

# Outputs of Paired Gabor Filters Summed Across the Background Frame of Reference Predict the Direction of Movement

TERI B. LAWTON

**Abstract**—A cortical neural network that computes the visibility of shifts in the direction of movement is proposed that computes: 1) the magnitude of the position difference between the test and background patterns, 2) localized contrast differences at different spatial scales analyzed by computing temporal gradients of the difference and sum of the outputs of paired even- and odd-symmetric bandpass filters convolved with the input pattern, and 3) using global processes that pool the output from paired even- and odd-symmetric simple and complex cells across the spatial extent of the background frame of reference to determine the direction a test pattern moved relative to a textured background. Evidence is presented that magnocellular pathways are used to discriminate the direction of movement. Since magnocellular pathways are used to discriminate the direction of movement, this task is not affected by small pattern changes such as jitter, short presentations, blurring, and different background contrasts that result when the veiling illumination in a scene changes.

## INTRODUCTION

THE MOVEMENT of objects relative to their background is used to infer the three-dimensional structure and motion of object surfaces. Apparent movement is perceived by the observer when an object appears at one spatial position and then appears at a second nearby spatial position a short time later [1]; for example, the movement seen when two nearby lights flash asynchronously in the night. The shift in the spatial position of contrast differences (light against a dark background) over a short time interval induces the perception of movement. The direction an object is perceived to move is judged relative to a background frame of reference [2]–[4]. Figure-ground segmentation precedes the determination of the direction of movement. When navigating through the environment, objects are perceived to move relative to a textured stationary background. Both the spatio-temporal characteristics of the object and the background frame of reference are used to determine the perceived direction of movement. Studying the visibility of shifts in the direction a pattern moves relative to a background using discrete sequential flashed stimuli has the advantage of providing a more “analytic” stimulus with which to separately manipulate the spatial and temporal aspects of movement.

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The author is with Robotics Teleoperators, Human Factors Research Group, Jet Propulsion Laboratory, California Institute of Technology, Pasadena, CA 91109.

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Optical flow, an important cue for navigation, is determined by measuring the rate of movement over time, divided by the rate of movement across space [5]. Determining the direction an object moves relative to the observer is used to disambiguate objects from the background frame of reference. To navigate effectively, the optical flow of objects in the environment, relative to the observer and other objects, is used by both human and computer vision systems.

## SPATIO-TEMPORAL CHARACTERISTICS THAT AFFECT DIRECTION DISCRIMINATION

Visual psychophysics research has uncovered several important properties of the spatio-temporal characteristics of test and background patterns that determine the direction a simple pattern is seen to move, such as a sinewave grating, relative to a textured background. The contrast, position or spatial phase, the spatial frequencies, and the temporal frequencies that characterize the test object and its background affect the direction a pattern is perceived to move, relative to its background. When identifying patterns where the test sinewave grating is shifted in position, relative to a textured background composed of single and multiple spatial-frequency components, the visibility of left–right movement was found to be predicted by spatially-localized paired Gabor [6] filters (paired even- and odd-symmetric filters optimally tuned to a 90° phase difference) summed across the background frame of reference [4], [7].

*The visibility of shifts in the direction of movement increased (a lower contrast was needed to identify the direction of movement):*

1) As the spatial-phase difference (between the peak luminance of the test pattern relative to the background) increased from a minimum phase difference of 4° [8] up to a maximum phase difference of 90° [9]–[11]. Increasing the phase difference from 90 to 180° did not change the visibility of shifts in the direction of movement. Paired Gabor filters which are orthogonal filters tuned to a spatial-phase difference of 90°, that is, they are in quadrature phase, predict these results [11].

2) As the temporal duration was increased when measuring the minimum spatial-phase difference needed to discriminate the direction of movement [12]. Yet once the test and background spatial-frequencies differ in spatial-

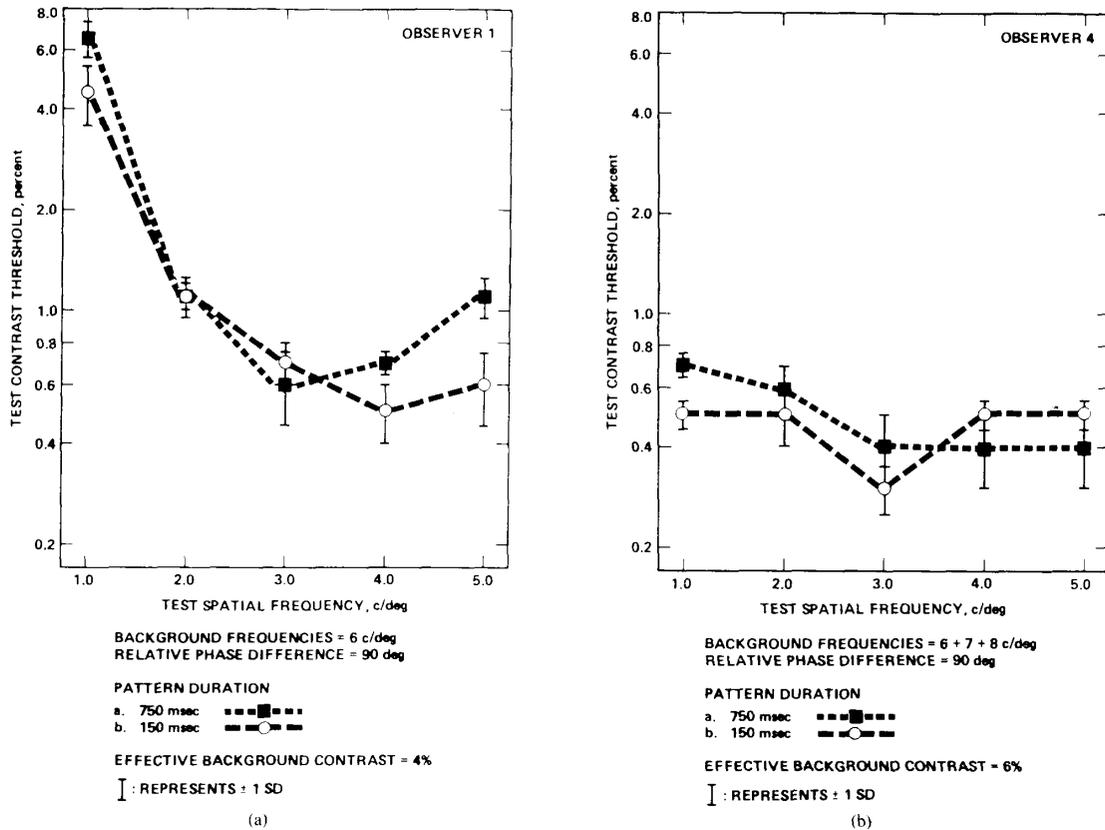


Fig. 1. The visibility of shifts in the direction of movement as the temporal frequency was increased by reducing: 1) the test and comparison pattern durations, Fig. 1(a)–(c) or 2) the duration between each pair of patterns, Fig. 1(d). To measure the effects of increasing the temporal frequency on the visibility of shifts in the direction a test pattern moved relative to a textured background, the peak luminance of the test spatial-frequency in test and comparison patterns differed in position optimally ( $90^\circ$ ) relative to the peak luminance of single [Fig. 1(a)] and multifrequency backgrounds [Fig. 1(b)–(d)]. The test sinusoidal grating was either shifted  $45^\circ$  to the left or to the right of the background's peak luminance, before being added to the background. The temporal frequency was increased by reducing the duration of test and comparison pattern 1) from 750 ms to 150 ms for a) a 6 cyc/deg background in Fig. 1(a) and (b) a 6 + 7 + 8 cycle/deg background in Fig. 1(b), and 2) from 150 ms down to 25 ms for a 6 + 7 + 8 cycle/deg background in Fig. 1(c). The temporal frequency was also increased by reducing the duration between each pair of test and comparison patterns from 500 ms down to 50 ms for a 6 + 7 + 8 cycle/deg background in Fig. 1(d). Contrast thresholds were obtained using a two-alternative temporal forced-choice staircase procedure [4], [10] for the data presented in all figures. Auditory feedback was always given following each pair of test and comparison patterns. The interstimulus interval (ISI) separating tone-cued test and comparison patterns that were presented abruptly equalled the pattern duration, except for Fig. 1(d) where this stimulus parameter was varied. The mean luminance of pattern and interstimulus intervals was a constant  $48 \text{ cd/m}^2$  surrounded by a  $20^\circ$  equal-luminance surround for data presented in all figures. Vertical test and background gratings were seen through a circular aperture that subtended  $4^\circ$  of visual angle.

phase optimally (by  $90^\circ$ ), then increasing the temporal frequency by decreasing: a) the duration of test and comparison patterns from 750 ms down to 150 ms (from 1.3 to 20 c/s), or b) the duration between test and comparison patterns from 500 ms down to 50 ms (from 2 to 20 c/s)

did not change the contrast needed to discriminate the direction of movement, see Fig. 1. To determine specificity it is important to present patterns that optimally activate the mechanisms being studied.

3) As the contrast of a low frequency background was

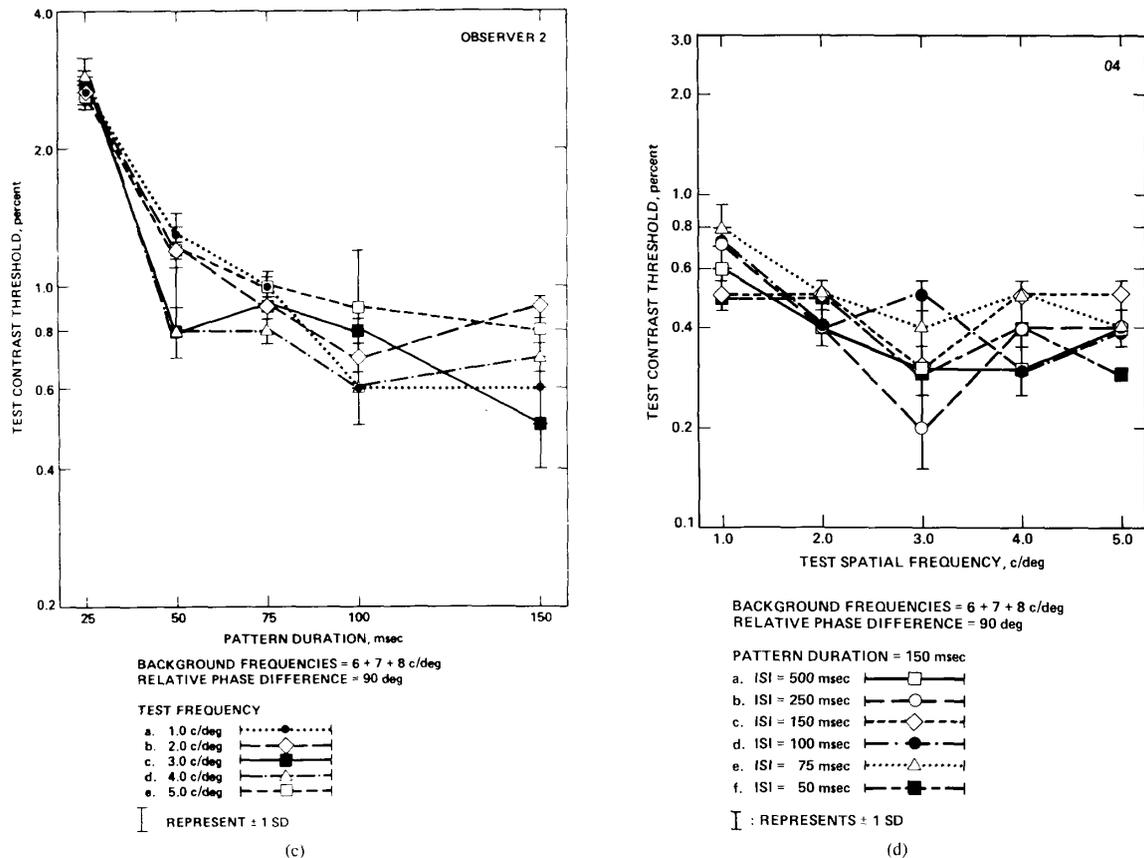


Fig. 1. (Continued.)

increased from 0.5 to 2 percent [13]. On the other hand, increasing the increasing the contrast of a single middle spatial-frequency background from 1 to 16 percent significantly reduced the visibility of shifts in the direction of movement [13]. However, if the background was composed of several middle spatial frequencies that repeat over a wide  $1^\circ$  area, then increasing the effective contrast of the background from 0.6 to 20 percent did not reduce the visibility of shifts in the direction of movement, see Fig. 2. The contrast needed to discriminate the direction a test pattern moved, relative to a clearly visible wide background frame of reference are all low, averaging 1 percent contrast. Since increasing the contrast of the middle spatial-frequency components of the background did not reduce the visibility of apparent movement, as found for backgrounds composed of a single spatial frequency [13], then it is the wide spatial extent of the background (analyzed by global processes in the cortex), and not the individual background frequencies that provides the frame of reference that is used to discriminate the direction of movement.

4) When the test spatial frequency was a harmonic of the background's fundamental frequency, that is, it repeats within the background frame of reference, as op-

posed to when the test frequency is not a higher harmonic of the background's fundamental frequency [4], [10], [14]. Global contrast differences that correspond to the width of the textured background provide the frame of reference used to discriminate the direction of movement.

5) When the test pattern was shifted relative to a wide background, such as 6 + 7 + 8 cycle/deg that repeats over a  $1^\circ$  area, as opposed to being shifted relative to a narrow background, such as 6 cycle/deg that repeats over a  $0.17^\circ$  area [4], [7], see Fig. 1(a), (b). Contrast thresholds are low for twice as wide a range of spatial frequencies (3 octaves as opposed to  $1\frac{1}{2}$  octaves) when added to a wide background composed of middle spatial frequencies, such as 6 + 7 cycle/deg as opposed to when added to a single middle spatial frequency background, such as 6 cycle/deg [4], [10]. All scales higher in spatial frequency than the fundamental frequency of the background pattern are used to detect the test pattern to discriminate the direction the test pattern moves. The range of scales that is used to discriminate the direction of movement is determined by the fundamental frequency of the background, that is, by the width of the background frame of reference.

6) As the contrast of middle background spatial fre-

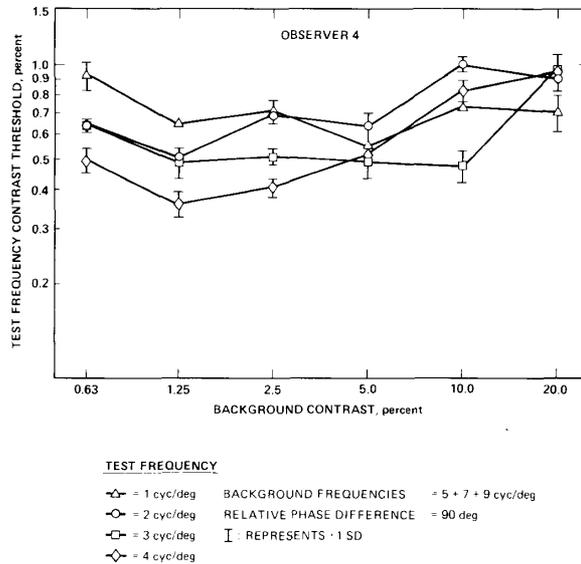


Fig. 2. The visibility of shifts in the direction a test pattern moved, as the contrast of a multifrequency background that provides a wide background frame of reference was increased from 0.6 up to 20 percent. Test spatial frequencies (between 1 and 4 cycle/deg) differed in position optimally ( $90^\circ$ ) relative to a 6 + 7 + 8 cycle/deg multifrequency background. The background frequencies are combined together in cosine phase. The tone-cued test and comparison patterns were presented gradually, using a half sinewave function, for 250 ms each, separated by a 250 ms interstimulus interval.

quencies (5 + 7 + 9 cycle/deg that repeats over a  $1^\circ$  area) are selectively reduced by placing a blur glass in front of the patterns, see Fig. 3. The global low frequency contrast differences within the background provide the frame of reference for discriminating movement. The higher component background spatial frequencies are not as important for discriminating the direction of movement as is the wide frame of reference that corresponds to the spatial extent of the background.

Both the global analysis of groups of edges across the background frame of reference, and the localized computation of contrast differences by paired even- and odd-symmetric Gabor filters within the frame of reference are computed to determine the direction of movement. Both the spatial-frequency composition and the spatial extent of the interval over which the test and background patterns repeat changes the visibility of the direction of movement [4], [10]. The importance of spatial frequency is related to the use of bandpass filtering by the channels used to detect different spatial-frequency components [15]–[18]. The importance of spatial extent is related to the use of a wide background frame of reference to improve the visibility of left–right movement discrimination [4], [10]. Only when discriminating movement relative to a multifrequency background, instead of a background consisting of a single spatial frequency, can the relative contribution of 1) global contrast differences corresponding to the background frame of reference, as opposed to 2) localized contrast differences between individual fre-

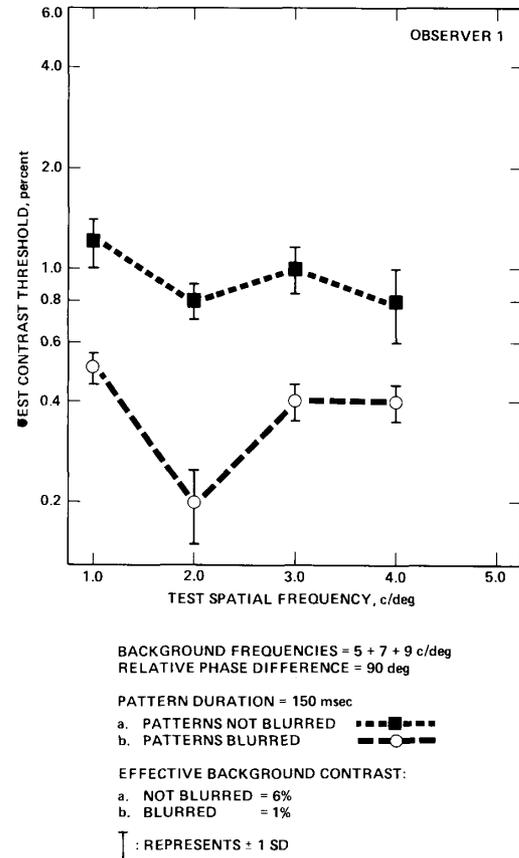


Fig. 3. The visibility of shifts in the direction of movement, relative to a wide multifrequency background, as the contrast of the high background frequencies were selectively reduced (low-pass filtering) by placing a ground glass in front of the patterns. A 6 + 7 + 8 cycle/deg background (repeats every  $1^\circ$ ) was used in Fig. 3(a), and a 5.6 + 6.6 + 7.6 cycle/deg background (repeats every  $5^\circ$ ) was used in Fig. 3(b). The ground glass reduced the contrast of a 2 cycle/deg pattern by a factor of 2 whereas for frequencies 8 cycle/deg or higher no contrast differences were transmitted through the ground glass. The test and comparison patterns were presented abruptly for 150 ms, each separated by a 150 ms interstimulus interval.

quency components be analyzed independently. The results that were found when using patterns that optimally activate direction-selective mechanisms indicate that the output of paired Gabor filters (in quadrature phase) are summed across the background frame of reference to discriminate the direction of movement.

#### OUTPUT FROM PAIRED GABOR FILTERS SUMMED ACROSS BACKGROUND FRAME OF REFERENCE USED TO DETERMINE THE DIRECTION OF MOVEMENT

Paired Gabor [6] filters are used to predict the direction of movement [4], [19]–[21]. A pattern's image intensity is encoded by separable spatio-temporal filters, consisting of paired even- and odd-symmetric simple cells (bar and edge detectors) in quadrature phase, optimally tuned to a  $90^\circ$  spatial-phase difference. For each combination of paired odd- and even-symmetric filters at each spatial scale

being analyzed, the input signal passes through the spatial and temporal filters to produce the four separable responses: each paired spatial filter being processed during two different time intervals by both 1) a low-pass temporal filter, and 2) a bandpass temporal filter optimally tuned to 10 c/s [22], [23]. Sums and differences of paired filters in quadrature phase are taken to produce the spatio-temporally oriented nonlinear responses that are selective for the direction of motion. The mathematical expressions that describe an even-symmetric Gabor function,  $F_{ES}$ , and an odd-symmetric Gabor function  $F_{OS}$  are [6]

$$F_{ES}(f, x, \sigma^2) = \cos(2\pi fx) e^{-(x-x_0)^2/2\sigma^2}$$

$$F_{OS}(f, x, \sigma^2) = \sin(2\pi fx) e^{-(x-x_0)^2/2\sigma^2}$$

where  $f$  corresponds to the spatial frequency of the pattern,  $x$  corresponds to the horizontal spatial position being examined,  $x_0$  corresponds to the observer's fixation point, and  $\sigma^2$  corresponds to the variability within the pattern's spatial period in locating the position of the most salient contrast difference  $x_0$ .

Why do we choose Gabor filters? The receptive fields of even-symmetric and odd-symmetric simple cells in the visual cortex that are used to discriminate the direction of movement can be characterized optimally by Gabor filters [24]. The Gabor [6] filter is either a sine or a cosine multiplied times a Gaussian function. Gabor functions optimize resolution on a linear scale in both the spatial position and spatial-frequency domains. Gabor functions optimize processing across space and over time. The Gaussian function acts as a spatially-localized smoothing function, significantly reducing the sensitivity of the cell as the pattern moves away from the center of the cell's receptive field. As the variance of the Gaussian filter is reduced: 1) the width of the sidebands of the even-symmetric filter is reduced relative to the center, and 2) the spatial-frequency bandwidth of the filter is reduced. The sine and cosine function of the Gabor filter acts like a bandpass spatial-frequency function that extracts the contrasts at each spatial position being examined. An even-symmetric filter computes the smoothed contrast at each spatial position being examined, whereas an odd-symmetric filter computes the corresponding contrast difference or spatial gradient. Therefore, by examining the output from *paired* even- and odd-symmetric Gabor filters, both the smoothed contrast at each spatial position being examined and the corresponding spatial gradients are computed. The spatially-localized paired sine and cosine functions enable the position of contrast differences to be measured using the smallest number of channels. Paired Gabor filters provide an encoding scheme for the visual cortex which maximizes signal-to-noise ratios given a fixed number of neurons [25]. The need for paired even- and odd-symmetric filters to predict the direction of movement is also indicated by psychophysical data that found increasing the position difference between the peak luminance of test and background patterns from a minimum phase difference, up to 90° increased the visibility

of the shifts in the direction of movement, and any larger phase difference did not affect movement discrimination [4], [9] [10].

For test and background patterns having peak luminances that differ in position by 90°, an even-symmetric filter would be used to detect the background, and an odd-symmetric filter would be used to detect the direction the test grating moved relative to the background. By examining the output from *paired* even- and odd-symmetric Gabor filters, both the smoothed contrast at each spatial position being examined and the corresponding spatial gradients are computed. Many computational models that predict movement, see Hildreth and Koch [5], implement a smoothing operation over the moving object, and then compute the spatial and temporal gradients of the smoothed object. These models, like those proposed to account for movement discrimination for simple patterns [12], [26], do not take into account the importance of 1) paired even- and odd-symmetric filtering functions, 2) global contrast differences that correspond to the background frame of reference, 3) a nonlinear contrast response, and 4) the spatial [8] and temporal [see Fig. 1(c)] thresholds that are inherent when computing spatial and temporal gradients. Therefore, these computational models cannot explain all of the psychophysical results that must be accounted for by a robust model that predicts the direction of movement.

Previous models that propose paired Gabor filters are used to predict the direction of movement [19]-[21] are extended by including: 1) threshold mechanisms dependent a pattern's spatial and temporal frequencies, 2) a nonlinear contrast transducer function, and 3) summing the outputs of the difference and sum of paired even- and odd-symmetric filters over the background's spatial extent, which provides the frame of reference used to judge the direction of movement at all spatial scales that are higher in spatial frequency than the background's fundamental frequency.

The direction a pattern moves relative to its background at two different times is discriminated whenever the output from mechanisms that compute the difference and sum of paired odd- and even-symmetric bandpass channels pooled across the background frame of reference exceeds threshold. The following model is proposed to predict the visibility of shifts in the direction of a test pattern (detected by temporal bandpass  $F_{OS}$ ) moves relative to a multifrequency background (detected by temporal low-pass  $F_{ES}$ ):

$$\frac{\delta}{\delta t} (F_{ES} \pm F_{OS})$$

$$= \left[ \sum_{x=x_0-(\beta/2)}^{x=x_0+(\beta/2)} \frac{k_j C_b^n + k_{fb}}{C_b^n + C_o} F_{ES}^m \pm \frac{k_i C_t^n + k_{ft}}{C_t^n + C_o} F_{OS}^m \right]_{t_2}^0$$

$$- \left[ \sum_{x=x_0-(\beta/2)}^{x=x_0+(\beta/2)} \frac{k_j C_b^n + k_{fb}}{C_b^n + C_o} F_{ES}^m \pm \frac{k_i C_t^n + k_{ft}}{C_t^n + C_o} F_{OS}^m \right]_{t_1}^0$$

where  $C_t$  corresponds to the contrast of the test pattern;

$k_{ft}$  corresponds to the contrast threshold for the test frequency;  $C_b$  corresponds to the contrast of the background pattern;  $k_{fb}$  corresponds to the contrast threshold for the background frequencies;  $C_o$  that depends on the temporal frequency, is a constant that corresponds to the signal-to-noise ratio used when detecting left-right movement of a test pattern relative to the background;  $n$  corresponds to the slope of the contrast response function (usually  $n$  is approximately 2 since the contrast response functions of simple and complex cells in the striate cortex are rectified [27], [28]);  $m$  usually is 1 but sometimes equals 2 as a result of low signal-to-ratios which only occur at high temporal frequencies and low contrasts,  $m \times o = 1$ ;  $\beta$  corresponds to the spatial period of the background frame of reference;  $x_o$  corresponds to the zero crossing or contrast difference that the observer uses as the point of reference to judge the direction the test pattern moved between the two pattern presentations  $t_1$  and  $t_2$ ; and  $k_i, k_j$  are constants for the gain of the contrast sensitivity that is changed by feedback. The difference and sum of paired even- and odd-symmetric filters are summed across the background frame of reference, and then differenced at times  $t_2$  and  $t_1$  to discriminate the direction of movement. Suppose the observer is practiced and has stored a template of the phase-shifted test pattern. Then, only one temporal interval is needed to identify the direction of movement by using the texture pattern of contrast differences [4]. However, the output from both temporal intervals must be compared to identify the direction of movement using the lowest contrasts possible [4].

To compute the direction a test pattern moves relative to a multifrequency background, the difference and sum of the output of paired Gabor filters computed during each of the temporal intervals being examined must be computed and compared. Leftward movement of a bright bar is signaled by the difference between the outputs of paired odd- and even-symmetric functions whereas rightward movement is signaled by the sum of the outputs of paired odd- and even-symmetric filters. Left-right movement at one spatial position is discriminated when the difference or sum of paired even- or odd-symmetric filters at time  $t_1$  differs significantly from the difference or sum at time  $t_2$ . Squaring the output of paired filters introduces a component at the difference frequency, which plays an important role in discriminating the direction of movement [4], [10], [29]. The sign of the temporal gradient will determine whether the test pattern moved to the right or moved to the left of the background's peak luminance.

The contrast of each pattern component is detected using filters tuned to spatial frequencies having a bandwidth of 1 to  $1\frac{1}{2}$  octaves [15]–[18]. A hyperbolic contrast response function, which optimally characterizes the contrast transducer function of normal observers [30] and simple and complex cells in the striate cortex [27], is used to predict the minimum contrast needed to discriminate the direction of movement. The hyperbolic contrast transducer function is a nonlinear function that contains both a nonlinear power function for the contrast of the test pattern  $C^n$ , and thresholding factors  $C_o, k_{ft}$ , and  $k_{fb}$ .

#### MODEL TO DISCRIMINATE DIRECTION OF MOVEMENT PREDICTS PSYCHOPHYSICAL RESULTS

The proposed model predicts that the output of odd-symmetric filters relative to paired even-symmetric filters will increase as the spatial-phase difference increases, up to  $90^\circ$ . There is a tradeoff in: 1) the phase difference between test and background patterns, and 2) the contrast of the test frequency that is needed to discriminate the direction of movement. As the spatial-phase difference is increased up to  $90^\circ$ , smaller contrasts are needed to discriminate the direction of movement [11]. There is both a minimum spatial position [8] and a minimum temporal duration [see Fig. 1(c)] that is needed to discriminate the direction a pattern moves relative to the background. Movement discrimination requires that the relative activation of both the test and background patterns, as measured by the output of paired Gabor filters (optimally tuned to  $90^\circ$  spatial-phase differences), be above threshold.

When the contrast of the background frame of reference is above threshold and below the saturation level of its contrast response function, for example from 0.6 to 20 percent, see Fig. 2, then the visibility of the direction of movement is not changed by the contrast of the background. The model proposed above predicts this result since at each temporal interval, the output of odd-symmetric filters, which compute the spatial gradient at each position being examined, is both summed and differenced from paired even-symmetric filters that are activated by the background frame of reference. As long as the difference between the sum and difference of the output of paired Gabor filters is greater than a threshold amount, then the direction of movement is discriminated. The contrast threshold for the test frequency is independent of the contrast of a suprathreshold background since  $(C_b + C_t) - (C_b - C_t) = 2C_t$ .

The background pattern composed of spatial frequencies combined in cosine phase acts as the frame of reference to judge the direction a pattern moves relative to a multifrequency background [4], [10]. Since the low fundamental frequency of the background is more important than the higher component spatial frequencies, see Fig. 3, this indicates that the multifrequency background that repeats over a wide  $1^\circ$  area operates like a low-pass filter. The increased visibility of the direction of movement when judged relative to a wide as opposed to a narrow background frame of reference has been found psychophysically [4], [7]. In addition, the direction of movement is visible at lower contrasts when the test spatial frequency is a harmonic of the background spatial frequencies, that is when it repeats within the background frame of reference, compared to when the test and background frequencies are not harmonically-related [4], [10]. The low-pass filtering which determines the background frame of reference is represented in the model as the sum across the spatial period of the background  $\beta$ , of the output of the difference and sum of paired Gabor filters, at all spatial scales that are an integral multiple of the background's fundamental frequency. The most salient con-

trast differences  $x_0$  are identified and used as a point of reference within the background frame of reference to judge the direction a pattern moves relative to a multifrequency background.

#### NEURAL NETWORK THAT CAN BE USED TO DISCRIMINATE THE DIRECTION OF MOVEMENT

Discriminating the direction of movement is a task determined in the cortex by paired even-symmetric and odd-symmetric simple cells consisting of excitatory and inhibitory subfields [31]–[34]. Finding that the receptive fields of even- and odd-symmetric simple cells vary in size allows for the coding of an image at different spatial scales [35]–[37]. There are cells tuned to all different spatial-phase angles [38]. However, paired odd- and even-symmetric simple cells in visual area V1 of the cortex are optimally tuned to a spatial-phase difference of  $90^\circ$  [33], [34]. These physiological results are consistent with visual psychophysics studying the direction a test pattern moved relative to simple and multifrequency backgrounds. Both 1) the center phase did not change the visibility of the direction of movement, only the phase difference changed an observer's sensitivity for discriminating the direction of movement, and 2) the visibility of shifts in the direction of movement was optimally tuned to a phase difference of  $90^\circ$  [11].

The neural network used to discriminate the direction of movement that is suggested by psychophysical and neurophysiological data is that the output of paired even- and odd-symmetric simple and complex cells in the visual cortex activated by both local and global contrast differences are used to discriminate the direction of shifts in the positions of contrast differences over time. Recent physiological data found a nonlinear output response from X-like cells in the cat's lateral geniculate nucleus (LGN) [39] and complex cells in the cat's striate cortex [28] that corresponds to the difference frequency of a compound grating. A difference in spatial frequency between the test and background is needed to discriminate the direction of movement, as found in our laboratory and others [9]. The nonlinear component that corresponds to the amplitude of the output at the difference frequency can be predicted as a result of rectification (a squaring of the output response) [28], [39]. The output of cortical cells are nonlinear, primarily due to: 1) thresholds that must exceed the spontaneous cortical activity; 2) rectification of the output response; 3) changes in the gain, such as those found following contrast adaptation; and 4) saturation of the contrast response working range. All of these nonlinearities are incorporated in the proposed model. The outputs of paired even- and odd-symmetric simple cells at different spatial scales are squared as a result of rectification. The sum and difference of the outputs of paired cells, implemented by pairs of simple cells having opposite polarity, are summed across the background frame of reference. Low-frequency contrast differences corresponding to the background frame of reference provide the fundamental scale that is used to compute the direction of

movement. The contrast differences induced by the position difference between test and background gratings are computed at all spatial scales tuned to spatial frequencies equal to and higher than the background's fundamental frequency [4].

Previous models [19]–[21] for predicting the direction of movement propose that spatio-temporal filters corresponding to paired Gabor filters are summed and differenced over time using a low-pass temporal filter that delays the response, being compared with a higher bandpass temporal filter optimally tuned to 10 cycle/deg. The low-pass temporal filter could be the result of: 1) simple cells being summed over time, or 2) complex cells in magnocellular pathways. Psychophysical data finds that only relative shifts in position, and not absolute shifts in position, are used to judge the direction of movement, see Fig. 4. Therefore, it is likely that complex cells, in addition to simple cells, are used to discriminate the direction of movement. The only directionally-selective neurons in the striate cortex of the cat that are invariant to the absolute position of a pattern are complex cells [40]. The response of a complex cell can be regarded as a sum of the responses of the underlying subunits having lateral antagonistic interactions that provide the complex cell with spatial-frequency tuning and direction-selectivity [40], [42]. It's likely that the summing of contrast differences, detected by paired odd- and even-symmetric simple cells, across the background's spatial period is done by complex cells. Complex cells are found primarily in magnocellular pathways.

Research suggests that magnocellular pathways play a major role in discriminating the direction of movement.

1) Neurons in magnocellular pathways are tuned to a much lower range of contrasts (0.1–10 percent contrasts) than are neurons in parvocellular pathways (10–100 percent contrasts) [42]–[44]. When discriminating the direction of movement between patterns that optimally activate the visual mechanisms used for this task, then only contrasts from 0.2 to 2 percent are needed to discriminate the direction of movement [4], [10], [11]. In fact, the contrast threshold for discriminating whether a grating moves to the right or to the left is the same as the contrast threshold for detecting the stimulus [45]. For patterns that optimally activate the channels used to discriminate movement, the visibility of the direction of movement relative to a wide background frame of reference was visible at low contrasts (below 1 percent) for a wide range of background contrasts (0.6–20 percent, see Fig. 2).

2) Neurons in magnocellular pathways are tuned to a lower range of spatial-frequencies than are neurons in parvocellular pathways [42], [44], [46]. Visual psychophysical data found that 1) motion detection is tuned to low spatial frequencies [47]–[49] and 2) low frequency backgrounds facilitate apparent movement discrimination [4], [13], [50], [51]. Additional evidence for the importance of a wide background frame of reference for determining the direction of movement is provided by finding that: 1) discriminating the direction of movement is facilitated for a wider range of spatial frequencies when judged relative

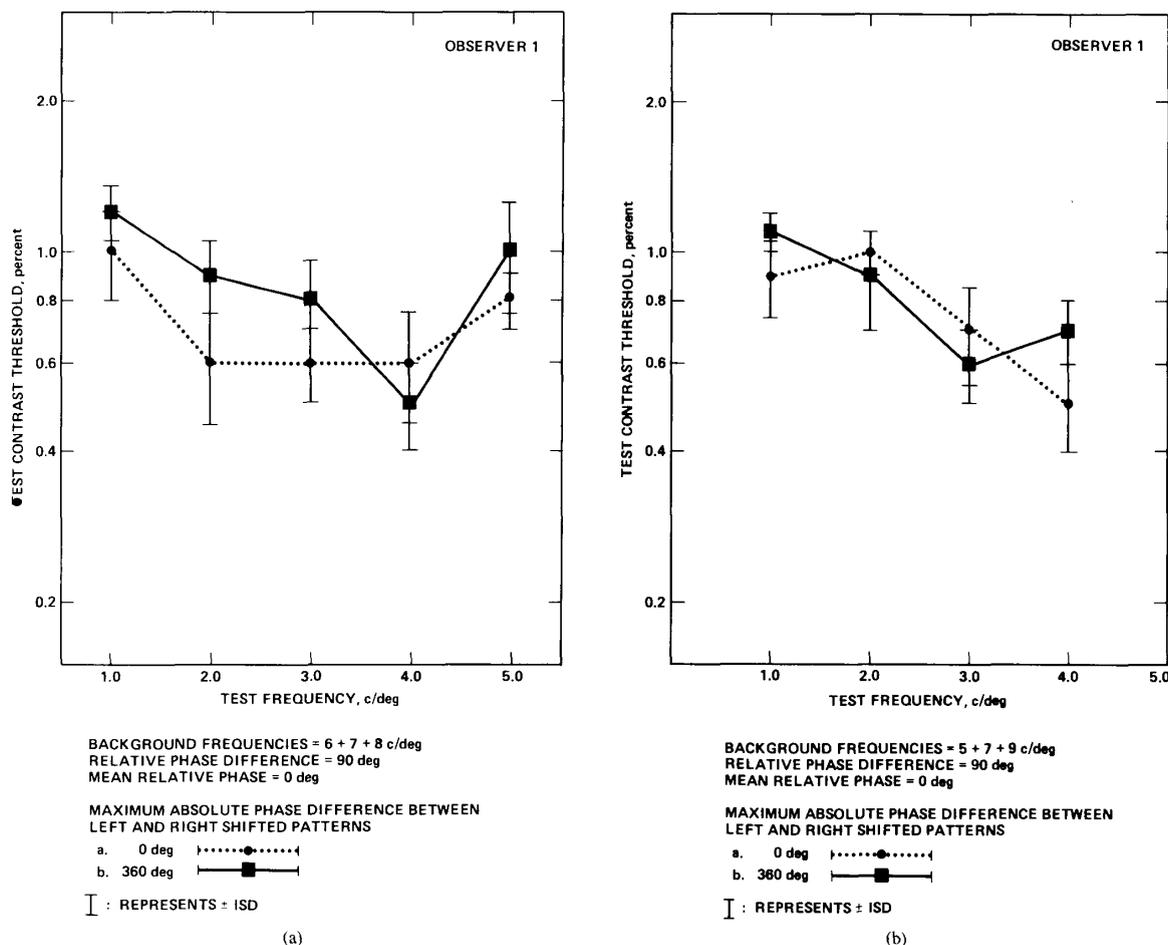


Fig. 4. The visibility of shifts in the direction of movement as the absolute position between test and comparison patterns was jittered randomly over 1 cycle of the background's spatial period. The position of the peak luminance of the test spatial-frequency relative to the peak background luminance always remained constant, only the position between test and comparison patterns varied. The contrast thresholds needed to discriminate the direction of movement on 1) a 6 + 7 + 8 cycle/deg background is shown in Fig. 4(a), and on 2) a 5 + 7 + 9 cycle/deg background is shown in Fig. 4(b). A two-alternative temporal forced-choice staircase procedure with auditory feedback [4], [11] was used to measure contrast thresholds to discriminate the direction a test pattern moved relative to a wide multifrequency background. The tone-cued patterns were presented abruptly for 250 ms separated by a 250 ms interstimulus interval.

to a low frequency background, than when judged relative to a higher frequency background [4], see Fig. 1(a), (b), and 2) blurring a 5 + 7 + 9 cycle/deg background that repeats over a  $1^\circ$  area (low-pass filtering by reducing the contrast of the middle spatial-frequency components), see Fig. 3, increased the visibility of the direction a test pattern moved. Thus, low-pass filtering increased the visibility of the direction a test object moved. In addition, previous studies found that shifts in the position between test and background patterns cannot be seen if: 1) the test and background frequencies are both above 6 cycle/deg [52], or 2) the background consists of a single high contrast middle spatial-frequency [12].

3) Neurons in magnocellular pathways are tuned to higher temporal-frequencies than are neurons in parvocellular pathways [42], [44], [46]. Psychophysical data found that as the temporal frequency was *increased* for test patterns that differed in position optimally (by  $90^\circ$ ) relative to a wide background frame of reference, then there was no change in the visibility of shifts in the direction of movement when either: 1) the durations of test and comparison patterns were reduced from 1.3 to 20 cycle/sec, or 2) the interval between the 2 patterns was reduced from 2 to 20 cycle/sec, see Fig. 1. Thus, shifts in the direction of movement relative to a wide background frame of reference are visible for a wide range of

temporal frequencies. These data indicate that magnocellular pathways are used to discriminate the direction of movement.

Likely sites in the magnocellular pathways for feedforward and feedback interactions to predict the direction of movement are 1) layer 4B in V1 (striate cortex) and 2) MT (middle temporal cortex) [53]–[55]. Magnocellular layers of the LGN project to layer 4C $\alpha$  in V1 [54]. Layer 4B receives most of its input from neurons in layer 4C $\alpha$ ; [54], [56]. Direction-selective cells in V1, composed primarily of even- and odd-symmetric simple cells that may change their direction-selectivity with a reversal of contrast [53], are especially concentrated in layer 4B [53], [57]. Although direction-selective cells in the striate cortex are tuned to a range of optimal displacements, direction-selective cells in the striate cortex of the cat resemble low-level “short-range” motion in human observers [40]. “Long-range” motion [58] where the global analysis of groups of edges across the background frame of reference is analyzed probably occurs at higher levels in the cortical hierarchy, such as MT.

Layer 4B is the major source of the projection from V1 to MT [55], [56]. MT is an area in the cortical hierarchy in which a selective emphasis on motion analysis is apparent [62]. MT has a higher incidence of direction-selective cells than do other cortical areas [56], [59]. The receptive fields in MT are two orders of magnitude larger than those in V1 [60], reflecting a high degree of convergence in this pathway. Cells in MT, unlike those in V1, have pronounced surround interactions, in which responses to stimulation within the excitatory receptive field can be inhibited by motion in other parts of the visual field [61], and may be involved in figure-ground discrimination. Whereas 40 percent of the cells in MT responded to the motion of individual spatial-frequency components, 25 percent of the cells in MT responded to the motion of the pattern as a whole and not to the motion of individual spatial-frequency components [62]. Based on these results, it seems likely that cells in MT are signaling the motion of objects relative to the background frame of reference, in conjunction with the magnocellular neurons from Layer 4B in V1 that are signaling the relative motion of a pattern's component spatial frequencies.

A cortical neural network that computes the visibility of shifts in the direction of movement was proposed that computes: 1) the magnitude of the position difference between the test and background patterns; 2) localized contrast differences at different spatial scales analyzed by computing temporal gradients of the difference and sum of the output of paired even- and odd-symmetric bandpass filters convolved with the input pattern; and 3) using global processes that pool the output from paired even- and odd-symmetric simple and complex cells across the spatial extent of the background frame of reference. Evidence was presented that magnocellular pathways are used to discriminate the direction of movement using patterns that optimize an observer's ability to discriminate the direction a pattern moved relative to a textured background. Since magnocellular pathways are used to discriminate the

direction of movement, this task is not affected by small pattern changes such as jitter, short presentations, blurring, and different background contrasts that result when the veiling illumination in a scene changes.

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Teri B. Lawton, photograph and biography not available at the time of publication.