



Central and peripheral interactions in the perception of optic flow

Claudine Habak *, Christian Casanova, Jocelyn Faubert

School of Optometry, Université de Montréal, 3744 Jean-Brillant # 260-7, Montreal, Que., Canada H3T 1P1

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Abstract

The purpose of this work was to evaluate the effects of central and peripheral stimulation on the perception of optic flow over large spatial extents. Coherence thresholds were measured for RDKs simulating observer translation and radial motion. Experiments 1 and 3a measured sensitivity to a range of speeds for a circular central region, for several annular regions of increasing eccentricity, and for a full-field stimulus (80° diameter). Results suggest that the spatial extent over which signals are integrated may vary in order to maximize the information available for perceptual representations. Experiments 2 and 3b evaluated central and peripheral interactions in a direction discrimination task, by comparing the effects of different signal strengths and directions in one of the two regions. The presence of noise dots (0% coherence) in either center or periphery led to a performance decrease from baseline measures. A similar decrease was observed when dots in the two regions moved in opposite directions. When dots in both regions moved in the same direction, a stronger peripheral signal led to facilitation of direction discrimination, whereas a stronger central signal did not. These findings suggest that central and peripheral inputs are not separable in the integration of optic flow, that they contribute equally to the percept under normal conditions (equal signal strength), and that peripheral stimulation seems important under ecologically relevant conditions such as poor visibility.

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1. Introduction

Optic flow consists of a projection of the visual scene on the retina during observer displacement (Gibson, 1979); a change that involves the entire visual environment. The underlying mechanism shows large areas of integration as evidenced psychophysically by regions of spatial summation up to 70° (Burr, Morrone, & Vaina, 1998), and by optic-flow sensitive neurons with receptive fields estimated to extend up to 100° in diameter in primates (Duffy & Wurtz, 1991). Such integration covers an extensive part of the visual field and the importance that central and peripheral vision may have in determining optic flow percepts is of interest. Much work has addressed this question (see below), but little has assessed how these regions interact to affect the integration of signals across the visual field. The purpose of the

present work is thus to evaluate the influence of central and peripheral stimulation on the perception of motion direction in optic-flow patterns.

The work evaluating the importance of central and peripheral vision in the perception of optic flow is only highlighted here as it has been reviewed elsewhere (Bardy, Warren, & Kay, 1999; Warren & Kurtz, 1992). Based on a variety of experimental findings using measures of vection (self-motion perception), postural adjustments, and/or heading, three separate theories have been proposed in the perception of optic flow. The peripheral dominance theory, originally proposed by Brandt, Dichgans, and Koenig (1973) suggested that peripheral stimulation determined the sensation of vection (Berthoz, Pavard, & Young, 1975; Brandt et al., 1973) and flow-induced postural adjustments (Lestienne, Shoenberger, & Berthoz, 1977). Much subsequent work has shown that the theory of peripheral dominance did not hold and that the reported effect resulted from a variety of factors (for a review see Warren & Kurtz, 1992). These include spatio-temporal characteristics that may lead one region to dominate over another (Palmisano & Gillam, 1998), the area of stimulation (Post,

* Corresponding author. Tel.: +1-514-343-6111x8824; fax: +1-514-343-2382.

E-mail address: claudine.habak@umontreal.ca (C. Habak).

1988), and foreground–background percepts, which suggest that the region perceived as the background elicits the strongest vection sensation (Howard & Heckmann, 1989; Ohmi, Howard, & Landolt, 1987). Functional specialization, the second theory, proposed by Warren and Kurtz (1992), suggested that central vision was specialized for radial and lamellar motion and peripheral vision for lamellar motion. Crowell and Banks (1993) reported that this finding resulted from increased error in heading judgements in the periphery and showed that heading estimates were equally good across the visual field for optic flow patterns, thus the retinal invariance hypothesis. Later work showed that this last theory also held for postural control (Bardy et al., 1999). The proposal of retinal invariance seems to be in accordance with much of the work that controlled for factors that may lead one region to take over another.

Information from central and peripheral visual fields thus appears to contribute equally to heading, postural control, and vection. The purpose of the present work is to evaluate the interactions that may exist between information from center and periphery, and the influence that one region may bear on the other. It is expected that both areas would influence each other equally because of the existence of large areas of integration and of equal sensitivity across the retina.

In order to equate the strength of central and peripheral information in the present work, the first experiment consists of measuring sensitivity to optic-flow stimuli (simulating observer translation) of varying speeds and at several eccentricities. Measures are carried out for full-field stimulation in addition to those for limited regions. The second experiment assesses the influence of central and peripheral information on the perception of motion direction by evaluating the effects of differing motion signals (direction and strength) in one of the two regions (central or peripheral) on the other. The third and fourth experiments are controls, the last of which assesses whether changes in performance are related to motion capture or sensitivity.

2. Experiment 1: speed sensitivity

2.1. Methods

2.1.1. Observers

Four observers participated in the study and had normal or corrected-to-normal acuity. Subjects consisted of two of the authors (CH and JF) and two naive observers (AB and OBL). All subjects except for OBL were psychophysically experienced, and none were aware of ongoing results. Only OBL and CH participated in experiment 1.

2.1.2. Apparatus and stimuli

Stimuli were generated on a Power Macintosh G3 and were rear-projected onto a Da-Lite Fast-Fold 2.44×1.83 m screen, from a distance of 4.10 m. The image was projected on the screen using an InFocus LP725 projector scanning at 75 Hz with a resolution of 800×600 . The projected image subtended $116^\circ \times 86.5^\circ$ from the viewing distance of 114 cm.

Optic-flow stimuli used in the present experiment simulated observer translation through a circular tunnel, and flow parameters such as speed and dot distribution are described in 2-D space (as represented on the screen) except where otherwise specified. Stimuli were presented in a circular 80° (diameter) field containing 150 hard-edged square dots. In 3-D space (world coordinates), dots were placed along the tunnel wall with a uniform random distribution (Fig. 1a). When viewed head-on (2-D space), as when moving down the tunnel, dots appeared more sparsely distributed with distance from center (as dictated by perspective, Fig. 1b). Dots subtended $0.5^\circ \times 0.5^\circ$ with a luminance of 10 cd/m^2 , and background luminance was 1.8 cd/m^2 , for a Michelson

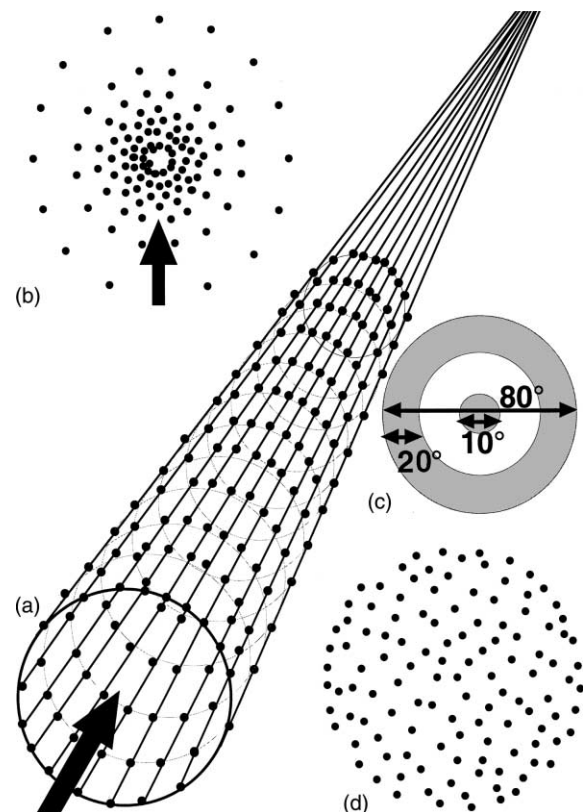


Fig. 1. (a) Illustration of dots on a tunnel wall with perspective information when viewed from the side (Note: dots in the actual stimulus were randomly distributed along the tunnel wall, unlike the regular spacing illustrated here). (b) Head-on view, as in experiments 1 and 2: stimulus with density and speed gradients. (c) Illustration of spatial layout used for measuring central–peripheral interactions in experiments 2, 3b, and 4. (d) Illustration of stimulus with uniform density and constant speed used in experiments 3 and 4.

Table 1

Dot velocities (deg/s) yielded by different jump sizes for a given region expressed in 2-D coordinates as dot moves along screen

Jump size (spatial unit)	Corresponding speed range for each eccentricity region (deg/s) in 2-D coordinates (dot displacement on screen)			
	Central 1.25°–5° ecc	5°–10° ecc	10°–20° ecc	20°–40° ecc
0.0625				
0.09375				2.813–11.25
0.125		0.2344–0.9375	0.9375–3.750	3.750–15.00
0.1875				5.625–22.50
0.25		0.4688–1.875	1.875–7.500	7.500–30.00
0.375				11.25–45.00
0.5		0.9375–3.750	3.750–15.00	15.00–60.00
0.75				22.50–90.00
1	0.1172–1.875	1.875–7.500	7.500–30.00	
1.5	0.1758–2.813		11.25–45.00	
2	0.2344–3.750	3.750–15.00		
4	0.4688–7.500	7.500–30.00		
8	0.9375–15.00			
12	1.406–22.50			
16	1.875–30.00			

contrast of 70%. A circular central region of 1.15° (diameter) around fixation was left blank. A red dot subtending 0.5°, marked the center of the display and served as a fixation point. The stimulus consisted of four-frame random-dot kinematograms simulating translation down a tunnel. Dot lifetime was two frames (1 jump), after which a dot was randomly repositioned as signal or noise. Noise dots appeared to move in random directions along the same trajectories. One frame lasted 26.7 ms and the inter-frame interval was 26.7 ms; total stimulus presentation time was 186.7 ms. A relatively short presentation time was used to minimize eye movements.

In order to simulate the optic-flow field during translation down a tunnel, dot speed increased with the square of the distance from the center of expansion. In other words, dot speed increased by a factor of four as the distance doubled. For example, for a displacement (jump) size of 1 spatial unit (see below), a dot with a speed of 1.875 deg/s at a radius (or eccentricity) of 5° would travel at a speed of 7.5 deg/s at 10°, 30 deg/s at 20°, and 120 deg/s at 40°. The size of the spatial displacement that dots covered between frames (jump size) could be controlled so that dots traveled greater distances and thus appeared to move faster. For example, a displacement of 1 spatial unit corresponded to a dot speed of 1.875 deg/s at a radius (or eccentricity) of 5° and a displacement of 2, to 3.75 deg/s at this same eccentricity. The current stimulus configuration (speed increases and tunnel) was chosen to better simulate optic-flow in the natural environment, where speed changes are larger for nearer than for further areas. Dot size was not increased with eccentricity because previous work showed similar thresholds whether dots were scaled for size (to mimic optic flow) or not (Habak, Casanova, & Faubert, 2000).

In order to measure speed sensitivity at various eccentricities, stimuli were curtailed in various ways. Dots were visible within a central region subtending 10° in

diameter, or within annuli whose inner and outer diameters subtended 10°–20° (5°–10° eccentricity), 20°–40° (10°–20° eccentricity), or 40°–80° (20°–40° eccentricity). A full-field stimulus condition (80° diameter field) was also tested. Isolated regions were obtained by masking the full-field stimulus so that dot number and speed in each region were equal to their respective distributions in the full-field condition. As optic-flow stimuli contain a speed gradient, speeds tested are expressed in jump size units (described above) to allow for direct comparison of curtailed regions and full-field stimuli. Displacement (jump) sizes tested here and their corresponding 2-D speed values in deg/s (dot speed moving along the screen) are shown for each region (eccentricity) in Table 1.

2.1.3. Procedure

Coherence thresholds (minimum proportion of dots moving in the same direction that yields a coherent percept) taken at 75% of correct responses were measured using the method of constant stimuli (levels along log steps). The stimulus was presented in one interval; subjects were required to discriminate whether the flow field was expanding or contracting. Subjects initiated each trial with a key-press and indicated their response with a key-press. Testing was carried out for one eccentricity at a time and the various speeds were randomly interleaved within this bloc. The order of conditions (eccentricity) was randomized from session to session and across subjects. Each point (given speed at a given eccentricity) was tested a minimum of three times so as to yield a measure of standard error.

2.2. Results

Results show that stimulation of each visual field region yielded sensitivity to a limited range of speeds (Fig. 2a). In general, sensitivity to lower speeds decreased with

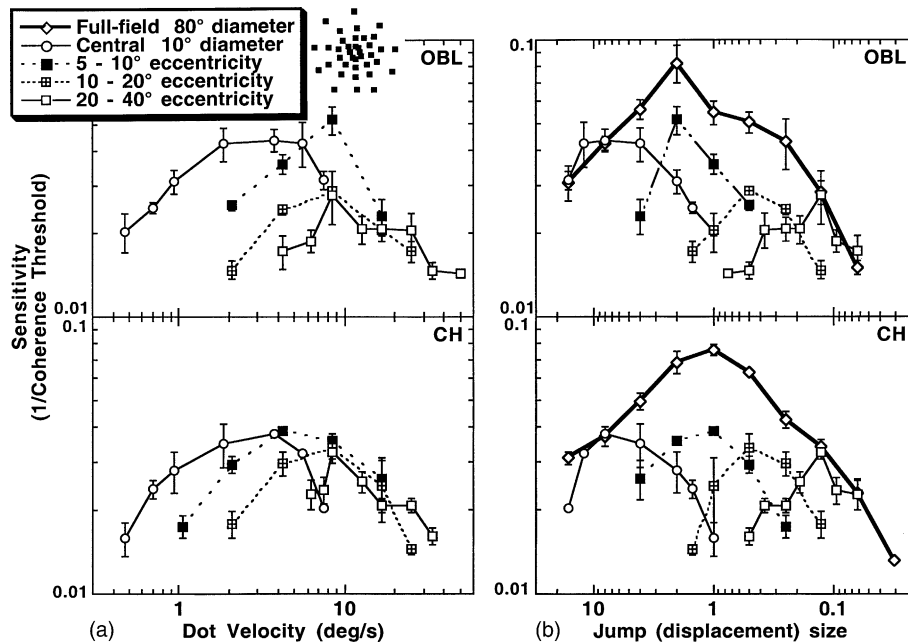


Fig. 2. Experiment 1: (a) Sensitivity (1/coherence threshold) for each region tested, as a function of dot velocity across the screen (2-D space) for the stimulus with density and speed gradients. Because of the speed gradient, dot velocity for a given region is taken at mid-radius (e.g. for the 20°–40° eccentricity region, dot velocity at 30° of eccentricity is used on the graph). (b) Sensitivity (1/coherence threshold) for each region and for the full-field stimulus as a function of jump size. Bars represent the standard error of the mean.

eccentricity, and the peak speed sensitivity for a given region increased with eccentricity. Peak sensitivity (≈ 0.033) was similar for all regions except for the most peripheral region (≈ 0.025). In Fig. 2b, results are plotted as a function of jump size to allow for a point by point comparison of a given curtailed region and the full-field stimulus. Results for full-field (80°) stimulation show an increase in sensitivity by factors of up to 1.5 (OBL) and 2 (CH) at mid-range speeds (jump sizes) when compared to sensitivity for each region alone. At the extremes (very high or very low speeds), sensitivity measured for the full-field is no better than that for each region alone.

3. Experiment 2: central and peripheral interactions

3.1. Methods

Apparatus and stimuli are generally the same as those in experiment 1. In order to probe central and peripheral visual fields, dots were curtailed to a central circular region subtending 10° in diameter or a peripheral annulus with inner and outer diameters of 40° and 80° (20°–40° eccentricity) respectively. Based on experiment 1, each region was tested at a jump size that yielded approximately equal sensitivities for the two regions. Specifically, central stimuli were presented at a jump size of 2 units (dot speed ranging from 0.23 to 3.75 deg/s)

and peripheral stimuli at 0.25 units (dot speed ranging from 7.5 to 30 deg/s).

3.1.1. Baseline conditions

Dot coherence thresholds using the same procedure as described in experiment 1 were made for the central region alone (C), the peripheral region alone (P), and for the two regions shown simultaneously with the same dot coherence level and direction of motion (C + P). When dots are said to move in the “same” direction in both regions, the motion pattern in the two regions is the same (i.e. motion in both regions is either expanding or contracting).

3.1.2. Test conditions

A set of conditions in which subjects attended to a given region (while maintaining fixation) was tested. Subjects were instructed to report whether the central region only appeared to expand or contract, regardless of any peripheral information. Dots in the peripheral annulus could appear to move in the same direction as those in the central region (“same”), in the opposite direction (“opposite”), or in random directions (0% coherence; termed “noise”). Dots in the peripheral field were presented at 100% coherence when moving in the same direction as, or opposite to dots in the central region. These various apparent motion directions were randomly interleaved in the same bloc of trials while coherence thresholds were measured for the central re-

gion (central measure). A condition, in which the reverse was tested, consisted of measuring coherence thresholds for the peripheral annulus when information in the central region was the same, opposite, or contained noise (peripheral measure). Observers were instructed to report the direction of motion of the peripheral annulus regardless of any central information. Coherence threshold calculations were made as above and were based solely on dots appearing in the target region (central for central measure and peripheral for peripheral measure). Testing order for all conditions was randomized from one session to another and across subjects. Each point was tested a minimum of three times so as to yield a measure of standard error.

3.2. Results

Group results for baseline and test conditions are shown in Fig. 3, and individual data in Table 2.

Baseline conditions: Generally, coherence thresholds are similar for both central (C) and peripheral (P) regions and are lower when both regions (C + P) are presented simultaneously.

Test conditions: Generally, the presence of noise and of dots moving in the opposite direction led to an increase in threshold whether measures were central (mean magnitude of increase in dot coherence threshold for noise of 3.79 ± 12.3 and for opposite-direction dots of 20.7 ± 17.0) or peripheral (magnitude of increase of 4.41 and 14.2 for noise and opposite-direction dots, respectively). Same-direction peripheral-measure thresholds were approximately equal to the baseline measure when both regions are present, whereas central-measure thresholds show a decrease of ≈ 14.9 (dot coherence) below this baseline (JF: 15.2, OBL: 1.1, AB: 25.7, CH: 17.6).

4. Experiment 3: uniform dot density and constant speed control

Experiments 1 and 2 were conducted with an ecologically valid optic-flow stimulus, in which dot density

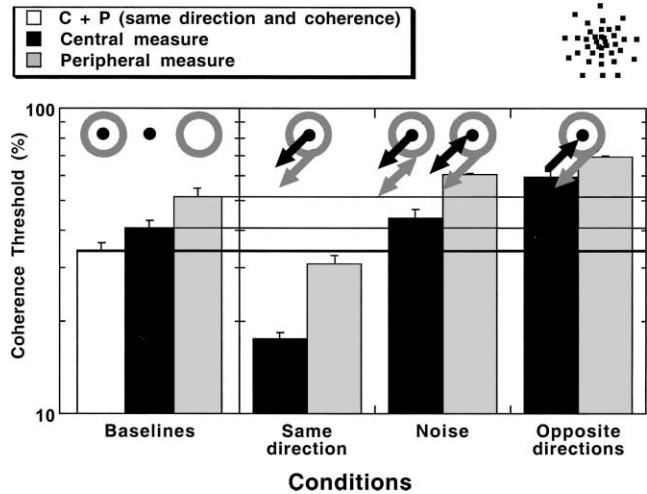


Fig. 3. Experiment 2: group mean ($n = 4$) direction discrimination coherence thresholds as a function of dot direction in the periphery for the stimulus with density and speed gradients. Baseline measures are shown on the left-hand side for both central and peripheral regions when dots move in the same direction and have the same coherence (C + P: hollow bar), for the central region alone (black) and for the peripheral region alone (grey). The right-hand side of the graph shows thresholds when subjects are instructed to attend to a given region (attend central: black bars; attend peripheral: grey bars) while dots in the other region move in the same direction, randomly (noise), or in the opposite direction. Bars show the standard error of the mean.

and speed varied with distance from the center. These gradients may lead to the summation pattern reported in experiment 1 and to the facilitation asymmetry between central and peripheral regions reported in experiment 2. The purpose of the current controls is to assess whether the findings may be generalized to radial motion stimuli in which dot density and speed are constant (Fig. 1d).

Speed sensitivity (CH) and central and peripheral interactions (AB, CH, OBL) were assessed by replicating experiments 1 and 2, using the same methods, with certain aspects of the stimulus that differed. Specifically, radial motion RDKs in which dot speed was constant and dot density uniform at 0.41 dots/deg^2 (2048 dots for the 80° field) were used.

Table 2 Individual coherence thresholds for all conditions in experiment 2, mean (standard error of the mean)

	Baseline conditions		Test conditions		
	C + P	Central measure	Same	Noise	Opposite
jf	33.28 (2.2)	46.74 (4.6)	18.08 (3.35)	38.65 (3.41)	55.39
obl	25.06 (2.8)	37.96 (6.5)	23.97 (1.6)	34.53 (1.0)	41.83 (6.5)
ab	52.22 (7.0)	55.15 (5.6)	16.53 (10.7)	69.90 (3.9)	91.52
ch	31.40 (3.0)	27.83 (2.0)	13.84 (5.2)	39.92 (1.8)	60.82 (1.2)
		<i>Peripheral measure</i>			
jf		45.13 (4.9)	20.95 (4.5)	58.52 (1.9)	63.76 (10.9)
obl		42.64 (3.1)	30.06 (4.0)	59.68 (7.4)	67.390
ab		80.02 (1.2)	44.50 (4.4)	65.89 (4.5)	70.21 (3.5)
ch		45.96 (6.3)	33.13 (2.8)	58.67 (3.5)	75.41 (3.0)

4.1. Experiment 3a: speed sensitivity

In order to assess sensitivity to speed (experiment 3a), thresholds were measured for the full-field stimulus and for each region separately at a range of speeds: 0.5, 0.75, 1, 2, 4, 6, 8, 16, 24, 32, and 48 deg/s.

Speed sensitivity results (Fig. 4) show that stimulation of each region yielded sensitivity to most of the speeds tested. Sensitivity was similar for the 10°–20°, 20°–40°, and the full-field regions with a peak of 0.1–0.2 at ≈ 4–6 deg/s. For the central region and the 5°–10° annulus, sensitivity was similar to that of the other regions for speeds up to 4–6 deg/s but dropped off beyond this point. Sensitivity to slower speeds (below 4 deg/s) is similar for the regions tested here and for the full-field stimulus in experiment 1. At 4 deg/s and beyond, sensitivity for the peripheral (10°–20° and 20°–40°) and full-

field regions exceeds that of the full-field stimulus in experiment 1 by a factor of ≈2.5–3.

4.2. Experiment 3b: central and peripheral interactions

In order to measure central and peripheral interactions (experiment 3b), speed was maintained at 6 deg/s; a speed at which sensitivity was approximately equal for each of the two regions.

Central and peripheral interaction results show a similar pattern to those of experiment 2. Group results for baseline and test conditions are shown in Fig. 5, and individual data in Table 3.

Baseline conditions: Generally, coherence thresholds are similar for each of the central (C) and peripheral (P)

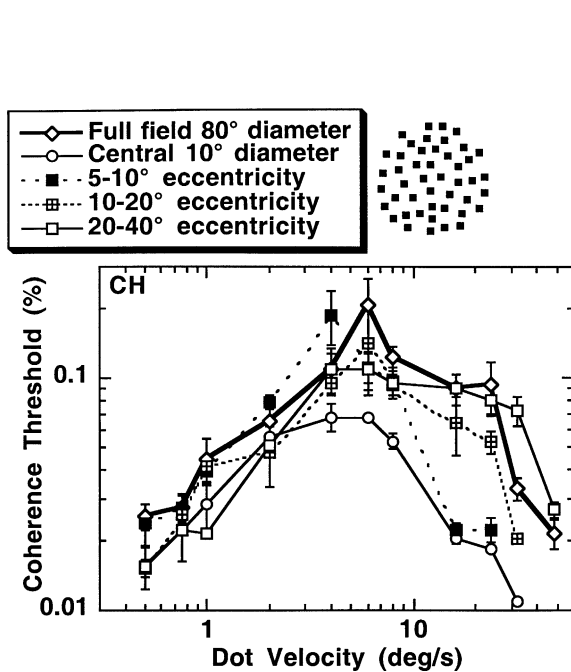


Fig. 4. Experiment 3a: sensitivity (1/coherence threshold) for each region tested, as a function of dot velocity across the screen (2-D space) for the stimulus with uniform density and constant speed. Bars represent the standard error of the mean.

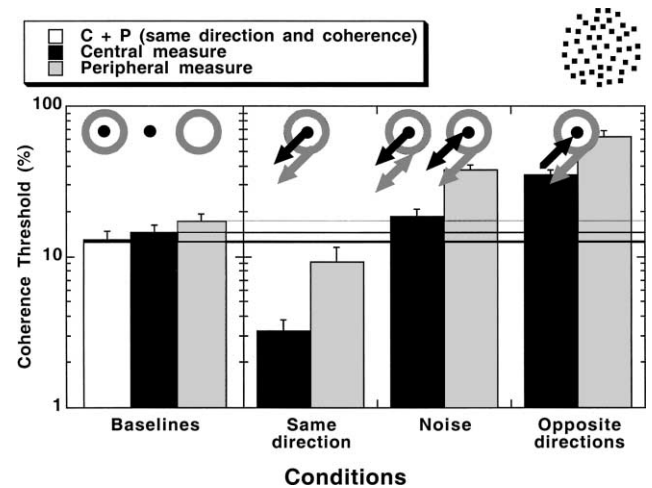


Fig. 5. Experiment 3b: group mean ($n = 3$) direction discrimination coherence thresholds as a function of dot direction in the periphery for the stimulus with uniform density and constant speed. Baseline measures are shown on the left-hand side for both central and peripheral regions when dots move in the same direction and have the same coherence (C + P: hollow bar), for the central region alone (black) and for the peripheral region alone (grey). The right-hand side of the graph shows thresholds when subjects are instructed to attend to a given region (attend central: black bars; attend peripheral: grey bars) while dots in the other region move in the same direction, randomly (noise), or in the opposite direction. Bars show the standard error of the mean.

Table 3

Individual coherence thresholds for all conditions in experiment 3b, mean (standard error of the mean)

	Baseline conditions		Test conditions		
	C + P	Central measure	Same	Noise	Opposite
obl	10.56 (2.5)	13.45 (2.6)	2.75 (0.5)	20.58 (2.4)	24.85 (1.2)
ab	25.56 (2.0)	25.22 (2.3)	10.16 (4.5)	28.82 (3.5)	45.81 (9.3)
ch	7.67 (2.9)	8.72 (1.5)	1.16 (0.07)	10.49 (5.2)	37.56 (5.6)
		Peripheral measure			
obl		16.00 (2.3)	3.634 (2.13)	36.06 (0.9)	87.68 (2.1)
ab		27.85 (4.3)	31.78 (8.0)	55.19 (6.7)	70.22 (8.9)
ch		11.49 (1.5)	6.778 (1.4)	26.68 (4.9)	39.34 (5.8)

regions presented alone and for both regions presented simultaneously (C + P).

4.2.1. Test conditions

Generally, the presence of noise dots had little effect on central measures (slight increase) but led to an increase in threshold for peripheral measures (mean magnitude of dot coherence threshold increase: 5.26 ± 4.14 and 24.6 ± 5.51 , respectively). Dots moving in the opposite direction led to an increase in threshold whether measures were central (mean magnitude of increase 21.4 ± 7.71) or peripheral (increase of 51.0 ± 23.5), but the increase was larger for the latter. Same-direction peripheral-measure thresholds were approximately equal to baseline measures, whereas central-measure thresholds showed a decrease of ≈ 10.0 (dot coherence) below this baseline (OBL: 7.8, AB: 15, CH: 6.8).

5. Experiment 4: sensitivity change or motion capture?

The pattern of results revealed thus far for central and peripheral interactions may arise from two sources. The first is that facilitation and masking may reflect actual changes in sensitivity. The second possible source is motion capture, where the percept (motion direction) is biased towards the direction of motion in the region with the stronger signal. In order to assess whether changes resulted from shifts in sensitivity alone, a 2IFC paradigm was used to measure detection thresholds. Any threshold change that arises would most likely result from changes in sensitivity because the perceived direction of motion is not required in responses per se. Observer CH reported which of the two intervals contained coherent motion in the target/attended region (central or peripheral).

The same stimulus and methods as in the uniform dot density and constant speed control (experiment 3b) were used. As in the experiments above, the observer attended to the central region for central measures and to the peripheral annulus for peripheral measures.

Results (CH) for baseline and test conditions are shown in Fig. 6 and show a somewhat different pattern from those in previous experiments.

Baseline conditions: Generally, coherence thresholds are similar for the three measures (C, P, and C + P).

Test conditions: Generally, central measure thresholds varied from baseline measures, and little change in threshold was evident for peripheral measures. The presence of noise dots led to little or no increase for both central and peripheral measures. The presence of dots moving in the opposite direction led to a large increase in coherence threshold for the central measure (magnitude of increase: 28.6) and a small one for the peripheral measure (magnitude of increase: 7.37). Thresholds for

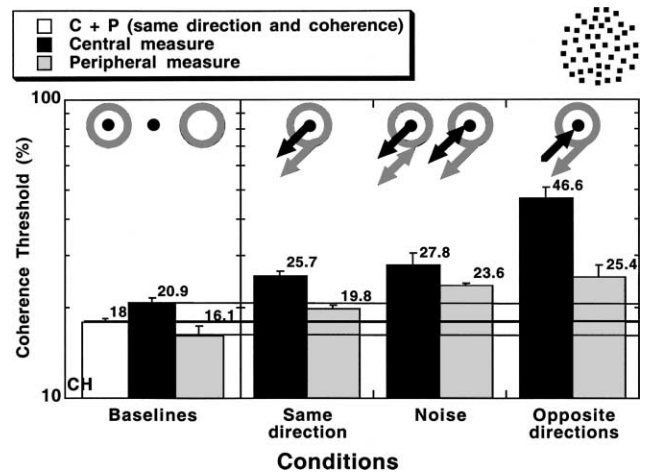


Fig. 6. Experiment 4: detection coherence thresholds as a function of dot direction in the periphery for the stimulus with uniform density and constant speed ($n = 1$). Baseline measures are shown on the left-hand side for both central and peripheral regions when dots move in the same direction and have the same coherence (C + P: hollow bar), for the central region alone (black) and for the peripheral region alone (grey). The right-hand side of the graph shows thresholds when subjects are instructed to attend to a given region (attend central: black bars; attend peripheral: grey bars) while dots in the other region move in the same direction, randomly (noise), or in the opposite direction. Bars show the standard error of the mean.

the same-direction condition were similar to baseline measures.

6. General discussion

6.1. Speed sensitivity

In summary, results from experiment 1 show that sensitivity to slower speeds decreases with eccentricity and that the best measures for each region alone are comparable across regions. When a uniform density and constant speed stimulus is used (experiment 3a), speed sensitivity is similar for all regions, but drops off at mid- to high-range speeds for smaller (more central) regions. Generally, these findings are consistent with those of Burr et al. (1998) who measured speed sensitivity for circular-trajectory RDKs with a constant speed profile, and with other studies that have assessed motion sensitivity throughout the visual field (van de Grind, van Doorn, & Koenderink, 1983). In comparing the speed sensitivity measured with the two different stimuli, it becomes apparent that sensitivity to slower speeds is similar for both stimuli, whereas sensitivity to faster speeds is generally higher for the uniform density and constant speed pattern. In experiment 1 (stimulus with density and speed gradients) sensitivity to slower speeds was largely dominated by the more central regions. These regions contained a relatively high number of

dots, and density was comparable to that of similar regions in experiment 3a (uniform density and constant speed stimulus). In contrast, the peripheral annuli in experiment 1 contained much fewer dots (≈ 10 for the farthest annulus) than the annuli with uniform density and constant speed. This extremely low dot density may have made for a weaker signal, whereas the larger number of dots may have provided a stronger signal.

Another point of interest is that sensitivity for the full-field stimulus was higher than that for any region alone when using the flow stimulus with density and speed gradients (experiment 2) but not the radial motion stimulus (uniform density and speed). This suggests summation within the optic-flow mechanism (consistent with existing data demonstrating extensive areas of integration, Burr et al., 1998; Duffy & Wurtz, 1991). In order to better understand the relative contribution of different sectors and to compare the findings from both stimulus types, the full-field data of each was compared to fits (data and fits for experiment 1 shown in Fig. 7a, and those for experiment 2 in Fig. 7b). The first predicted that full-field sensitivity was determined by simple linear summation of responses across all regions at a given point. The second used the same computation as the first with the constraint that responses from only the two most sensitive adjacent regions are summed linearly (this implies that the inner or outer sector was always discarded). The third fit only plotted points from the single most sensitive region (winner-take-all). For the stimulus with density and speed gradients, Fig. 7a shows that simple linear summation across all regions overestimates full-field sensitivity at mid-range speeds,

whereas the addition of the constraint predicts the pattern of sensitivity almost perfectly (more so for OBL than CH). This suggests that the optic-flow mechanism seems to sum information linearly across the two most sensitive regions, and that any additional responses may not be taken into account. In contrast, for the uniform density and constant speed stimulus (Fig. 7b), fits 1 and 2 over-estimated sensitivity, and the third fit predicted the full-field data almost perfectly. This suggests that additional responses may not be taken into account. For this last fit, full-field sensitivity matched that of the 5° – 10° or 10° – 20° annulus for speeds of 8 deg/s or less, and that of the 20° – 40° annulus for speeds above 8 deg/s.

This pattern suggests that when not saturated (as in experiment 1), the optic-flow mechanism sums across larger regions, whereas more optimal stimuli do not require such large areas of integration. In other words, the spatial extent over which the optic-flow mechanism integrates seems to be flexible. The purpose of such a mechanism may be to maximize the information available to the system and thus to provide a more robust percept.

6.2. Center-periphery interactions

Similar patterns are found for the radial motion stimulus with density and speed gradients (experiment 2) and for the stimulus with uniform density and constant speed (experiment 3b); these are thus considered together in this section. The presence of dots moving in random directions (noise) or in directions opposite to those in the measured (target) region lead to threshold elevations (masking) in direction discrimination. Dots in the opposite direction lead to larger elevations than noise. The masking caused by the presence of noise and opposite-direction motion signals over a large spatial distance (15°) is consistent with summation within a large-extent mechanism as shown by Burr et al. (1998). Present results also suggest that this mechanism is extremely robust, as peripheral signals affected threshold measures when subjects were instructed to attend to the central region and ignore any other stimulation.

The presence of noise dots in either center or periphery led to similar threshold elevations, though the effect of central noise dots on the periphery was slightly larger. Dots moving in the opposite direction led to a threshold elevation (consistent with Mather & Moulden, 1980, 1983 though for different measures) of larger magnitude but of similar pattern to that of noise dots. These results suggest that central and peripheral stimulation do not have a differential effect on the perception of optic flow. These findings taken with those from experiment 1 are consistent with the retinal invariance theory, in that sensitivity is similar irrespective of eccentricity, and that various regions have equal effects on integration.

When dots in both central and peripheral regions appeared to move in the same direction, thresholds de-

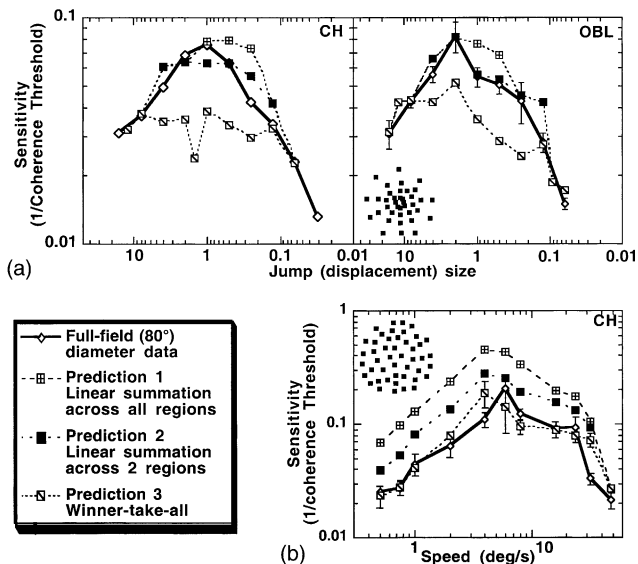


Fig. 7. Full-field (80° diameter) shown with three possible fits: 1—linear summation across all regions, 2—linear summation with the constraint that only responses from the two most sensitive adjacent regions are considered, 3—no summation across regions, the single most sensitive region is considered (winner-take-all).

creased to baseline for the peripheral measure, and to below-baseline for the central measure. In other words, peripheral signals had a dramatic facilitatory effect on central measures, but not the reverse. The much larger area of peripheral (3769.9 deg^2) as opposed to central (78.5 deg^2) stimulation may be responsible for this asymmetrical facilitatory effect of periphery on center. Two reasons make this explanation unlikely however. The first is that coherence thresholds for each region measured alone (baseline) were similar, and slightly better for the central region. More importantly, the presence of noise and opposite-direction dots in either central or peripheral regions had similar effects on threshold measures. If area of stimulation were a factor, noise and opposite-direction dots would have led to larger threshold elevations when present in the periphery than when in the center. Facilitation reached the same absolute levels as the sensitivity peak for the full-field stimulus (80°) in experiment 1 and was slightly better than those of the full-field in experiment 3b (conditions compared to their respective stimulus). This suggests that threshold decrease (facilitation) may only be as good as the system's maximum sensitivity (best threshold for full-field stimulus). Another possible explanation for the extensive asymmetrical facilitation when dots move in the same direction is that subjects may have relied entirely on the peripheral region to determine the percept. This explanation is unlikely however, because presentations were randomly interleaved; in other words, subjects did not know whether noise, same-, or opposite-direction dots were to appear. Two patterns would have emerged had subjects based their judgement entirely on the peripheral region. The first is that thresholds would have increased extensively for the noise condition. The second is that performance would have approached 0% correct responses for the opposite-direction condition, which was not the case as performance at low-coherence levels (central-measure) was no worse than chance. The finding of an asymmetrical facilitation may explain some of the earlier peripheral dominance hypothesis results (Berthoz et al., 1975; Brandt et al., 1973), in that peripheral signals were often more salient than central ones.

6.3. Facilitation and masking: sensitivity or bias?

The facilitation and masking effects described above may result from changes in sensitivity, from the motion in one region biasing the perceived direction of motion in the other (bias or motion capture), or from a combination of the two. The last experiment measured detection thresholds and was not subject to such bias. A summary of changes in threshold for all three experiments (observer CH) is shown in Fig. 8. Masking effects persisted in the last experiment (right-hand side panel) whereas facilitation disappeared completely. This pat-

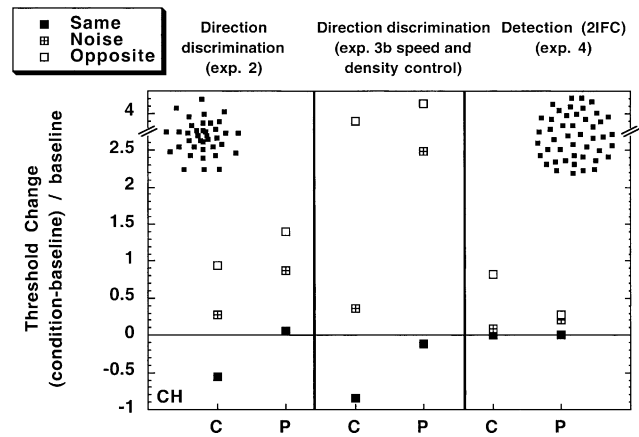


Fig. 8. Threshold change when dots in the non-target region move in the same direction as (full symbols), randomly (crossed symbols), or in a direction opposite (hollow symbols) to that in the attended region. Data re-plotted from experiments 2, 3b, and 4 and are shown for each of the attended regions. Note: for experiment 4, thresholds for each condition were subtracted from the "same direction" thresholds instead of baseline values because the former were slightly elevated when compared to baseline.

tern suggests that dots moving in the opposite direction lead to changes in sensitivity (certainly for central measures) and that facilitation most likely arises from motion capture. This is not absolute however, as dots moving in opposite directions may also provide some bias because masking effects are much larger in direction discrimination tasks (experiment 3b, center panel) than in coherent motion detection tasks (experiment 4, right-hand side panel).

The question remains however, as to why sensitivity changes in the detection task occur for opposite-direction dots, whereas facilitation in direction discrimination tasks occurs for same-direction dots. The threshold elevation for the detection task in the present work may arise from the larger area of stimulation of the peripheral annulus or from a different representation. The representation may differ, in that opposing signals in different spatial locations may be interpreted as a large deforming pattern (as opposed to an expansion and a contraction). Some support for this suggestion comes from work using a compound stimulus made up of two superimposed components, each of which moved in opposite directions (Meese & Harris, 2001). Detection thresholds for a compound deformation stimulus were higher (inhibition) than for each component alone, whereas summation was reported for compound radial-motion stimuli. Though counter-intuitive, this finding relates to the present work in that opposite-direction signals in the stimuli used here are spatially distinct. The different opposing motions in various parts of space, may simply appear as two planes or as a deformation.

In terms of the facilitation of periphery on center for same-direction dots, the direction discrimination task with large stimuli relates to navigation. Ecological

factors may provide a reason for the existence of a facilitation effect that seems to be asymmetrical when discriminating motion direction. Under the present conditions, a rich motion signal in the periphery (100% coherence) captured the perceived direction of motion in the center where signals were less prominent (dot coherence was modified in order to measure thresholds), but not the reverse. Conditions of low-visibility such as fog, low-illumination, or dense foliage often lead to poor visibility at far-distances (central vision) and clearer near-by views (peripheral vision), whereas the reverse is not observed. Under such conditions, a mechanism may have evolved to aid in the perception of optic flow, in which peripheral signals capture central information, whereas the reverse is simply not necessary. These conditions may be likened to poor (lower coherence) signals from the central portion of the visual field and richer signals (100% coherence) from the periphery in the present study.

7. Conclusion

In conclusion, central and peripheral vision provide equal input to the mechanism underlying the perception of optic flow. Central and peripheral information should be considered as a single entity for optic-flow mechanisms, which simply integrate information over large spatial extents, irrespective of location. This integration is quite robust as it takes place even when subjects are instructed to ignore distant information. An asymmetry arises when strong signals are present in one region and weak signals in the other. For direction discrimination, strong signals from the periphery facilitate the percept when central signals are weaker, but not the reverse. Generally, opposing signals lead to an increase in both detection and direction discrimination thresholds. These findings are consistent with ecological phenomena.

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