Reversed phi revisited

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Two briefly flashed lines shown in rapid succession evoke a sensation of motion in human observers. This is examined quantitatively such that line separation, temporal offset, and contrast polarity are varied. Line pairs are presented on a gray background and are either both bright or both dark (equal contrast polarity) or one line is bright and the other is dark (opposite contrast polarity). Observers are instructed to indicate the perceived direction of motion. With foveal viewing, perceived direction is veridical for line pairs with equal contrast polarity but is reversed for line pairs with opposite contrast polarity, with spatial separations between 0 and 12 arcmin, and with temporal offsets between 8 and 33 ms. When separations, temporal offsets, or both are further increased, perception reverts to veridical. When lines of opposite contrast polarity are presented in the parafovea, reversal of perceived direction is also observed. The psychophysical results correlate well with those of recent intracellular recordings from directionally selective simple cells in the primary visual cortex of anesthetized cats (N. J. Priebe & D. Ferster, 2005).

Keywords: short-range motion, long-range motion, phi phenomenon, reversed phi, contrast polarity, directional selectivity, striate cortex

Introduction

Wertheimer (1912) reported that two briefly flashed lines shown in rapid succession evoke a sensation of motion beyond that of seeing the line in two successive positions. Wertheimer coined the term “phi” phenomenon to emphasize the phenomenal experience of motion.

The “reversed phi” phenomenon was discovered by Anstis (1970). If stroboscopically presented pairs of visual patterns are shifted in space and their contrast polarity is inverted simultaneously, motion is perceived in a direction reversed to that of the stimulus.

These counterintuitive results were predicted by a model originally created to describe the turning responses of insects to moving periodic patterns (Hassenstein & Reichardt, 1951; Reichardt, 1987). Briefly, a Reichardt correlator receives input from two adjacent points (1 and 2) in space. A moving stimulus successively activates photoreceptors and second-order neurons corresponding to Point 1 and Point 2. In the model, the first activation is delayed with respect to the second, such that both arrive simultaneously at the correlator, a multiplicative unit. This generates a large output, whose sign indicates the direction of motion. For stimuli with equal contrast polarity, the sign is always positive. However, if the stimulus contrast is reversed while the stimulus is traveling from Point 1 to Point 2, the activation elicited in one of them has a sign different from that activated in the other. Thus, the result of the multiplication is negative in sign, that is, in a direction opposite to the previous situation.

Motion stimuli, such as those used in this study, differ in luminance from the background on which they are presented. A Reichardt motion detector responds to these stimuli. It is possible to construct stimuli that lack overall luminance changes but can elicit a motion percept (http://www.brl.ntt.co.jp/people/nishida/demo/motionindex.html). A Reichardt detector does not respond to such stimuli (Chubb & Sperling, 1988). The distinction between first-order motion stimuli (luminance driven) and second-order motion stimuli (no luminance changes present; Chubb & Sperling, 1989) was introduced.

An example for second-order motion is a shifting random checkerboard pattern, in which each check is either a patch of random dots (uncorrelated between frames) or a patch of uniform gray, of the same luminance as that averaged over the random dots. If the checkerboard is moved coherently between frames, observers correctly perceive the direction of motion for a range of spatial offsets. However, if random dot patches and gray patches are exchanged between frames, perceived direction of motion is reversed (Nishida, 1993). This led to the extended definitions for patterns of first-order reversed phi and second-order reversed phi (Lu & Sperling, 1999; Mo & Koch, 2003, but see Cavanagh & Mather, 1989).

The maximal shift where humans can see the direction of spatial shifts of random dot patterns is 18 arcmin (Braddick, 1974). This short-range mechanism is complementary to a long-range one, active when looking at other patterns, for seeing shifts across several degrees.

This study has its origin in the observation that the temporal order of two lines separated by 3 arcmin can be correctly identified with a precision of 3–5 ms (Wehrhahn & Rapf, 1992; Westheimer & McKee, 1977). For separations \( \Delta \chi > 3 \) arcmin, temporal thresholds increase with line separation. Here, I explore the perceived direction of
motion elicited by two lines briefly flashed in succession (two pulses in space and time) on a gray background. Line pairs are either both bright or both dark or one line is bright and the other is dark. In the sense of the definitions given above, these are first-order motion stimuli.

These stimuli are sharply circumscribed in space (two thin lines presented at various separations) and time (duration of 2 ms), yielding a particularly focused tool; when it comes to the parameters of interest here, I quantify the spatial separation as well as the temporal offset in each stimulus with satisfactory precision.

**Methods**

In all experiments, two vertical lines of predetermined contrast and separation were flashed in succession on a gray background. Lines were 15 arcmin high and 2 or 3 arcmin wide for foveal stimulation. Their temporal order was randomly selected from seven equally spaced intervals that included synchrony. The time latencies were multiples of 8.33 ms, constrained by the refresh rate of the monitor. The duration of each flash as measured by a photodiode was about 2 ms. Figure 1 illustrates the display sequence, with a small fixation point shown prior to the two flashes, such that no interaction with the task occurred.

Observers viewed the stimuli on a flat-screen monitor placed at a distance of 193 cm. On each trial, a binary response was registered, with participants pressing either of two mouse buttons to indicate the perceived direction of motion. No error feedback was provided. Trials, in runs of 150, occurred at fixed time intervals of a few seconds. Each point in the graphs is based on at least three runs (i.e., 450 trials) for that condition, obtained on different days.

The proportion correct \((p = r/n)\) was computed from the ratio of responses to the right \((r)\) to the total number of presentations \((n)\) for each stimulus condition and its standard deviation \((SD)\) using the binomial formula \(SD = \sqrt{p \times (1 - p)/n}\). The formula is valid if the data follow a binomial distribution. This condition is satisfied if either \(p \times n > 5\) or \((1 - p) \times n > 5\), depending on whether \(p\) is close to 1 or to 0. I have found \((1 - p) \times n > 100\) for all averaged values close to 1 and 0, respectively. I therefore conclude that the data in this study do not differ significantly from a binomial distribution. When the responses were equally distributed between “seen right → left” and “seen left → right,” the probability is 0.5; the more secure the percept of “right → left,” the closer it is to 0, and the more secure the percept of “left → right,” the closer it is to 1.

Observers placed their head in a chin rest and used contact or spectacle lenses as needed. Dim general illumination (≈1 cd/m²) in the room allowed the outlines of the monitor to be seen. The screen luminance \(L\) of lines and the background was calibrated using a Minolta luminance meter, allowing adequate characterization of contrast using Michelson’s formula \((L_{\text{max}} - L_{\text{min}})/(L_{\text{max}} + L_{\text{min}})\). Routinely, the screen luminance of the gray background was 55 cd/m². Bright and dark lines had a luminance of 110 and ≈5 cd/m², respectively. Michelson contrast values were 0.33 and 0.9, respectively. The refresh rate of the monitor was set to 120 Hz. For Observer 2, a refresh rate of 60 Hz was used.

Two observers were highly experienced in this task. The third observer was naive with respect to the goal of the experiment. Vision of all participants was corrected to normal. Each experiment included at least one observer who was naive to the task. Taking into account that practice may improve performance (Wehrhahn & Rapf, 2001), all results reported were taken when performance had reached a stable level.

**Results**

A schematic outline of the experiments is shown in Figure 1. Two vertical lines are presented on a gray background. During each run, the separation \(\Delta x\) (i.e., the distance between the inner edges of the two lines) remained constant and the temporal offset \(\Delta t\) (i.e., the time interval between the onset of the two lines) varied randomly from trial to trial.

In Figure 2, the proportion of correct responses is plotted as a function of the temporal offset \((\Delta t)\) for the two line stimuli shown in the insets. In the top panel, line
separation ($\Delta x$) is 0 arcmin; that is, for a line width of 2 arcmin, the line edges touch. For both conditions (see insets), proportion correct is at about chance value (0.5) for $\Delta t = 0$. For equal contrast polarity, proportion correct increases with increasing $\Delta t$, but for opposite contrast polarity, proportion correct decreases to below 0.25 for temporal offsets between 8.3 and 25 ms and only increases again between 33 and 50 ms. Thus, for the shorter temporal offsets, perceived direction is veridical for two black lines flashed in succession but is reversed in most cases, if one black line and one white line are presented. This confirms and extends earlier results (Anstis, 1970; Chubb & Sperling, 1989).

If line separation $\Delta x$ is 18 arcmin (Figure 2, bottom panel), the perceived direction of motion elicted by the line pairs and that of the stimuli is the same, independent of the polarity of line pairs, although the two proportion correct functions obtained for equal and opposite contrast stimuli differ slightly. The transition between the situations described in the two panels of Figure 2 is gradual (data not shown), indicating that the influence of the presumed short-range mechanism is strong for a separation of 0 arcmin (top panel) but weakened or absent at 18 arcmin (bottom panel).

Figure 3 shows the proportion correct for stimuli with opposite contrast polarity in Observer 2. Here, temporal and spatial offsets used are almost twice as large as those in the previous experiment. I note that at a separation of 0 min and temporal offsets of 17 and 33 ms, the white–black line pair yields significantly reversed responses. At a temporal offset of 50 ms, values are still below 0.5. At 67 ms, the proportion correct is back to 0.5 with a significant increase to 0.74 (correct perception of direction is reasonably certain) at 100 ms. For a stimulus of two white lines at a separation of 0 arcmin, perception in this observer is veridical. At the larger separation (30 arcmin), the white–black line pair yields veridical responses. For the larger spatiotemporal offsets required in this observer, this corresponds to the results shown in Figure 2.

If reversed perception of direction due to opposite contrast stimuli is generated by the short-range mechanism, it should depend on eccentricity in a way similar to
short-range motion (Foster, Thorson, McIlwain, & Biederman-Thorson, 1981; Thorson, Lange, & Biederman-Thorson, 1969; Westheimer, 1983). This was tested in the next experiment presenting equal and opposite contrast stimuli in the parafovea at an eccentricity of 4 deg. Stimulus dimensions and line separation (12 arcmin) match those presented in the fovea, assuming that cortical magnification factor predicts the respective spatial parameters (Westheimer, 1983). The data show that perceived direction is reversed when a white line and a black line are presented (top panel). For identical line parameters with both lines being white, a rapid increase into saturation is observed. For a distance of 48 arcmin, perceived direction is veridical for both conditions tested (bottom panel).

Moreover, with these stimuli, I am able to delineate the transition between the conditions where strong reversed phi is observed (small separations) and those where this is not the case (large separations). On the basis of the arguments laid out in the Discussion section, I propose that this is equivalent to the parameters constraining the short-range system. As can be seen when comparing Figure 2 with Figures 3 and 4, the temporal offset is much larger in Observer 2 as compared with Observer 1. The results from Observer 3 to the conditions of Figures 2, 5, and 6 are shown as an auxiliary file. They are very similar in all other respects to those of Observer 1. The range of spatial separations within which reversed phi is observed is similar among all three observers.

The curves in Figures 2, 3, and 4 are based on about 1,000 trials. I obtained the data represented in such curves in two observers for six line separations, each with dark → bright, bright → dark, bright → bright, and dark → dark sequences. Following the convention introduced by Adelson and Bergen (1985), the results are presented as space–time diagrams. In Figure 5, the proportions of correct responses are shown as squares whose color represents the perceived direction and whose areas indicate the proportion of correct choices.

For this and the other two observers, the range of the space–time diagram in which dark → bright and bright → dark stimuli elicit inverted direction of motion is surrounded on both sides by a region in which this is not the case. The black squares indicating perception in a direction opposite to the stimulus are oriented along a diagonal tilted...
to the left. This is consistent with predictions arising from the energy model (Adelson & Bergen, 1985; Emerson, Bergen, & Adelson, 1992).

As a control, the space–time plot of proportions correct for stimuli of equal contrast polarity is shown in Figure 6 (same observer as in Figure 5). As expected, equal contrast polarity sequences are perceived to correspond to the direction of the stimulus throughout. I note that for both the smallest and largest separation, proportions correct increase more slowly with increasing temporal offset.

More data for Observer 1 and a whole set for yet another observer show that the phenomena described here are independent of whether pairs of black lines or pairs of white lines are shown. Reversed phi is reliably obtained irrespective of whether the white line or the dark line is presented first (see auxiliary data).

**Discussion**

In the experiments presented here, computation of the direction of visual motion requires a comparison of luminance changes of the two stimulus components in space and time. The experiments in this study constrain that parameter range in which the responses to a pair of lines of opposite contrast polarity change from reversed phi to phi. For the conditions in this study, the maximal time window within which the signals arising from the two lines are integrated by the short-range mechanism amounts to 33 ± 8 ms. The maximal spatial separation of lines processed by this mechanism is 12–18 arcmin. This means that for a reliable judgment of the direction of a moving stimulus, a speed range between 3 and 40 deg/s is required. The values obtained are specific to the stimuli used here and may be different in other conditions. They are consistent with many earlier results (Exner, 1875; Thorson et al., 1969; Wehrhahn & Rapf, 1992; Wertheimer, 1912; Westheimer 1983; Westheimer & McKee, 1977). This indicates that the stimuli used in those earlier experiments probably had activated the short-range mechanism too.

Several previous studies have used two dots flashed in succession to “probe the neural connectivity in the human visual system.” The results in these previous studies are comparable to those found in the experiments with peripheral stimulation in this study (Foster, Gravano, & Tomoszek, 1989; Foster et al., 1981; Thorson et al., 1969).

Directionally selective neurons were described in the visual cortex right from the outset of single-unit recordings (Hubel & Wiesel, 1962). The understanding of their underlying mechanism was significantly advanced by the use of the reverse-correlation technique originated by McLean and Palmer (1989) and developed and applied in the cat by Emerson et al. (1992) and De Angelis, Ohzawa, and Freeman (1993) as well as in the monkey by De Valois and Cottaris (1998) and by Livingston and Conway (2003) or Conway and Livingston (2003).

Motion stimuli can be represented in the space–time plane. Plotting subsequent positions of an object moving with constant speed yields a straight line that is slanted to the right. Inverting the direction of motion inverts the sign of the spatial component and, thus, the slant. Increasing or decreasing object speed increases or decreases the slope of the line. Orientation of the line in the space–time plane thus completely describes object motion (Adelson & Bergen, 1985).

Because the perceived direction of motion considered here is a binary decision, the stimuli leading to the perception of the same direction are functionally equivalent and so must be the mechanisms achieving this. First, I take into account that the sequences black → black and white → white are processed by different mechanisms that presumably receive reciprocal inputs from thalamic On and Off pathways (Edwards & Badcock, 1994; Shechter & Hochstein, 1990; Snowden & Edmunds, 1999; van der Smagt & van de Grind, 1999; Wehrhahn & Rapf, 1992). The experiments reported in this study are consistent with the assumption that each of these directionally selective mechanisms is also sensitive to an opposite contrast polarity pair moving in the opposite direction (Figure 5).

Assuming that the mechanisms just add up neuronal inputs, as proposed by Priebe and Ferster (2005), this also means that the net effect of the opposite contrast line on the mechanism must be excitatory.

These considerations closely correspond to changes in the amplitude of the membrane potential observed in directionally selective simple cells in V1 of the cat, as...
measured with intracellular electrodes (Priebe & Ferster, 2005). The membrane potential of these cells is activated or inhibited by either white or black lines in a “push–pull” manner, thus exhibiting spatiotemporal opponent coding (for a review, see Hirsch & Martinez, 2006).

For example, consider a directionally selective On-center simple cell that is significantly depolarized by a sequence of two white bars moving in the preferred direction (left), and assume that this cell has an inhibitory lobe to the right of this region. For a white line stimulus briefly presented to the inhibitory region, the cell hyperpolarizes, but it depolarizes for a black line. As a consequence, when stimulated first with a white line in the receptive field center and subsequently with a black line at the position of the inhibitory lobe, the cell is significantly depolarized, although due to motion in the null direction of the cell (see Figure 4C and 4D; Priebe & Ferster, 2005). Thus, this cell processes the stimuli white → white moving left and white → black moving right in a way analogous to that observed in the experiments with human observers.

The results of these physiological experiments as well as those of the psychophysical experiments reported are consistent with the detailed circuitry provided by the energy model (Adelson & Bergen 1985). At a computational level, the reversed phi phenomenon is also explained by other models (Lu & Sperling, 1999; Reichardt, 1962, 1987; van Santen & Sperling, 1985; Watson & Ahumada, 1985).

The results of this study indicate that—for the parameters obtained by briefly presenting two adjacent lines in rapid succession—there is one zone of operation of the physiologically characterized mechanism, which supports both phi and reversed phi (short range) and another zone supported by another physiological mechanism (long range). Assuming that equal and opposite contrast polarity stimuli show about the same dependence on spatial offset, the short-range mechanism present in the fovea appears to be ineffective or absent for a line separation of 20 arcmin and larger. At this offset, the response of the observers in this study to line pairs with opposite contrast polarity is veridical and, hence, indistinguishable from the responses to line pairs of equal contrast polarity. Such a behavior can be explained by models including a quadrature step, which is not required for the explanation of the responses for short spatial offsets presented here (van Santen & Sperling, 1985; Watson & Ahumada, 1985; see also Adelson & Bergen, 1985). The physiological implementation is thought to be located in area MT. Responses of neurons in this area are insensitive to the sign of contrast polarity (Croner & Albright, 1999; Krekelberg & Albright, 2005; Livingstone, Pack, & Born, 2001).

I have shown that the perceived direction of two briefly flashed lines of equal and opposite contrast polarity shown in rapid succession correlates well to intracellular responses of simple cells in the primary visual cortex of cats stimulated in a very similar fashion. I interpret this as an indication for the existence of analogous directionally selective simple cells in the primary visual cortex of humans. This means that the spatial extent of the short-range motion mechanism is constrained by the physiological properties of such cells. Because simple cells are luminance driven, these conclusions are restricted to first-order mechanisms.

The results can be used to define the zone of short-range motion in humans as that given by the spatial extent of the reversed responses to opposite contrast stimuli. The longer range of the veridical responses to line pairs of both opposite and equal contrast polarity indicates that there is another—long-range—motion mechanism (Braddick, 1974). For same-contrast stimulus pairs, both mechanisms, the long-range and short-range give responses in the same direction, and if there is a division of labor between them, this would have to demonstrated by other means than the reverse-phi approach adopted in this study, for example through contrast or chromaticity effects (Wehrhahn & Westheimer, 2005). But should the correct temporal-order judgments for large separations be called a perception of motion? The two targets clearly occur one after the other, but whether it is possible to differentiate this experience from one that is truly a movement is a matter that would need investigation in somewhat more nuanced terms than the simple—right or left—binary decisions required of the observers in this study.

**Conclusions**

Earlier findings indicated a separation of pathways into subsystems selectively responding to motion of white → white and black → black line pairs. I assume that horizontal motion is processed by separate mechanisms, each of which having respective excitatory and inhibitory inputs from On and Off pathways and, thus, being sensitive to motion of white or black line pairs and to motion either to the right or to the left. The experiments in this study suggest that these mechanisms are also sensitive to a sequence of lines with opposite contrast polarities moving in the respective opposite direction. Applying the simple additive rule of excitatory neuronal inputs proposed by Priebe and Ferster (2005), this means that the effect of the opposite contrast line is excitatory.

**Acknowledgments**

I thank Nikos Logothetis for support. Gerald Westheimer’s help as host, programmer, observer, and discussant is gratefully acknowledged. I also thank Crystal Tan for running numerous experiments and for help in drawing figures.
Kuno Kirschfeld and Andreas Tolias provided helpful comments on an earlier version of the manuscript.

Commercial relationships: none.
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