



# Cardinal axes for radial and circular motion, revealed by summation and by masking

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## Abstract

Both electro-physiological and psychophysical studies point to the existence of detectors specialised for the analysis of optic flow. However, it is unclear whether these detectors are tuned to specific ‘cardinal directions’ (such as radial and circular motion), or whether they respond equally to all directions of optic-flow motion, including intermediate spiral motions. Here summation and masking studies of motion coherence sensitivity are reported that suggest that optic flow may be tuned to radial and circular cardinal directions. Strong summation was found between two orthogonal directions of spiral motion, but much weaker summation between radial and circular motion. As orthogonal spiral motions always contain a common radial or circular component, the stronger summation for these motions implies that detectors are tuned to radial and circular directions. Similarly, the most effective masking stimuli (placed adjacent to but not superimposed on the test stimuli) tended to be those in the radial or circular directions, even for spiral targets, further suggesting that flow-field motion is detected and discriminated by mechanisms tuned to these ‘cardinal’ directions. © 2001 Elsevier Science Ltd. All rights reserved.

*Keywords:* Visual motion; Optic flow; Cardinal directions; Coherence ratios

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## 1. Introduction

When animals move they generate flows of pattern information across their retinæ which are capable of signalling not only the relative motion and shape of objects in the environment but also the movement of the observer (Gibson, 1950; Nakayama, 1985; Warren, Morris, & Kalish, 1988; Warren, 1998). Gibson highlighted the global properties of this pattern of retinal motions and drew attention to the need for the visual system to uncover invariants in the optic array to guide navigation within a crowded environment. Gibson noted that when observers moved towards a point that they were fixating, an expanding pattern of retinal motion was produced with the focus of expansion coinciding with the fixated object. This simple pattern of flow is rare. Pursuit eye movements made by moving

observers add translational components to the flow field. Surfaces closer to the observer produce greater retinal velocities and frequently this produces asymmetries in the flow field. The observer’s task is to distinguish those signals that relate to self-motion from those which relate to object properties.

Formal analysis reveals that the first order components of the flow field can be reduced locally to four fundamental components (Koenderink, 1986): divergence (expansion or contraction), curl (rotation about the axis of motion) and two components of deformation (a change in shape with no change in area produced by a greater rate of expansion/contraction on one axis). These differential invariants constitute an orthogonal set in Euclidean space and the components could form cardinal axes in a space representing motion.

One useful strategy for deriving the radial structure of the flow field would be to decompose the pattern of motion into signals along each cardinal direction (Warren, 1998). This model has the virtue of requiring the

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minimum number of mechanisms to represent the motion. An alternative would be to filter the flow fields using mechanisms that were tuned to particular combinations of these orthogonal components (Duffy & Wurtz, 1991b; Graziano, Andersen & Snowden, 1994). The current paper attempts to determine which of these two alternatives is favoured by the human visual system.

The existence of detectors in the human system sensitive to div, curl and translation would be consistent with a large body of physiological evidence showing single cells tuned to those global properties in cortical area MSTd of the motion pathway in monkeys (Saito, Yuki, Tanaka, Hikosaka, Fukada & Iwai, 1986; Duffy & Wurtz, 1991a; Orban, Lagae, Verri, Raiguel, Xiao, Maes & Torre, 1992; Graziano et al., 1994). Duffy and Wurtz (1991a,b) found that many units were sensitive to either radial, circular or translational motion and that their receptive fields were very large, often more than a hemifield. Duffy and Wurtz, 1991 and Graziano et al., 1994 have also provided evidence that many neurones were tuned to particular combinations of radial, rotary and translational motion. The results suggest that cells in monkey MSTd are not tuned only cardinal axes for optic flow, but also to various combinations of these components. However, it is also possible that the combined signals could be de-multiplexed by combinations of units leaving independent estimates of the strength of each orthogonal motion component.

The human psychophysical data also fail to point clearly to either alternative. (Regan & Beverley, 1973a,b, 1978a,b, 1979, 1980, 1981) used a selective adaptation paradigm to demonstrate functional independence of expanding flow fields and frontoparallel motion. The mechanisms revealed by Regan and colleagues are well suited for the required global analysis of the flow field, although their evidence suggested that the analysis was restricted to small areas, of the order of  $1^\circ$  (Beverley & Regan, 1979). More recently, Morrone, Burr, and Vaina (1995) have applied a different technique, 'summation', to demonstrate the existence of integration units for complex flow motion. Their results suggest that the integration can occur over very extensive areas,  $10\text{--}80^\circ$  (Burr, Morrone, & Vaina, 1998). Further support for this form of integration comes from the demonstration of Snowden and Milne (1997) that adaptation in one region of the visual field transfers to unadapted regions, as would be expected if the receptive fields were very large.

Studies explicitly aiming to determine the existence of cardinal mechanisms for optic flow detection have produced mixed conclusions. Freeman and Harris (1992), Lappin, Norman, and Mowafry (1991) and Te Pas, Kappers, and Koenderink (1996) all used masking techniques. The performance in conditions where the dots moved along one cardinal axis (e.g. expansion) was

compared with conditions where dots moved in non-cardinal directions, such as an expanding clockwise spiral. These studies all point to different processing mechanisms for radial and circular motion. However, Te Pas et al. (1996), noted that in their study the results could also be produced by observers simply noting local deviations from parallel motion and concluded that the data did not strongly support the existence of cardinal mechanisms. This objection could also apply to the critical experiments in the other two studies. Snowden and Milne (1996) also note that in a system with an array of detectors tuned to narrow ranges of orientation in this cardinal space, signals  $90^\circ$  apart are likely to be detected independently and hence this does not constitute a critical test between the two alternatives.

More recently Morrone, Burr, Di Pietro, and Stefanelli (1999) measured minimum coherence thresholds for a wide range of vector directions in this cardinal space. At these low coherence levels local parallelism is not available as a cue. Individual results gave no clear picture, but a principal components analysis led to the conclusion that performance could be supported by orthogonal detectors for curl and div. However, Snowden and Milne (1996) reached different conclusions. They adapted to specific directions in this cardinal space and then measured minimum motion coherence thresholds. They found adaptation effects were restricted to a narrow range of directions near to the adapting direction and concluded that the visual system must contain detectors tuned to a range of directions some of which were non-cardinal.

Physiological studies show that complex motion is analysed in cortical area MST, a relatively high level of the motion hierarchy that integrates local motion signals from lower levels of analysis (Tanaka & Saito, 1989; Duffy & Wurtz, 1997). Psychophysical studies also point to a 'second-stage' of analysis for flow-field motion that integrates local-motion signals. For example, high-pass filtering of optic flow stimuli show that the local signals are combined at a second stage of analysis, not merely integrated by early mechanisms operating at a low spatial scale (Smith, Snowden, & Milne, 1994). Morrone et al. (1995), showed that different techniques can tap different stages of analysis of flow-field motion: contrast sensitivity measures probe early mechanisms, that are limited by the contrast thresholds, while motion coherence thresholds seem to reveal properties of the higher-level mechanisms that integrate complex motion. Other evidence that the two techniques probe different sites comes from the very different estimates of integration period for the two techniques, about 200 ms for contrast thresholds and 2000 ms for motion coherence thresholds (Santoro & Burr, 1999). Thus, it may be that the adaptation stimuli of Snowden and Milne (1996) affected the low-level mechanisms rather than the global integrators. These

would of course show no tendency towards cardinal directions.

In this study we use both summation and masking paradigms to investigate cardinal directions for optic flow. In doing so, one takes advantage of the fact that optic flow mechanisms integrate over a wide region (Morrone et al., 1995; Snowden & Milne, 1997). It is therefore possible to separate spatially the mask from test stimuli, so they do not stimulate the same local-motion detectors. Under these conditions, evidence has been found for cardinal directions for optic flow, tuned to radial and circular motion.

## 2. Methods

### 2.1. Stimuli

The stimuli comprised a total of 100 randomly positioned dots, some of which were caused to move coherently in a radial or circular fashion, or in variable combinations of these motions (spiral motion). The motion of the dots is most easily described in polar co-ordinates,  $\dot{r}$  and  $\dot{\theta}$ , the radial and angular velocities of the dot (in degrees of visual angle and radians/s, respectively):

$$\dot{r} = v \cos \phi$$

$$\dot{\theta} = v/r \sin \phi \quad (1)$$

where  $v$  is local speed,  $6^\circ/\text{s}$ , and  $\phi$  gives the types of motion in the radial-rotation space. The  $0$  and  $180^\circ$  describe expansion and contraction (respectively), and  $90$  and  $270^\circ$  clockwise and counter-clockwise rotation. Intermediate angles produce spiral motions, combinations of radial and circular motion. The angle  $\phi$  also refers to the local direction at which the dots cross the right hand horizontal axis. Note that the local speed does not vary with distance from the origin (as it would for rigid rotation), but is constant for all positions (because of the normalisation by radius). In all cases the dots moved for a ‘limited lifetime’ of three frames (100 ms), after which they were reborn in a new random location. One third of the dots (or more generally,  $1/\text{lifetime}$ ) died and were reborn on each frame.

All stimuli were generated on the face of a Mitsubishi 4821 Monitor under the control of a Cambridge Research Systems VSG2/4 framestore. The framerate of the monitor was 150 Hz. Dots remained in their position for five video frames (33 ms), so the effective frame rate of dot motion was 30 Hz. Half the dots were luminance increments and half decrements against the mean background luminance of  $52 \text{ cd/m}^2$ , having a Michelson contrast of 90%. Each dot subtended 5 pixels ( $14'$  arc). The stimulus was a  $10^\circ$  diameter circle (at a viewing distance of 50 cm), with an empty  $1.5^\circ$

hole in the centre. If the trajectory of a dot took it outside the circle or into the central hole, it was reborn in a new random position. Throughout each trial, subjects fixated a clear fixation point in the centre of the screen.

The ‘noise’ dots were designed to move in a non-coherent way that was locally similar to the coherent flow-field motion. Each dot moved in a different randomly chosen flow-field trajectory for its lifetime (equal to that of the signal dots), by choosing a random value for  $\phi$  of Eq. (1). On rebirth in a new random position, it was assigned a new randomly chosen  $\phi$ . All experiments measured sensitivity by measuring the maximum proportion of non-coherent dots that could be tolerated for the target to be correctly identified or discriminated. The total number of dots was always constant (and equal to 100), but the proportion of coherently moving dots varied.

Two measurements of motion sensitivity were used in this study: direction discrimination (for the summation experiment) and detection (for masking). For the direction discrimination task there was a single presentation where the direction of motion was chosen from two opposites (e.g. expansion from contraction:  $0$  from  $180^\circ$ ) from which the subject was required to choose. For the detection task the observer had to identify the interval containing the target, in a two-interval presentation. In all experiments the ratio of coherent to non-coherent dots was varied dynamically by the QUEST routine (Watson & Pelli, 1983), that homed in near threshold (87% criterion). Thresholds were then calculated offline, by fitting probability of seeing curves with a cumulative Gaussian function. In all conditions at least three separate QUEST sessions were run, each with 30 trials.

### 2.2. Summation and masking

The two techniques employed to test for cardinal axes were ‘summation’ and ‘masking’. In both cases the screen was divided into 16 virtual sectors, each subtending  $22.5$  clock degrees. The summation experiment was designed to examine how optic flow motions in orthogonal directions sum to increase sensitivity. In one condition only one type of motion was displayed, but all dots (both coherent and non-coherent) were confined to alternate sectors (a total of 50 dots on the screen in this case, so dot density was the same as in other conditions), with the other sectors set to average mean luminance. In the other condition the alternating sectors contained a motion stimulus in the orthogonal direction in optic flow space. In both conditions the task of the subjects was to distinguish the direction of motion from its opposite; for example clockwise rotation plus expansion from anticlockwise rotation plus contraction. The coherence ratios of the two directions

of motion were yoked to vary together. The position of the sectors was randomised from presentation to presentation.

In the masking experiment, the test was presented together with a mask, a stimulus where all dots moved in a coherent direction, but the direction of motion was non-informative for the task. The masks always comprised 75% of the stimulus dots, but could be displayed either adjacent to the target sectors, or superimposed on the target stimulus, covering the whole of the screen. In the case of adjacent masks, the target motion was confined to four maximally separated sectors, each  $22.5^\circ$  wide. The masks filled the spaces between them, four sectors each subtending  $67.5^\circ$ . Again, the position of the target sectors was randomised from trial to trial (but always maintaining the cross formation). When the mask was superimposed on the target motion, 75% of the dots (75 dots) comprised the mask, and moved coherently in the mask direction. The remaining 25 dots formed the test, either as coherent dots in the direction of the test, or random noise. The direction of the mask motion varied considerably over the entire range.

If a dot crossed a sector, it took on the characteristics of the new sector for the remainder of its lifetime. This has the effect of reducing slightly the motion signal, particularly for circular motion. In previous studies, where sensitivity was measured as a function of sector number, the actual signal strength was calculated by cross-correlation and corrected for this artefact (Burr, Morrone, & Vaina, 1998). However, the procedure is laborious and cannot be performed on-line, and results in only minor changes. As one was not interested in comparing absolute thresholds for circular versus radial motion, or in varying sector size in this experiment, the correction is unnecessary in this study.

The three authors, all with correct to normal vision served as observers for these experiments.

### 3. Results

#### 3.1. Summation

This experiment was designed to study interactions between different directions of optic flow by measuring sensitivity to motion in a single direction of optic flow, and comparing that sensitivity to that of two orthogonal directions, displayed in adjacent sectors. As described above, the circular screen was divided into 16 equal virtual sectors, and a target stimulus (together with its noise) was displayed in alternate sectors. In one condition the other sectors remained blank, while in the other they contained coherent motion in the orthogonal direction. In both cases ob-

servers were required to discriminate the direction of motion from its opposite.

Fig. 1 compares sensitivity for detecting the direction of motion in a single direction (open squares) with that for a dual presentation (filled circles), with the intermediate sectors showing motion in the orthogonal direction. Sensitivity was always higher for

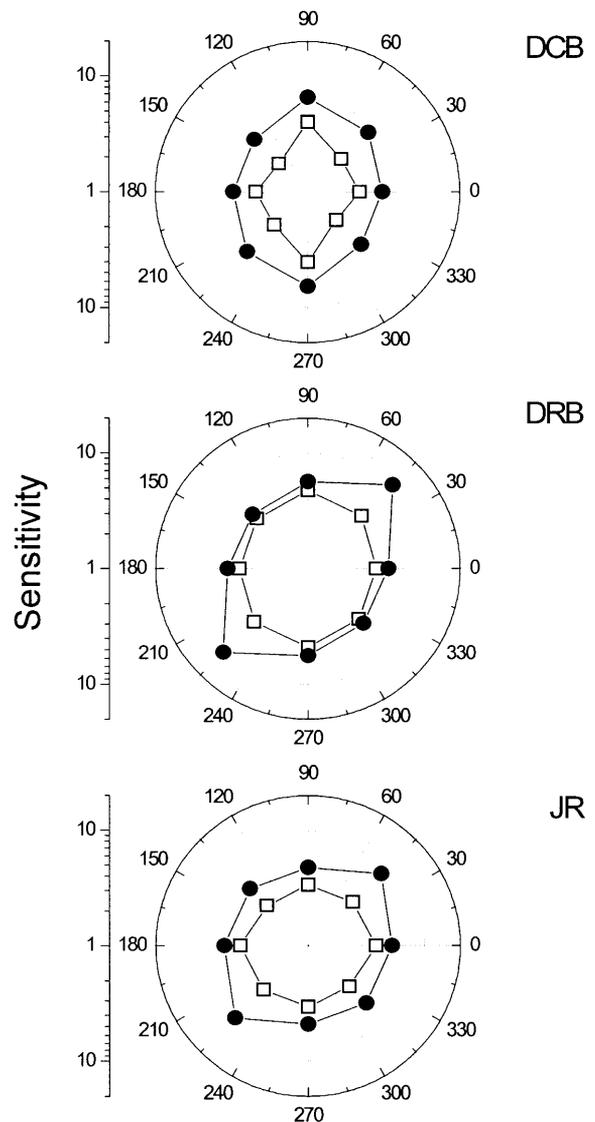


Fig. 1. Coherence sensitivity for discriminating the direction of motion of optic-flow stimuli. Open squares show sensitivity for a motion stimulus in single direction, displayed in alternate sectors (8 out of 16), with the other sectors set to mean luminance. Filled circles show sensitivity for double motion stimulus, comprising both the direction indicated by the polar plot and the orthogonal direction. Direction discriminations were performed for target angles:  $0-180$ ,  $45-225$ ,  $90-270$  and  $135-315^\circ$  (summed together with  $90-270$ ,  $135-315$ ,  $180-270$  and  $225-45^\circ$ , respectively). The supplementary points on the curve are therefore identical. The increase in sensitivity for two directions of motion was highest when the motion was in the non-cardinal than in the cardinal directions. In this and subsequent figures, the average standard error of the mean was about 0.06 log-units.

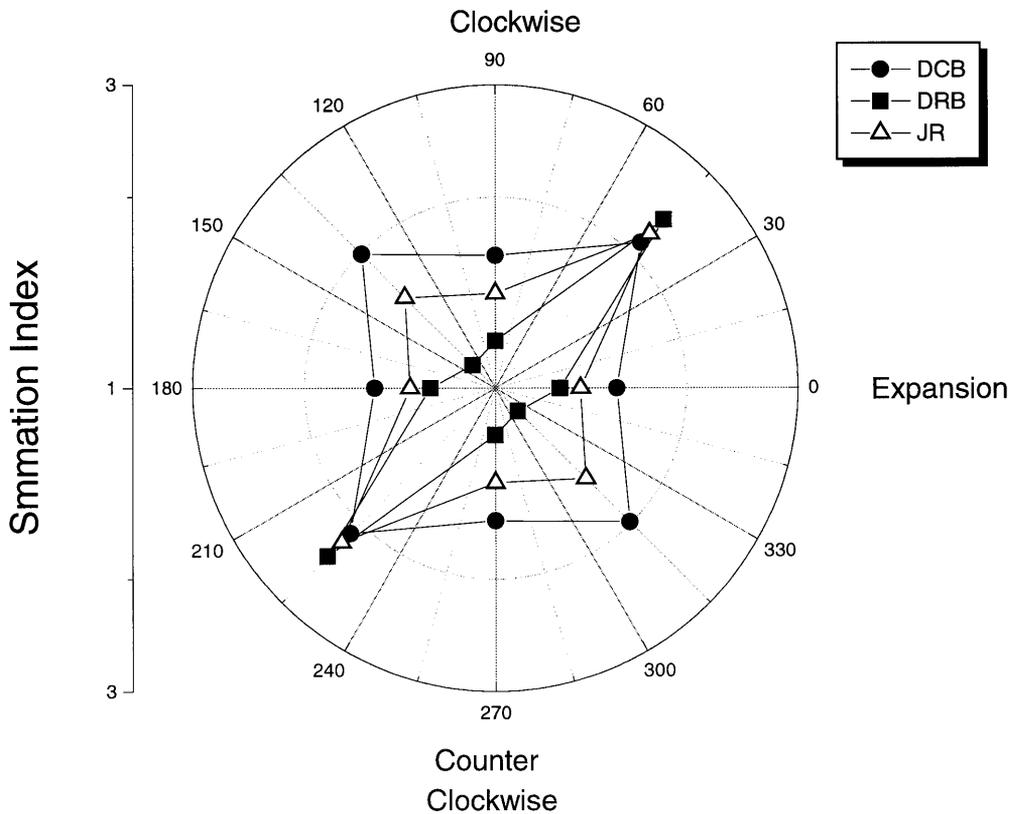


Fig. 2. Summation between two orthogonal motions, as a function of the spiral angle of one of the motion fields (the other was that plus  $90^\circ$ ). The summation index is defined as the ratio of the thresholds for direction discrimination for a single motion stimulus to that with orthogonal motion interspersed in the intermediate sectors (data from Fig. 1).

the dual presentation, but the advantage tended to be greater when the stimuli moved in non-cardinal than in cardinal directions, particularly for stimuli of  $45^\circ$  (together with  $225^\circ$ ). This tendency is brought out more clearly by calculating a 'summation index', defined as the ratio of thresholds of the target alone to those with an orthogonal target in adjacent sectors. An index of 1 means that sensitivity was the same for the single and double presentation. These results are shown in Fig. 2. As sensitivity to the double stimulus was always higher than that for single stimuli, the summation index was always greater than unity. However, the clear star shape of the curve, especially for DCB and JR, shows that summation was much stronger for  $45^\circ$  and  $225^\circ$  than for  $0^\circ$  and  $90^\circ$ . This suggests that the direction discrimination was based on detectors tuned to the cardinal axes of circular and radial motion. A combination of  $45^\circ$  and  $135^\circ$  both contain a circular component at  $90^\circ$ : if this is the information used for detection, then the target angles should summate, increasing sensitivity. On the other hand,  $0^\circ$  and  $90^\circ$  lie on independent cardinal directions, so there should be no direct summation, unless there also existed detectors tuned to  $45^\circ$  and  $135^\circ$ . In fact sensitivity did improve in these conditions, but by a smaller amount, probably ascribable to 'probability summation' (Graham, 1977).

### 3.2. Adjacent masks

Another technique to study interactions between different stimuli is masking, where a high contrast stimulus 'mask' is presented together with the target. Unlike summation studies, the mask stimulus is uninformative in itself, but could influence the detectability of the target. The target and mask were not superimposed, but displayed in separate sectors. One quarter of the screen was dedicated to the target, and three quarters to the mask: four opposing sectors (each  $22.5^\circ$ ) contained the mask, while the intermediate sectors (each  $67.5^\circ$ ) contained the target. Three target stimuli were used for each subject: for DCB and DRB they were expansion ( $0^\circ$ ), clockwise rotation ( $90^\circ$ ) and a spiral mixture of the two ( $45^\circ$ ); for JR they were in the opposite direction,  $180^\circ$ ,  $270^\circ$  and  $225^\circ$ . The mask stimuli occupied a wide range of motion angles from  $0^\circ$  to  $360^\circ$ . In any given session, at least four different mask conditions were used, randomly intermingled from trial to trial. Each trial comprised two intervals in which subjects had to identify that containing the target and mask from that containing mask alone.

Here the prediction is that if there exist cardinal directions for complex motion, the maximum effect of the masks will always occur at cardinal directions,

especially 0 and 90°, both for the cardinal and non-cardinal stimuli. That is to say, if the 45° stimulus is detected by mechanisms tuned to 0 or 90°, rather than those tuned to 45°, masks at 0 and 90° should interfere maximally with detection.

Coherence thresholds are shown in Fig. 3. As expected from the above rationale, the tuning tended to follow cardinal directions more than the non-cardinal directions. For DCB and JR, the maximum masking for the cardinal targets was when masks moved in the same direction as the targets, 0° and 90° for DCB and 180 and 270° for JR. The non-cardinal direction, however, did not produce masking in that direction, but at 0° for DCB and 180° for JR. For DRB the tuning for all targets was less clear-cut, and that for 45° was quite broad.

The argument is based on the idea that if there exist only detectors tuned to cardinal motion directions (radial and circular motion), then the intermediate spiral motions should be detected by them alone. However, for 45°, detectors at either 0 or 90° could work equally well. It is possible that under different conditions different mechanisms respond to the target: when the mask is

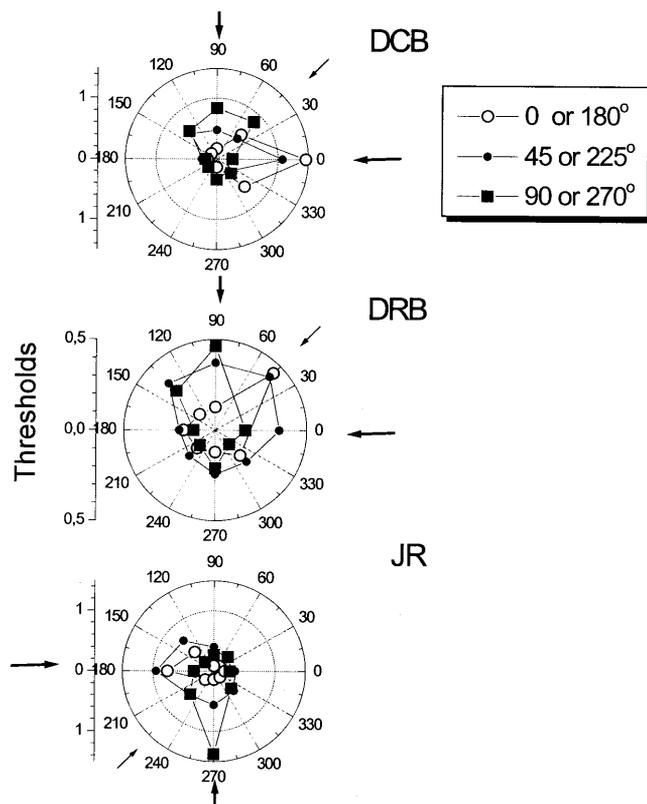


Fig. 3. Thresholds for detecting the interval in which a target appeared, as a function of the spiral angle of a masks positioned adjacent to the target. In different sessions, the target was expansion (0°), clockwise rotation (90°) or spiral expansion-rotation (45°) for DCB and DRB, and 180, 225 and 270° for JR. Average errors in this, and other graphs were about the size of the square symbols.

near 0 the 90° detectors may be more sensitive, and vice versa. To avoid this possibility of ‘off angle looking’, the experiment was repeated with a double mask, a mask containing two orthogonal directions of motion. For example, if the mask was at 0°, it was also at 90°; if at 225°, also at 315°.

The results are shown in Fig. 4. Recall that for each angle, the mask was also at 90° plus that angle. Here there is very little evidence for tuning at 45 or 225°, even for DRB. For all conditions the curves peaked around 0, 90, 180 or 270°.

### 3.3. Superimposed masks

In the previous experiments the masks were deliberately separated from the target to avoid the possibility of masking local-motion mechanisms, as they should only be combined with the target motion information at a later stage of integration along complex flow field directions. To investigate the importance of separating spatially the target and mask, the masking experiments were repeated with target and mask superimposed. Again, three quarters of the dots comprised the target, and one quarter the mask, but these were intermingled over the whole display area. Measurements were made for only two observers, for three target stimuli: expansion (0°), clockwise rotation (90°) and a spiral mixture of the two (45°).

The results are shown in Fig. 5. Tuning in these conditions is not very convincing at all. There is some tendency for the masking to be greatest when test and mask coincide, both in the cardinal directions and for the 45° stimulus. Certainly there is very little evidence for cardinal axes in these curves. A possible explanation for the difference between these results and those of the previous two figures is that local-motion signals could have been masked by the superimposed masks, so the results do not represent the characteristics of higher-stage integrating mechanisms.

## 4. Discussion

The aim was to determine whether the human visual system uses a cardinal decomposition to represent global motion or instead uses an array of mechanisms tuned to a wider range of flow directions. Although there is considerable variation from observer to observer, the results of the summation experiment suggest the existence of cardinal axes in global motion space, analogous to those observed for the red–green and yellow–blue axes in colour space (Krauskopf, Williams, & Heeley, 1982). The cleanest results are those of DCB. He shows little summation for rotary and radial motion (Fig. 2), and that small amount can probably be ascribed to probability summation, the small increase

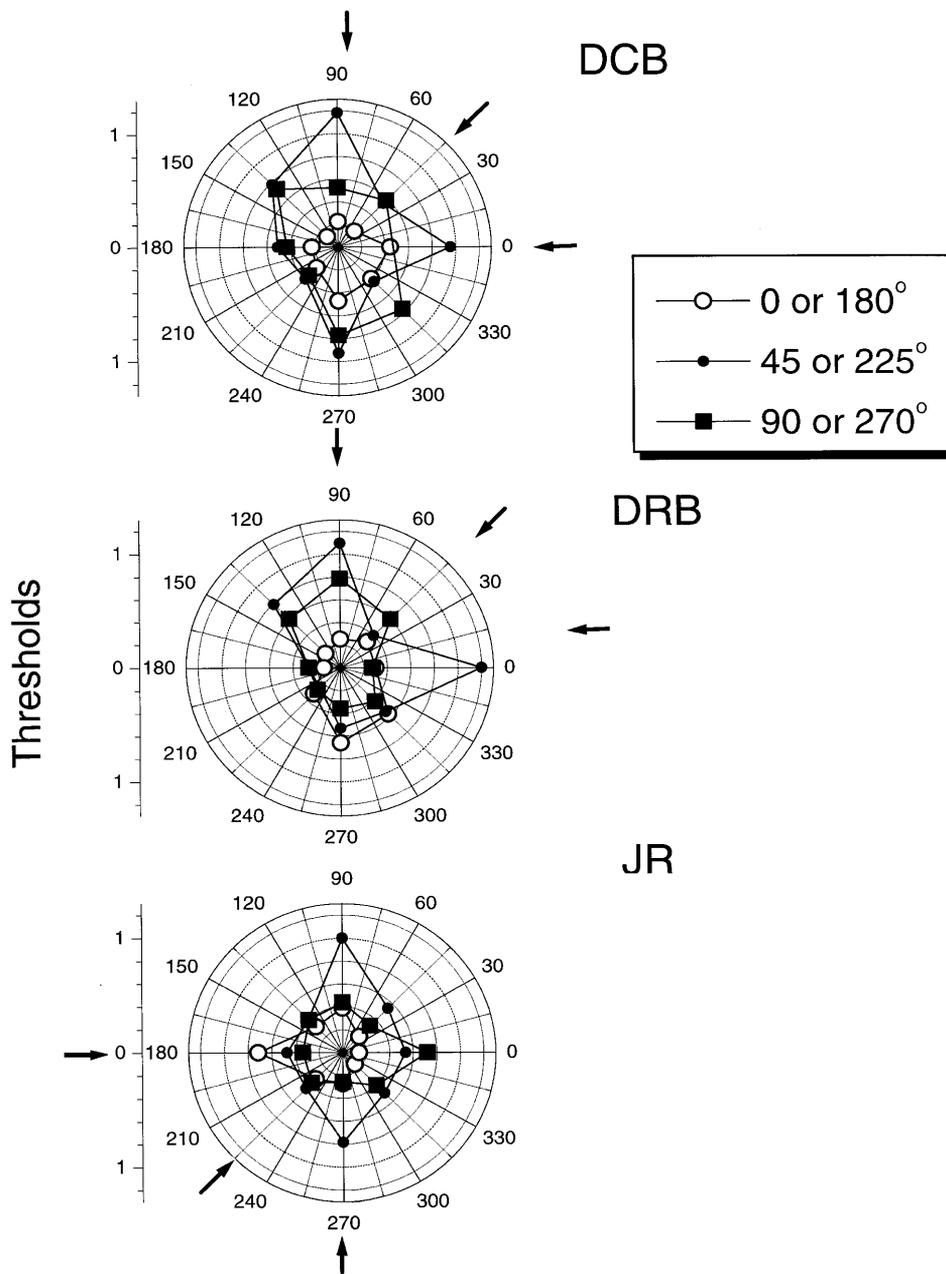


Fig. 4. Thresholds for detecting the interval in which a target appeared, as a function of the spiral angle of mask motion confined to sectors adjacent to the target. In this case the mask had two components, one at the angle indicated, another at that angle plus 90°. In different sessions, the target was expansion (0°), clockwise rotation (90°) or spiral expansion-rotation (45°) for DCB and DRB, and 180, 225 and 270° for JR.

expected on statistical grounds between independent detectors (Graham, 1977). But when the motion is spiral, incorporating both radial and rotational components, it summates with motion orthogonal to it, as would be expected if spiral motion is detected by virtue of its radial or circular components. The results of JR are less symmetrical than those of DCB, but again show greater summation for orthogonal spiral motions than for rotary and radial motion. DRB's results are quite asymmetric. He shows strong summation for one combination of orthogonal spiral motions, but very

little for another, suggesting an asymmetry in his analysis of optic flow, being less sensitive for radial motion (as direct measurements confirm).

The masking experiments with separated target and masks also supported the existence of cardinal directions in optic flow space. Rotary or rotational stimuli were masked little if at all by masks on orthogonal axes, and strongly by masks on the same axis. But spiral target stimuli (45 or 225°) are most strongly masked by stimuli on the cardinal axes. This pattern is clearly evident in the results of DCB and JR, less so in

the results of DRB. Evidence for cardinal directions was stronger still when adjacent double masks were employed to circumvent the possibility of ‘off-angle looking’. Spiral targets are much more strongly masked by rotary and radial masks than by spiral masks.

Superimposed masks provide little evidence to support the existence of cardinal axes. A likely reason for this is that the masks excite not only the mechanisms that integrate local-motion signals for optic flow analysis, but also the local-motion mechanisms themselves. Thus the masking effects may be predominately local, saying little about optic flow analysis. This may also explain the discrepancy between the results reported here and those of Snowden and Milne (1996). They used stimuli that adapted the whole field, and tested the same field. Again, the main adapting effects could have been on the level of local motion analysis rather than global.

The results reported here reinforce existing evidence for the appealing idea that complex flow-field motion can be represented with a minimal number of vectors (Lappin et al., 1991; Freeman & Harris, 1992; Te Pas et al., 1996; Morrone et al., 1999). However, it remains at variance with single-unit physiological studies of MSTd cells in macaque monkey, that have failed to find any tendency for cardinal axes (Tanaka & Saito, 1989;

Duffy & Wurtz, 1991a; Graziano et al., 1994). There could be many reasons for this discrepancy. The psychophysical techniques are likely to reveal the most sensitive neurones, whereas the single-unit studies should sample all neurones: there may well exist neurones with intermediate spiral tuning, that are less sensitive or fewer in number than those tuned to cardinal axes. It is also possible that there are inter-species differences, or that the cardinal axes do not reflect the action of MSTd cells, but another level of analysis.

Flow field analysis finds analogies in colour vision, where there has been clear evidence for the cardinal directions along the L–M and S–(L+M) axes (Krauskopf et al., 1982; Krauskopf & Farell, 1990). However, it is interesting to note that even in colour space, evidence is now emerging for central mechanisms that do not follow the cardinal directions (Cropper, Mullen, & Badcock, 1996; Krauskopf, Wu, & Farell, 1996; Krauskopf, 1999). It may well be that the evidence for cardinal directions for optic-flow does not describe completely these mechanisms, and should be considered with due caution. One obvious possibility is that the cardinal behaviour may only apply at near threshold coherence levels. If the physiologically revealed mechanisms, preferring other directions of flow, are active but less sensitive than at higher coherence levels the operation of these mechanisms may also be observable, and they may explain the differences found among observers.

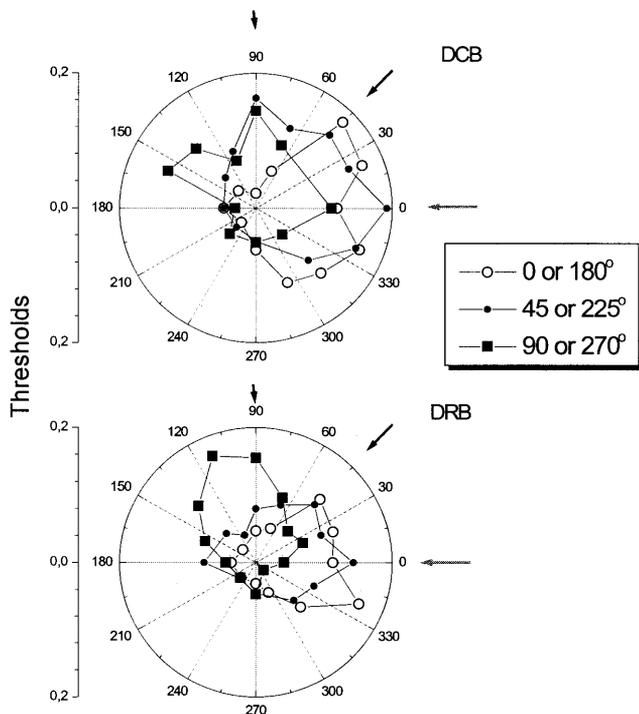


Fig. 5. Thresholds for detecting the interval in which a target appeared, as a function of the spiral angle of a superimposed mask. A total of 75% of dots moved coherently to form the mask, the other 25% comprising the target and random motion. In different sessions, the target was expansion ( $0^\circ$ ), clockwise rotation ( $90^\circ$ ) or spiral expansion-rotation ( $45^\circ$ ).

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