counter prediction 2).

For each observer seperately and for the composite observer, Table 2 shows the gradients to 2 decimal places (d.p.) of the linear fits to the data from this experiment. Note that for all observers and the composite observer, the gradient is close to zero in the 0% noise condition. The gradient increases significantly (by an order of magnitude) in the 50% noise condition and increases further for

[2] N.B. this analysis has been repeated using the raw angular difference between the real and perceived angle of probe motion ($\theta_R - \theta_P$). The results were very similar; the average difference in the calculated means for each condition was around 5%. Similarly the average difference in the fitted parameters was around 5%.

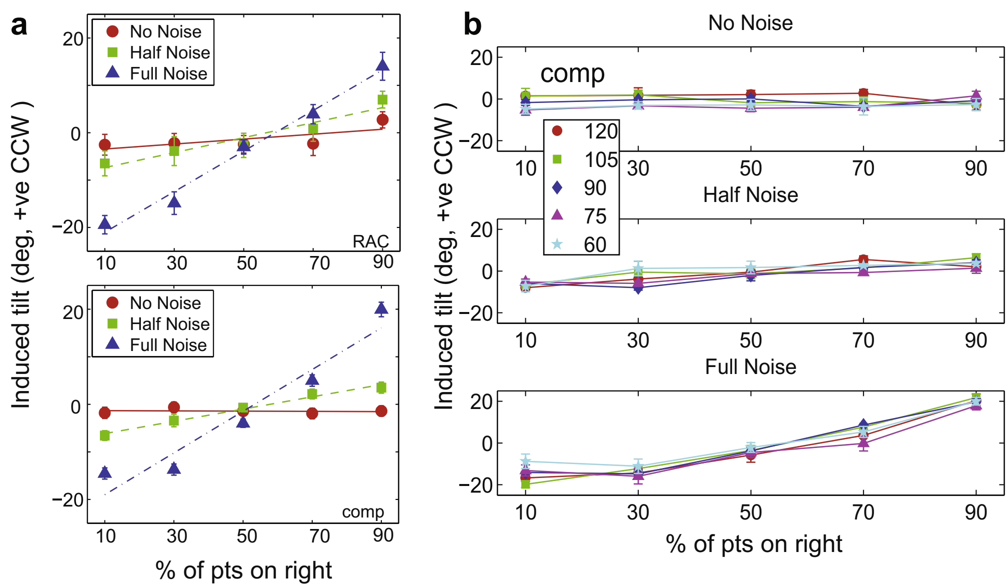

Fig. 3. Results of the first experiment: (a) The induced tilt measure is shown for a typical individual and the composite observer obtained by averaging over the six observers. The straight lines represent linear fits to the data (solid line, 0% noise; dashed line, 50% noise; dash-dot line, 100% noise). Error bars denote ±1 SE. (b) The same data shown separately for each of the physical probe directions.

Table 1
Average (over 6 participants) gradients of linear fits to perceived trajectory in Experiment 1 for the 5 different probe directions

Noise	−30 deg	−15 deg	0 deg	15 deg	30 deg
None	−3.81	−5.08	−0.71	6.40	1.95
Half	14.78	13.88	14.83	9.29	11.59
Full	46.07	51.60	45.51	38.97	37.04

the 100% noise condition. Consequently, as the consistency of the stimulus with a radial flow field is systematically degraded the tendency to perceive illusory motion is increased. We take these results as further evidence that the perception of object movement during self-movement relies fundamentally on the type of optic flow components present in the retinal image.

4. Experiment 2 results and discussion: Flow-parsing persists when local relative motion is removed

If the mechanism which drives the perception of 'illusory' motion in such displays is local in nature then it should pool motion information from adjacent background objects only. To test for this possibility or demonstrate that this mechanism is not just local in nature, but also involves some global processing (as might be expected if optic flow processing were implicated in the observed results), we ran a variant of the previous experiment. We removed all the dots within 4cm (approximately 3 deg) of the probe dot. Note that in this experiment we are simply interested in ruling out an explanation which involves only a local motion contrast mechanism rather than pinpointing the size of the mask which completely destroys the observed effect (although see discussion of this experiment below). If after removal of the nearest dots surrounding the probe the results indicate a difference between perceived and physical trajectory in the different noise conditions then local processes must be determining performance in this task. Alternatively if the effect persists then there must be some global processing taking place as might be expected if an area with large receptive fields such as MT+ were involved in this process.

This experiment also served as a useful control; due to the shuffling process the motion of the dots immediately surrounding the probe is likely to be different in the radial flow and non-radial flow conditions. Under a local motion contrast account, this difference might drive the observed results.

Fig. 4 shows the results obtained in this experiment for a typical observer and the composite observer. Once again each induced tilt value is calculated as the average of 15 data points. The results are strikingly similar to those obtained in the first experiment (Fig. 3). Table 3 shows the fitted gradients for the six observers in this experiment and the associated composite observer. The gradients are similar to those seen in the previous experiment; when none of the motion vectors are shuffled the gradients are close to zero, however, as the proportion of shuffled dots increased the gradients increase by an order of magnitude (see Table 3).

Once again these results seem consistent with the predictions of the flow parsing hypothesis. A two-way repeated measures ANOVA was conducted to formally test these results. In agreement with the predictions of the flow parsing hypothesis there was a significant interaction between the amount of noise present and level of symmetry ($F(8,40) = 29.32$, $p < 0.001$).

These results demonstrate that the perceived trajectory is not driven by a purely local mechanism and it argues against a simple local motion contrast account. Further-

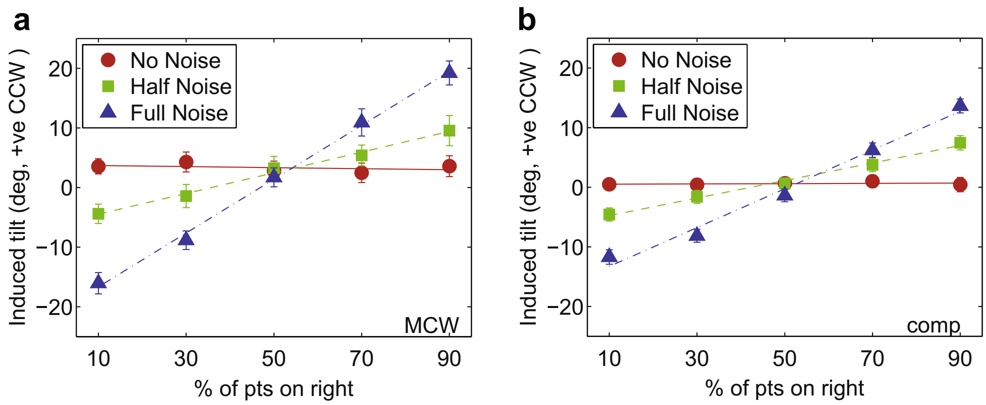

Fig. 4. Results of the second experiment in which a mask was placed around the probe: (a) The induced tilt measure is shown for a typical individual and the composite observer obtained by averaging over the six observers. The straight lines represent linear fits to the data (solid line, 0% noise; dashed line, 50% noise; dash-dot line, 100% noise). Error bars denote ±1 SE. (b) The data for the composite observer.

Table 2
Gradients of linear fits to perceived trajectory data in Fig. 3

Observer	Noise condition		
	0%	50%	100%
PAW	0.02	0.10	0.29
JJN	−0.05	0.11	0.35
BLM	0.00	0.13	0.44
CHR	0.00	0.8	0.50
LXG	−0.04	0.20	0.62
RAC	0.05	0.15	0.42
COMP	−0.02	0.13	0.44
r^2	0.02	0.98	0.93

Table 3
Gradients of linear fits to perceived trajectory data in Fig. 4

Observer	Noise condition		
	0%	50%	100%
PAW	0.03	0.17	0.33
SKR	−0.02	0.12	0.25
AJK	0.03	0.18	0.27
CHR	−0.01	0.16	0.44
MCW	−0.09	0.17	0.45
MDK	−0.03	0.11	0.21
COMP	0.02	0.14	0.33
r^2	0.09	0.99	0.99

more, this control experiment indicates that our result is not attributable to the difference in the motion vectors surrounding the probe in the shuffled and unshuffled conditions. In a further control experiment we investigated the perceived probe trajectory as the size of the mask region increased. The results indicate that the pattern of perceived trajectories seen in Experiments 1 and 2 persists for masks with diameter of at least 12 deg of visual angle (Fig. 5a).

An anonymous reviewer suggested that the results presented here may be due to the fact that there are relatively more vertical or near vertical velocity vectors above and below the centre of the display in the non-shuffled condition. As a consequence it was suggested that the perceived probe trajectory might be constrained in the non-shuffled condition because observers were making comparisons with these vertical velocity vectors. To test this possibility, we ran an additional control study in which the central 6 deg portion of dots was removed together with the dots in a 70 deg wedge (±35 deg from vertical) above and below the centre of the display. The results were similar to those shown in the other studies reported in this paper (Fig. 5b). As a consequence we note that this result is remarkably robust to variations in the stimulus configuration.

5. Discussion

The results of the experiments reported here add to the body of evidence that is compatible with the use of flow-parsing in the estimation of object trajectory during self-movement (Rushton & Warren, 2005; Rushton et al., 2007; Warren & Rushton, 2007). In the first experiment we found an interaction between the symmetry of the flow field and the amount of noise (shuffle). This interaction was in-line with the predictions of the flow-parsing account; when the probe was displayed together with an asymmetric radial flow stimulus no illusory motion was perceived, in spite of the presence of net motion in the display. When the consistency of the stimulus with radial flow was systematically destroyed, illusory motion was perceived. In the second experiment, we removed motion in the immediate vicinity of the probe and still obtained the same pattern of results indicating that this effect is not due to a simple local motion contrast or a difference in the motion vectors in the region immediately surrounding the probe in the shuffled and un-shuffled conditions.

5.1. Relation to theories of induced motion

We have referred rather generically to an ‘induced motion account’ or accounts. Existing induced motion theories were not designed to predict what would happen in our radial flow display, therefore we are somewhat reticent

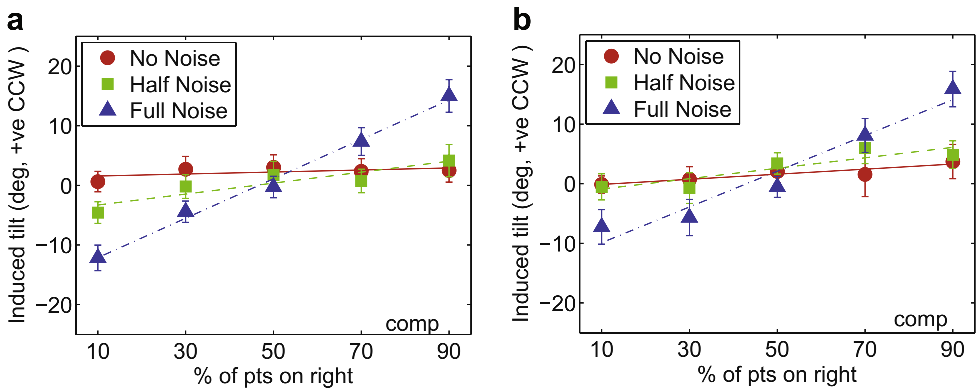

Fig. 5. Results of further control experiments to assess the impact of local interactions between the probe and velocity vectors: (a) Mask surrounding the probe object is increased in size to around 12 deg in diameter (average of 3 observers), (b) A wedge of 70 deg angular extent is removed from above and below the probe, together with a circular mask of around 6 deg diameter surrounding the probe (mean of 3 observers).

to attribute specific predictions to specific models. Reinhardt-Rutland (1988) provided a review of the theories of induced motion. He categorised the accounts into the following groups: Duncker's (1929/1938) Theory; Alteration of the Observer's Perception of Space; Felt & Cancelled Eye Movements; Induced Movement and "Intelligent" Perception; Sensory and Neural Processes. What we can state is that it is not apparent to us that any of the accounts, as currently developed, predict or can account for the results we report here. As an aside we note that in his review Reinhardt-Rutland suggests a future area of possible research derived from Gibson's work (see Gibson, 1950) and the movement of observers through an environment. We believe our work may be compatible with the idea he had in mind.

5.2. The optic flow illusion

It should be noted that the stimulus used in the asymmetric 50% noise condition has some similarities to displays associated with the optic flow illusion: in the optic flow illusion a pattern of radial motion is superimposed on a pattern of uniform planar motion and the perceived focus of expansion (FOE) is seen to shift in the direction of the planar flow (see Duffy & Wurtz, 1993; Lappe & Rauschecker, 1995; Royden & Conti, 2003). In the stimulus used in the present study, half of the dots are consistent with a radial flow pattern and the other half move over a range of directions which are not consistent with radial flow. However, since the motions of the latter half are actually also generated from the asymmetric radial flow pattern prior to shuffling, these dots will have a net horizontal motion. It is not a simple matter to interpret our results in terms of the induced motion illusion. First, we are not interested in the perceived focus of expansion of the flow pattern and secondly, in contrast to the common stimuli in studies of the OF illusion, our stimulus is asymmetric.

One account of the optic flow illusion from which we can derive predictions is that of Meese, Smith, and Harris (1994). Meese et al. (1994) explained the optic flow illusion in terms of induced motion. They suggested that the lateral flow induces an opposite illusory motion in the radial pattern leading to a shift in the FOE (Meese et al., 1994). Under this account, in our display the shuffled dots provide a net lateral motion and so this could shift the FOE. If the FOE is shifted then the probe dot will no longer be at the centre of the radial pattern. If the probe is moving through a peripheral part of the radial flow field then this could add an induced component of motion towards the focus of expansion. This prediction can be derived by considering the local velocity vectors which would be radiating outwards and so induce a motion inwards. The same prediction results from considering scene geometry; if an object remains at the same direction as the observer moves forwards, the object must be moving inwards, towards the locomotor path. However, note that this predicts the opposite pattern of perceived lateral movement to that observed in the present study. The probe object in our stimulus moves in the opposite direction to the net horizontal motion (i.e. the analogue of the superimposed uniform flow in the OF illusion stimuli).

An anonymous reviewer pointed out that alternatively, the position of the probe may simply be shifted by the net horizontal motion of the shuffled points in the same way that it is suggested the FOE shifts in the account discussed above. As a consequence, the shift in perceived trajectory would then be consistent with that seen in the present results.

5.3. Relation to "motion distortion" experiments

Whitney & Cavanagh (2000) investigated the influence of a structured motion field (a rotating radial grating) on the perceived relative position of two very briefly presented objects that were distant from the motion. The objects appeared displaced in the direction of the nearest motion, i.e. an object located to the right of a clockwise rotating grating was perceived shifted downwards, and object to the left was perceived shifted upwards.

One way of thinking of this finding is in terms of a roll movement (rotation along the line of sight) by the observer. If the grating rotates anti-clockwise then this is compatible with a clockwise roll of the observer. If the observer rolls then all stationary objects in the scene should move on a consistent circular trajectory. The Whitney & Cavanagh finding is compatible with such a roll movement. On first inspection this result appears at odds with what might be predicted under the flow parsing hypothesis. Flow parsing would predict that after parsing the roll component of optic flow the object should be seen to move in the opposite direction to the rotating grating.

However, it should be noted that in their study probe objects were presented very briefly for a period of 60 ms. It has been shown that the visual system has a bias towards the perception of scene stationarity (Wexler, Lamouret, & Droulez, 2001) and when an object is seen so briefly there is little chance for evidence to accumulate to suggest that the object is not scene stationary. Whitney & Cavanagh did investigate what happens when the probe objects are visible for longer periods of time. In the range they report, up to 250 ms, the shift in perceived displacement decreases. Whether the displacement asymptotes to zero or changes direction with longer presentation (as would be predicted under the flow parsing account) is not indicated.

5.4. Centre-surround motion-contrast models and models of MT neurons

Murakami & Shimojo proposed a motion contrast detector (Murakami & Shimojo, 1993) based on similar principles to that of Nakayama and Loomis (1974) and Nawrot and Sekuler (1990). Their model computes the relative motion (‘‘motion contrast’’) between the centre and surround and can explain induced motion type phenomena as well as the motion capture phenomenon seen in the peripheral visual field. The initial model was based upon contrast within the retinal image and therefore did not take depth relations into account. However, Murakami (1999) examined perception of induced motion of a target with planes of dots moving at different disparity defined depths. Induced motion was found to be determined by motion of the dots in the plane closest to the target. The results of the present study (Experiment 2) cannot be explained by such a local motion contrast mechanism.

5.5. Models of MST to support heading extraction

A number of models of optic flow processing in area MST have been proposed and suggested as candidate mechanisms for estimation of locomotor heading (e.g. Lappe & Rauschecker, 1993; Perrone, 1992; Perrone & Stone, 1994; Royden, 1997). These models are underpinned jointly by the biological characteristics of areas MT and MST as well as mathematical solutions to the problem of observer heading estimation from optic flow information (e.g. the differential schemes of Longuet-Higgins and Prazdny (1980), Rieger and Lawton (1985) and Hildreth (1992) as well as the subspace algorithm of Heeger and Jepson (1992)). Since the flow parsing hypothesis relies upon a similar analysis of optic flow information it is likely that such schemes will provide a good starting point from which to model the flow-parsing mechanism. Note, however, that none of these schemes explicitly encode the optic flow field. Instead, optic flow information is represented by a spatial template (Perrone, 1992; Perrone & Stone, 1994) a neural population code (Lappe & Rauschecker, 1993, 1995) or is processed locally by motion opponent operators (Royden, 1997). Clearly, flow parsing requires that flow fields are represented explicitly so that those components due to observer movement can be parsed from the retinal flow at a global level, leaving a resultant flow field due to object movement. It is therefore difficult to make predictions for the experiments reported here based on current models of MST motion processing.

5.6. Subtraction and filters

Although we describe parsing as a serial sequence of subtractions we do so simply for ease of exposition. It may well be more correct to conceive of the parsing in terms of multi-dimensional filters of the kind described by Perrone (1992), in which case we would say that in the 0% noise conditions only the radial flow components were filtered. In the noise conditions other filters were stimulated, namely those which are sensitive to retinal flow arising from eye rotation.

5.7. Vector analysis

We have previously noted that flow-parsing could be reformulated in terms of Johansson’s vector analysis (Warren & Rushton, 2007). The flow parsing hypothesis indicates that optic flow detectors act as filters, parsing retinal flow into distinct components due to observer and object movement. The component of retinal motion due to self movement can then be ‘subtracted’ from the total retinal flow, leaving only those components of motion due to movement of objects in the world. As a consequence, movement of an object relative to the background scene can be estimated as if the observer were stationary. Johansson (1974) suggested that the visual system decomposes a pattern of retinal motion into a common 2D component of motion and a relative motion component. In Johansson’s terms we are proposing that retinal motion is decomposed into a common 3D component of motion and a relative motion component. Such an account is also consistent with the theoretical work of Zemel and Sejnowski (1998) who suggest a computational model of MST which segments retinal motion due to self and object motion. This model of MST is then seen to encode relative motion between the observer and other objects in the scene.

5.8. Relation to previous flow-parsing results

It is interesting to note that previous results (e.g. see Warren & Rushton, 2004; Rushton & Warren, 2005) have indicated a special role for depth order and have suggested that stereo depth information may be necessary for flow-parsing. The results of this study demonstrate that, at least in some cases, flow-parsing can occur in the absence of stereo-defined depth information.

6. Summary and conclusions

To summarise we have shown a pattern of perceived probe motion that is in-line with the predictions of the flow-parsing hypothesis. We have previously shown that flow-parsing plays a role in detection of object movement (Rushton & Warren, 2005), perception of object trajectory (Warren & Rushton, 2007), and the pop-out of an object (Rushton et al., 2007). These previous studies relied upon depth dependent motion; here we demonstrate the influence of the structure and symmetry of the flow field on the perception of the trajectory of an object of interest. These data add further weight to the flow-parsing hypothesis and the suggestion that optic flow processing subserves the perception of object movement during self movement.

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