

Illusory motion perception in blindsight

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Edited* by Thomas D. Albright, The Salk Institute for Biological Studies, La Jolla, CA, and approved December 6, 2010 (received for review May 13, 2010)

Motion detection is typically spared in blindsight, which results from damage to the striate cortex (area V1) of the brain that is sufficient to eliminate conscious visual awareness and severely reduce sensitivity to luminance contrast, especially for high spatial and low temporal frequencies. Here we show that the discrimination of motion direction within cortically blind fields is not attributable to feature tracking (the detection of changes in position or shape), but is due instead to the detection of first-order motion energy (spatiotemporal changes in luminance). The key to this finding was a version of the line motion illusion entailing reverse-phi motion in which opposing motion directions are simultaneously cued by motion energy and changes in stimulus shape. In forced-choice tests, a blindsighted test subject selected the direction cued by shape change when the stimulus was presented in his intact field, but reliably selected the direction cued by motion energy when the same stimulus was presented in his blind field, where relevant position information was either inaccessible or invalid. Motion energy has been characterized as objectless, so reliance on motion energy detection is consistent with impaired access to shape information in blindsight. The dissociation of motion direction by visual field (cortically blind vs. intact) provides evidence that two pathways from the retina to MT/V5 (the cortical area specialized for motion perception) are functionally distinct: the retinogeniculate pathway through V1 is specialized for feature-based motion perception, whereas the retinocollicular pathway, which bypasses V1, is specialized for detecting motion energy.

superior colliculus | visual cortex | visual pathway | hemianopia

Blindsight is a rare phenomenon caused by damage to the primary visual cortex (striate cortex, or V1) of the brain that is sufficient to eliminate conscious visual awareness (1, 2). Visual sensitivity to luminance contrast is reduced in the corresponding part of the visual field, most severely for high spatial and low temporal frequencies (3). The fact that it is not completely abolished for low spatial and high temporal frequencies accounts for many of the residual visual capacities that have been reported in blindsight, including, in forced-choice tests, the ability to detect and discriminate stimuli presented in the field defect (2, 4). Evidence obtained from monkeys with striate cortex lesions as well as from cortically blind patients suggests that these capacities are mediated by neural pathways that project from the retina to extrastriate visual cortex, which normally bypass the main visual pathway that projects from the retina to the striate cortex via the lateral geniculate nucleus (the retinogeniculate pathway) and involve the superior colliculus of the midbrain and the lateral geniculate and pulvinar nuclei of the thalamus (5–13).

Blindsight is not merely normal vision without awareness. In addition to the loss of primary visual cortex, retrograde degeneration of relay neurons in the corresponding part of the lateral geniculate nucleus and concomitant transneuronal degeneration of up to 90% of retinal ganglion cells (specifically, P β ganglion cells) (14) accounts for severely reduced contrast sensitivity for low temporal and high spatial frequencies, with corresponding impairments in the ability to discriminate shape, slow movement, and wavelength (4)—abilities that normally depend on the parvocellular system (15).

Of the visual capacities typically spared in blindsight, the detection and discrimination of movement is the most robust (2, 16, 17). Several studies have indicated that cortically blind patients are able to discriminate the direction of movement of single spots (11, 18–20) and bars (21, 22), with a preference for faster-moving targets that reflects the selectively spared sensitivity to high temporal frequencies (3). However, there has been some doubt as to whether these abilities reflect sensitivity to motion-specifying stimulus information (e.g., first-order motion energy determined by spatiotemporal changes in luminance) (23), because the translational movement of spots and bars is confounded with changes in position, which can be discriminated within the field defect independently of motion (1). This is underlined by the fact that cortically blind patients are unable to discriminate the direction of motion of stimuli devoid of global changes of position, e.g., gratings and random dot kinematograms depicting translation, relative motion, and motion in depth (11, 22, 24). It remains possible, however, that direction discrimination for spots and bars differs from random kinematograms, gratings, etc., because these stimuli engage different motion-processing mechanisms, consistent with the differences between them in their local and global characteristics. On this basis, the possibility cannot be ruled out that direction is discriminated in the cortically blind visual field by virtue of a mechanism that directly detects motion information in the stimulus.

The objectives of the research reported in this article are (i) to show that the detection of motion-specifying stimulus information is possible independently of position and/or shape information that could serve as the basis for feature tracking, and (ii) to identify the motion detection mechanism that is responsible for direction discrimination in cortically blind visual fields. In the experiments that follow, a blindsighted observer was tested using a version of the line motion illusion (25) entailing the reverse-phi phenomenon (26). For this stimulus, opposing motion directions are cued simultaneously by motion energy and changes in stimulus shape and position. The findings show that motion direction discrimination within the field defect is not attributable to the detection of changes in position or motion-specifying changes in shape (feature tracking), but is instead due to the detection of first-order motion energy.

Results

Experiment 1: Replication of the Line Motion Illusion. In its standard form, the line motion illusion is obtained by first presenting a white square, and then presenting a colinear white rectangle adjacent to it. Although the entire rectangle is presented simultaneously, motion is perceived away from the square, as if the rectangle were being painted across the screen. It seems as if the square is gradually changing shape as it extends into an elongated rectangle. The opposite happens when the rectangle is removed; i.e., motion is perceived toward the square, and the

Author contributions: P.A. and H.S.H. designed research, performed research, analyzed data, and wrote the paper.

The authors declare no conflict of interest.

*This Direct Submission article had a prearranged editor.

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stimulus appears to change shape as it contracts from an elongated rectangle into a square.

In our version, the stimulus was composed of a two-frame sequence (frame 1 duration = 1,000 ms; frame 2 duration = 500 ms) in which two white rectangles of equal size (2.0° wide, 6.0° high) were presented against a black background, first singly and then one above the other by adding the second rectangle above or below the first (extension; Fig. 1A), or first one above the other and then singly by removing either the upper or lower rectangle (contraction; Fig. 1B).

First, we tested whether a person with blindsight is capable of discriminating the direction of motion determined by the line motion illusion. Our test subject was G.Y., a 50-y-old man with blindsight arising from unilateral damage to his left medial occipital cortex that caused a right, homonymous hemianopia, with macular sparing extending 3.5° into what is an otherwise a blind hemifield (27) (Fig. 2). A temporal, two-alternative forced-choice procedure was used in which the upward and downward variants of the rectangle-added or rectangle-removed stimuli were presented in randomly determined order in two intervals

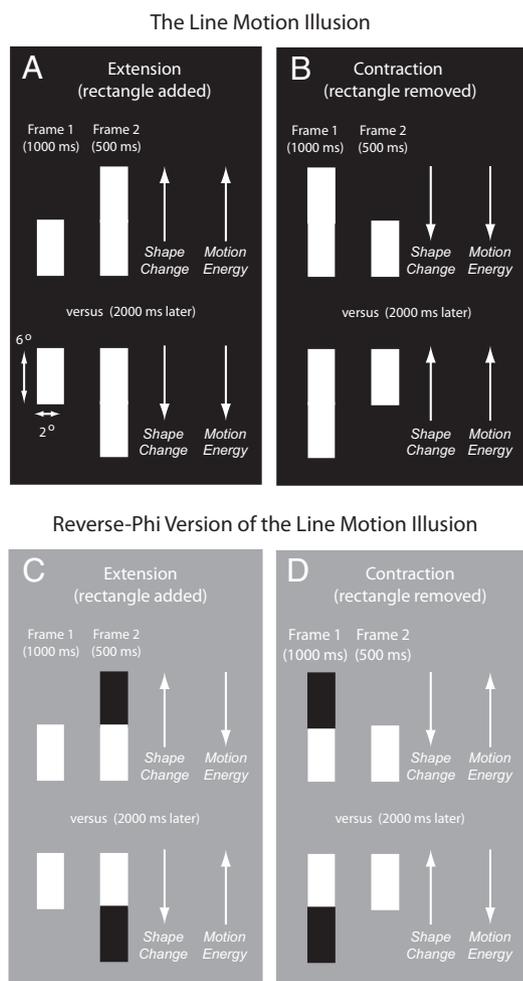


Fig. 1. Two-frame sequences in which motion is specified by shape change or motion energy. Experiment 1: Each panel illustrates the alternatives presented in random order in two-alternative forced-choice trials. Standard line motion stimulus for which the direction of motion specified by shape change and motion energy is the same for trials with shape extension (A) and trials with shape contraction (B). Experiment 2: Reverse-phi version of the line motion stimulus for which shape change and motion energy specify motion in opposite directions for trials with shape extension (C) and trials with shape contraction (D).

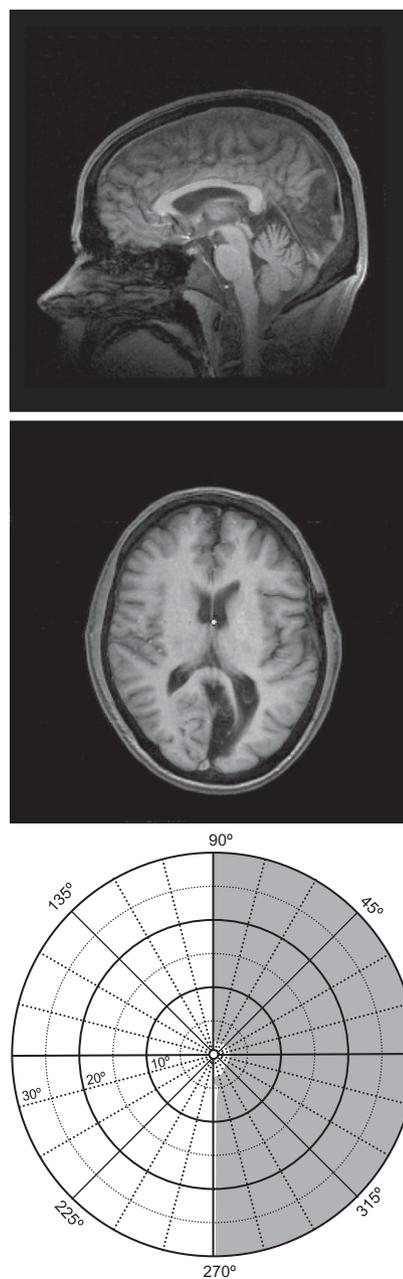


Fig. 2. G.Y.'s cortical lesion and corresponding field defect. The only remaining part of his left striate cortex is at the occipital pole, corresponding to 3.5° of macular sparing. The tests described here were carried out with stimuli centered 12° above the fixation point at 30° of eccentricity. (Reproduced with permission from ref. 22.)

(up during one interval, down during the other). G.Y. was required to indicate the interval during which he detected upward motion by pressing one of two keys. When the stimuli were presented in his intact, sighted visual field, G.Y. could always discriminate the motion direction determined by the line motion illusion (Fig. 3A). On every trial, he indicated that motion was upward in the temporal interval with upward extension (Fig. 1A Upper) or in the temporal interval with upward contraction (Fig. 1B Lower; Pearson's $\chi^2 > 40.0$, $df = 1$, $P < 0.0001$, $n = 80$). He could also discriminate the motion direction determined by the line motion illusion within his impaired visual field. That is, he indicated that motion was upward in the temporal interval with upward extension for 65% of the rectangle-added trials and in

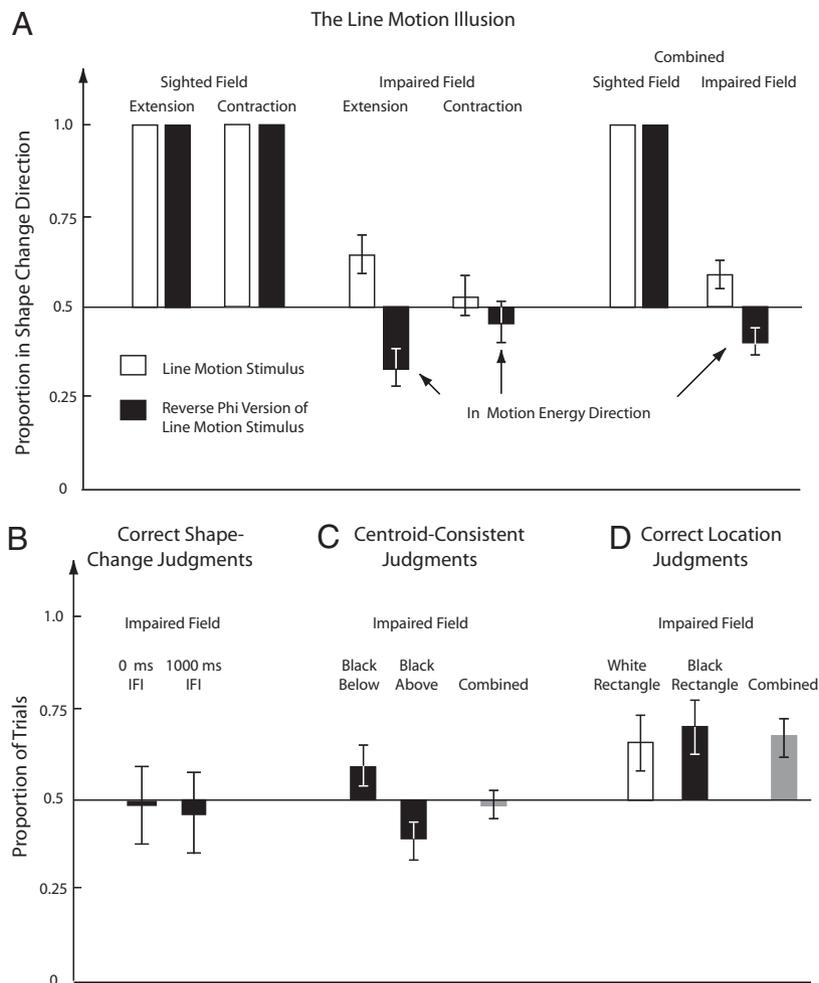


Fig. 3. Percent correct scores for the detection of motion direction, changes in shape, and changes in position plotted as deviations from chance (50%) in temporal two-alternative forced-choice tests. In each case, scores above 50% correspond to judgments favoring the motion direction implied by shape change or position information. (A) For the standard line motion stimulus, G.Y. most often chose the direction implied by both shape change and motion energy in both his sighted and cortically blind field, but for the reverse-phi version of the line motion stimulus he selected the direction specified by shape change in his sighted field, but chose the direction specified by motion energy in his blind field. (B) G.Y. could not discriminate between the shapes that had been presented in experiment 2, regardless of whether motion was possible, as was the case for the 0-ms but not the 1,000-ms IFI. (C) G.Y. could not discriminate between upward and downward displacements of the centroid of the reverse-phi stimulus in his blind field. (D) G.Y. could discriminate the location of the black and white components of the reverse-phi stimulus in his blind field, but this would provide invalid cues to the direction specified by motion energy, which was selected most often by G.Y. Error bars indicate 95% confidence limits.

the temporal interval with upward contraction for 53% of the rectangle-removed trials. Overall, upward motion was selected significantly more often than would be expected on the basis of chance (mean = 60% correct; Pearson's $\chi^2 = 6.44$, $v = 1$, $P = 0.0112$, $n = 160$). Throughout testing in this and subsequent experiments, G.Y. maintained that he was unaware of the stimuli presented in his impaired field, in keeping with the definition of type I blindsight, i.e., “visual capacity in a field defect in the absence of acknowledged awareness” (2). Thus, the direction of what has been characterized as an illusion was discriminated in his cortically blind field despite G.Y.’s acknowledged absence of conscious awareness.

Experiment 2: Reverse-Phi Variant of the Line Motion Illusion. In the experiment described above, in which a white rectangle was added or removed to create the line motion illusion, the discrimination of motion direction could have been due either to the tracking of stimulus features displaced in the course of shape change or to the detection of first-order motion energy in the same direction. These alternatives were distinguished by modi-

fying the line motion stimulus, making the added/removed rectangle black and changing the background to an intermediate gray. This reversal of luminance polarity created a reverse-phi (26) version of the line motion stimulus for which motion energy is in the opposite direction compared with the stimulus used in experiment 1 (both confirmed by the computational implementation of a motion energy detector) (23).

Within G.Y.’s intact visual field, changes in global shape predominated over motion energy in determining the perceived motion direction for the reverse-phi versions of the line motion stimuli. When the added/removed rectangle was black, he always indicated that motion was upward in the temporal interval with upward extension (Fig. 1C) or upward contraction (Fig. 1D; $n = 80$). G.Y. could also discriminate motion direction when the reverse-phi stimuli were presented within his cortically blind field, but not on the basis of shape change. Compared with his judgments with the standard line motion stimulus, the frequency with which G.Y. indicated that motion was upward in the temporal interval with upward extension decreased from 65% to 33%, with a smaller decrease from 54% to 46% for his reports of

upward contraction (Fig. 3A). The resultant interaction between the type of line motion stimulus (standard vs. reverse phi) and the type of shape change (extension vs. contraction) was significant (Mantel-Haenszel test, $\chi^2 = 4.692$, $P = 0.03$), but allowing for the interaction by means of a saturated logistic model, the difference between the frequencies with which G.Y. selected upward motion for the standard line motion stimulus (60% correct overall, combining both upward extension and upward contraction) and the reverse-phi version of the line motion stimulus (39.4% overall) was highly significant (logistic regression, odds ratio = 2.54, $P = 0.0045$).

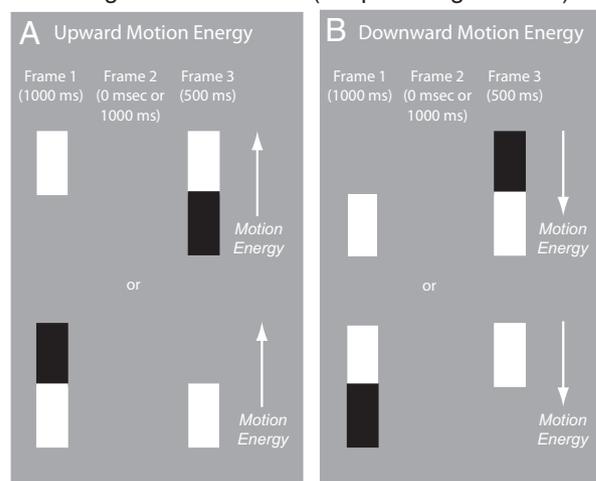
Judgments in the shape change direction decreased in G.Y.'s blind field for the reverse-phi stimulus because his directional judgments were most often determined by first-order motion energy, which was opposite to the directions determined by changes in shape. G.Y. indicated that motion was upward in the temporal interval with upward motion energy for 68% of the trials in which the black rectangle was added, and for 54% of the trials in which the black rectangle was removed. Overall, the temporal interval with upward motion in the direction determined by first-order motion energy was selected significantly more often than would be expected on the basis of chance (Pearson's $\chi^2 = 7.24$, $df = 1$, $P = 0.0071$, $n = 160$). Thus, in contrast to his sighted field, G.Y. discriminated the direction of motion for the reverse-phi stimulus in his blind field on the basis of first-order motion energy rather than shape change.[†]

Experiment 3: Control for the Detection of Shape Change. The stimuli in this experiment were the same as in experiment 2, but combined for forced-choice testing such that the alternatives were matched with respect to the direction specified by motion energy (Fig. 4A and B). G.Y. was asked to indicate whether the length of the stimulus increased (in one interval) or decreased (in the other interval). He was unable to discriminate between these shape changes, either when the interframe interval (IFI) was 0 ms, so motion was possible (49% correct; Pearson's $\chi^2 = 0.05$, $df = 1$, $P = 0.82$, $n = 80$), or when the IFI was 1,000 ms, so motion was not possible (46% correct; Pearson's $\chi^2 = 0.45$, $df = 1$, $P = 0.5$, $n = 80$; Fig. 3B). Although this does not preclude the possibility that other shapes might prove to be discriminable within cortically blind fields, G.Y.'s inability to discriminate changes in the shapes tested in experiment 2 indicated that the detection of motion energy in that experiment was indeed objectless.

Experiment 4: Control for Position Cues. It was confirmed in this experiment that direction discrimination in G.Y.'s cortically blind field was based on the detection of motion energy rather than being inferred from changes in the centroid of the stimulus' luminance profile (28), which are in the same direction as the motion energy. This was shown by having G.Y. compare the location of the white rectangle with the location of the combined white and black rectangles in his blind field (the possibility of motion detection was eliminated by temporally isolating their presentation by 2,000 ms, as illustrated in Fig. 4C and D). After each trial, G.Y. indicated the temporal interval during which the stimulus was higher. His choice of temporal interval was consistent with the shift in the centroid of the luminance profile for 49% of the trials, which did not differ significantly from chance (Pearson's $\chi^2 = 0.10$, $P = 0.752$, $n = 160$; Fig. 3C). The difference in the location of the centroid for the two stimuli could not be accessed for judgments of relative spatial location.

[†]Although G.Y. can discriminate the direction of second-order, contrast-determined motion energy in his blind field (22), the detection of second-order motion energy for the reverse-phi stimuli in the current study would have resulted in judgments of motion direction opposite to those selected most often by G.Y. in his blind field.

Length Discrimination (shape change control)



Centroid Shift (position control)

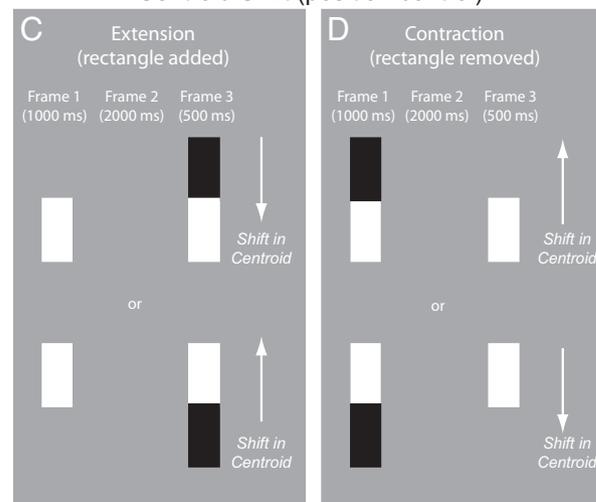


Fig. 4. Three-frame sequences that tested the detectability of changes in shape and the accessibility and validity of the position cues available for the motion stimuli tested in experiments 1 and 2. Each panel illustrates the alternatives presented in random order in two-alternative forced-choice trials. Experiment 3: Changes in shape with either a 0-ms or 1,000-ms IFI, with alternatives matched in upwards motion energy (A) and downward motion energy (B). Experiment 4: Centroid shifts induced by adding or removing a black rectangle to or from an adjacent position above or below a white rectangle for trials with shape extension (C) and trials with shape contraction (D).

Experiment 5: Control for Attentive Feature Tracking. Although G.Y. can orient attention within his cortically blind field (29), his discrimination of motion direction for the reverse-phi version of the line motion stimulus in experiment 2 was not the result of attentive feature tracking (30). This was shown by presenting a single white or black rectangle in the upper location of the reverse-phi line motion stimulus during one 1,000-ms temporal interval, and in the lower location of the line motion stimulus during the other 1,000-ms temporal interval (or vice versa, randomly determined). As in experiment 4, the two intervals were separated by 2,000 ms, so motion detection was not possible. G.Y. correctly indicated the temporal interval during which the rectangle was higher on 68% of the trials, significantly greater than would be expected on the basis of chance (Pearson's $\chi^2 = 9.80$, $df = 1$, $P = 0.0017$, $n = 80$; Fig. 3D). Although this made it plausible for motion direction to be determined by shifting at

tention from the location of the initially presented white rectangle to the location of the subsequently added black rectangle, the motion inferred on this basis would have been toward the black rectangle. This would have been opposite to the direction specified by first-order motion energy, which was the basis for G.Y.'s judgments of motion direction in his cortically blind field.

Discussion

G.Y.'s discrimination of motion direction was based on the detection of first-order motion energy when the reverse-phi stimuli illustrated in Fig. 2 *C* and *D* were presented within his cortically blind field. When the same stimuli were presented in his intact visual field, direction discrimination was based on the detection of changes in global shape. This difference maps onto the mechanisms proposed for the extraction of motion energy (by first- or second-order systems responsive to spatiotemporal changes in luminance or luminance contrast) vs. the detection of object motion (by a third-order system responsive to spatiotemporal changes in feature salience) (31). The characterization of motion energy as signaling objectless motion (31) is consistent with motion being perceived without extracting the boundary and surface features that determine a moving object's shape (23). The sparing of objectless motion energy detection in the cortically blind field thereby allows for motion direction to be discriminated regardless of deficits in object/shape perception in that field.

The evidence reported in this article for motion energy detection in cortically blind fields argues against the assertion that success discriminating motion direction for translating bars, but failure to do so for random kinematograms and drifting gratings, is the result of direction judgments being based on the detection of changes in position rather than motion (22). For random kinematograms, the fact that all of the dots move in the same direction does not preclude the stimulation of motion energy detectors with other directional selectivities, albeit more weakly. Similarly for drifting gratings, motion energy detectors selective to the direction of drift would be most strongly stimulated, but detectors with the opposite selectivity also would be stimulated. When striate cortex is intact and mechanisms associated with the perception of object motion are available, winner-take-all inhibitory interactions among detectors with different directional selectivity appear to be sufficient to suppress less strongly stimulated motion directions (33, 34). However, in the absence of V1 input to middle temporal (MT), competitive interactions among motion energy selective neurons in MT appear to be relatively "soft" (35), so directions other than the dominant direction remain active (36, 37), creating a multiplicity of conflicting motion signals. Whether this accounts for the difficulty discriminating motion direction for random kinematograms and drifting gratings within cortically blind visual fields remains to be determined.

When the stimuli that are the basis for the current report are presented to intact striate cortex, changes in object features predominate over motion energy. However, it has been found in a separate study that motion energy can predominate in the determination of motion direction within intact visual fields, provided the motion is fast (38). It is not surprising, therefore, that it is easier to discriminate motion direction within cortically blind visual fields when the motions are relatively fast (21, 22). Fast motion enhances the extraction of objectless motion energy, and the preference of motion energy detection for low spatial

frequencies (39, 40) as well as high speed corresponds nicely with the residual sensitivity to low spatial and high temporal frequency within the cortically blind visual field (3). Indeed, high-speed motion discriminations appear to be alike for both blind and intact visual fields (41), so the current findings suggest that motion energy extraction for high-speed motion perception is the same in blindsight as it is in normal vision.

The previously described speed dependence of motion energy extraction is consistent with the different neural pathways that appear to be activated as a function of the speed of apparent motion (42). For relatively slow speeds, spatial separation has corresponding effects on human judgments of motion, and on the activation of both area V1 and area MT/V5 neurons of the macaque, a correlation between V1 and MT/V5 activation that would be expected for the low-speed-preferring object motion pathway. For faster speeds, effects of spatial separation corresponded for human judgments and MT/V5 activation, but not for V1 activation. This is as expected if the high-speed-preferring motion energy pathway to MT/V5 bypasses V1. Experiments with monkeys combining single-unit recordings in MT with blindsight-inducing V1 lesions indicate that this pathway is routed via the superior colliculus (the retinocollicular pathway) (6–8), either through the pulvinar nucleus or through the lateral geniculate nucleus (9, 13).

It is tempting to speculate on the relevance of our results to motion detection pathways in the intact brain. It has been found that 80% of identified directionally selective macaque MT neurons extract motion energy from visual stimuli, whereas 20% respond to motion in the feature-determined direction (35). In addition, it has been shown that neural activity in MT depends in part on inputs from V1 and in part on inputs from the superior colliculus (6–8). Our evidence for the detection of motion energy without shape discrimination, together with the absence of definitive evidence that V1 neurons respond preferentially to motion energy in reverse-phi stimuli (35), suggest that the motion energy-selective MT neurons receive their inputs from the superior colliculus, whereas feature-selective MT neurons receive their inputs from V1. It is therefore possible, for intact brains, that the pathway from the superior colliculus to MT entails the extraction of objectless motion energy, whereas the parallel V1 pathway to MT entails mechanisms for the extraction of features that contribute to the perception of both an object's form and its motion.

Our findings show that motion discrimination is preserved in the field defect of a patient with blindsight. The dependence of motion energy on motion energy detection and its independence of object or feature detection is in keeping with previous studies (3, 43, 44) in suggesting that residual vision in blindsight is largely dependent on the detection of transient changes in luminance.

Materials and Methods

Visual stimuli were generated using a ViSaGe Stimulus Generator (Cambridge Research Systems) with custom software and presented on a 22-inch Mitsubishi Diamond Pro-20705B CRT monitor (100-Hz refresh rate). They were viewed monocularly (right eye) in a diffusely lighted room; the average reflectance of the light gray walls was 2.0 cd/m². The luminances of the white, gray, and black regions of the stimuli and background were 44.5, 20.2, and 0.23 cd/m², respectively. A viewing distance of 57 cm was maintained with a chin rest. The fixation point was located 6 cm outside the visible frame of the CRT monitor to avoid the possibility of raster artifacts being detected by the spared visual field (45). Fixation was monitored with closed-circuit TV. Rare trials in which the observer's eye moved by any discernible amount were aborted (with replacement). The stimuli were centered 12.0° above the fixation point, either 30.0° to the right in G.Y.'s blind field, precisely where his discrimination and awareness of moving stimuli had previously been characterized (22, 46), or 30.0° to the left for testing in his intact field.

All tests used a temporal, two-alternative forced-choice procedure, i.e., one in which both variants of the stimulus (up and down) were presented in

[†]Converging results have been obtained for a patient, D.F., who because of brain damage has great difficulty discriminating between different shapes. Although she can discriminate motion direction for a moving solid square, she cannot do so for moving illusory contours (Kanizsa squares) (32). With the impairment of her object/shape pathway, it is likely that she, like G.Y. in his blind field, relies on motion energy detection for judgments of motion direction. Based on the findings in the present article, we can now attribute her failure with Kanizsa squares to the absence of motion energy in those stimuli.

randomly determined order (up then down, or down then up), to eliminate any possibility of the responses being affected by response bias. The start of each interval and the end of each trial was signaled by a tone, the intervals being separated by 2,000 ms. After each trial, G.Y. indicated, by pressing one of two keys, the interval during which he detected upward motion (or position, or shape extension, according to the test). Responses were cast as contingency

tables and analyzed using Pearson's χ^2 tests, Mantel-Haenszel tests (tests of homogeneity for pairs of 2×2 contingency tables), and logistic regression (47).

ACKNOWLEDGMENTS. We thank G.Y. for his participation and Dr. A. D. Lunn for his expert advice on statistical analysis. This work was funded in part by a McDonnell European Network grant (to P.A.).

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