

Blindsight Modulation of Motion Perception

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Abstract

■ Monkey data suggest that of all perceptual abilities, motion perception is the most likely to survive striate damage. The results of studies on motion blindsight in humans, though, are mixed. We used an indirect strategy to examine how responses to visible stimuli were modulated by blind-field stimuli. In a 26-year-old man with focal striate lesions, discrimination of visible optic flow was enhanced about 7% by blind-field flow, even though discrimination of optic flow in the blind field alone (the direct strategy) was at chance. Pursuit of an imagined target using peripheral cues showed reduced variance but not

increased gain with blind-field cues. Preceding blind-field prompts shortened reaction times to visible targets by about 10 msec, but there was no attentional crowding of visible stimuli by blind-field distractors. A similar efficacy of indirect blind-field optic flow modulation was found in a second patient with residual vision after focal striate damage, but not in a third with more extensive medial occipito-temporal damage. We conclude that indirect modulatory strategies are more effective than direct forced-choice methods at revealing residual motion perception after focal striate lesions. ■

INTRODUCTION

Blindsight refers to retained visual ability without awareness, after cerebral lesions (Weiskrantz, Warrington, Sanders, & Marshall, 1974). There are several hypotheses concerning the anatomic basis of blindsight, which are not mutually exclusive. Initial reports of target localization in hemianopic fields were predicated upon the proposal that the superior colliculus alone may mediate some remnant visual function (Pöppel, Held, & Frost, 1973). More recent concepts of blindsight invoke the participation of surviving extrastriate visual cortex, via geniculate projections bypassing striate cortex or indirect relays involving the tectum and pulvinar (Stoerig & Cowey, 1997).

The theory that surviving extrastriate cortical function is at least partially responsible for blindsight is supported by studies of monkeys with striate lesions. These show residual visual responses in the middle temporal (MT) area (Girard, Salin, & Bullier, 1992; Gross, 1991; Rodman, Gross, & Albright, 1989) and area V3a (Girard, Salin, & Bullier, 1991). However, not all extrastriate regions show such remnant function: In similar studies, striate lesions were found to abolish visual activity in V2 (Girard & Bullier, 1989), V3 (Girard et al., 1991), and inferotemporal (IT) cortex (Gross, 1991). Since V5 and V3a are components of the “dorsal stream” of cortical visual processing, concerned more with target motion and spatial location, whereas IT is part of the ventral stream, concerned with object shape and identity, this suggests that responses to moving stimuli should be

particularly likely to survive striate lesions. Indeed, monkeys with striate lesions have been shown to possess residual motion detection and discrimination (Keating, 1980); on the other hand, studies of ocular pursuit of moving targets after striate ablation have produced both positive (Zee, Tusa, Herdman, Butler, & Gücer, 1987) and negative results (Segraves et al., 1987).

In humans, although a variety of blindsight abilities have been demonstrated, the evidence for remnant motion perception is less clear. Direction discrimination in 3 patients (Perenin, 1991) and illusions of self-motion in 2 of 10 patients (Heide, Koenig, & Dichgans, 1990) have been reported with large luminant gratings in the blind hemifield, but such stimuli are prone to scatter artefacts. Others have failed to duplicate the result (Verhagen, Huygen, & Mulleners, 1997) or found that only subjects with conscious residual vision detected small moving targets (Blythe, Kennard, & Ruddock, 1987). Using random dot stimuli, we did not find any direction discrimination, even in subjects with sparing of the lateral human motion area (Barton & Sharpe, 1997a). Regarding eye movements, residual optokinetic nystagmus was reported in one cortically blind patient (ter Braak, Schenk, & van Vliet, 1971), but neither in two others (Verhagen et al., 1997; Perenin, Ruel, & Hecaen, 1980) nor in three hemianopic patients (Perenin, 1991). Four children with cortical blindness and residual optokinetic nystagmus have been reported (van Hof-van Duin & Mohn, 1983), but confirming complete loss of vision in children is difficult: Of note, one child avoided walls when walking and another had residual visual evoked potentials. We did not detect residual pursuit in adult hemianopic patients with intact lateral occipito-temporal

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cortex (Barton & Sharpe, 1997b). Despite these mixed results, functional imaging studies in blindsight patient GY (Barbur, Watson, Frackowiak, & Zeki, 1993) and transcranial magnetic stimulation studies in normal subjects (Beckers & Zeki, 1995; ffytche, Guy, & Zeki, 1995) support the possibility that the human motion area may have activity that is not dependent upon input from striate cortex.

As with most blindsight studies, both our previous experiments and those of others tested for manual or ocular motor responses to stimuli in blind regions alone. An alternative method, which we use here, is to determine if blind-field stimuli can modulate responses to stimuli in the seeing hemifield. Studies of covert recognition in visual object agnosia draw a similar distinction

between direct strategies, which require forced-choice decisions about some attribute of the object, which is not overtly recognized, and indirect strategies, which examine how unconscious knowledge about the object influences responses to other stimuli (Young, 1994). An indirect strategy circumvents the awkwardness of asking patients to guess at properties of a stimulus that they do not acknowledge seeing, and has been reported superior to other blindsight techniques in a study of linguistic effects (Marcel, 1998). Other reports of blindsight modulation of responses to seen stimuli include saccade inhibition (Rafal, Smith, Krantz, Cohen, & Brennan, 1990), spatial and temporal summation in manual reaction times (with inconsistent results) (Tomaiuolo, Ptito, Marzi, Pau, & Ptito, 1997; Corbetta, Marzi, Tassinari, &

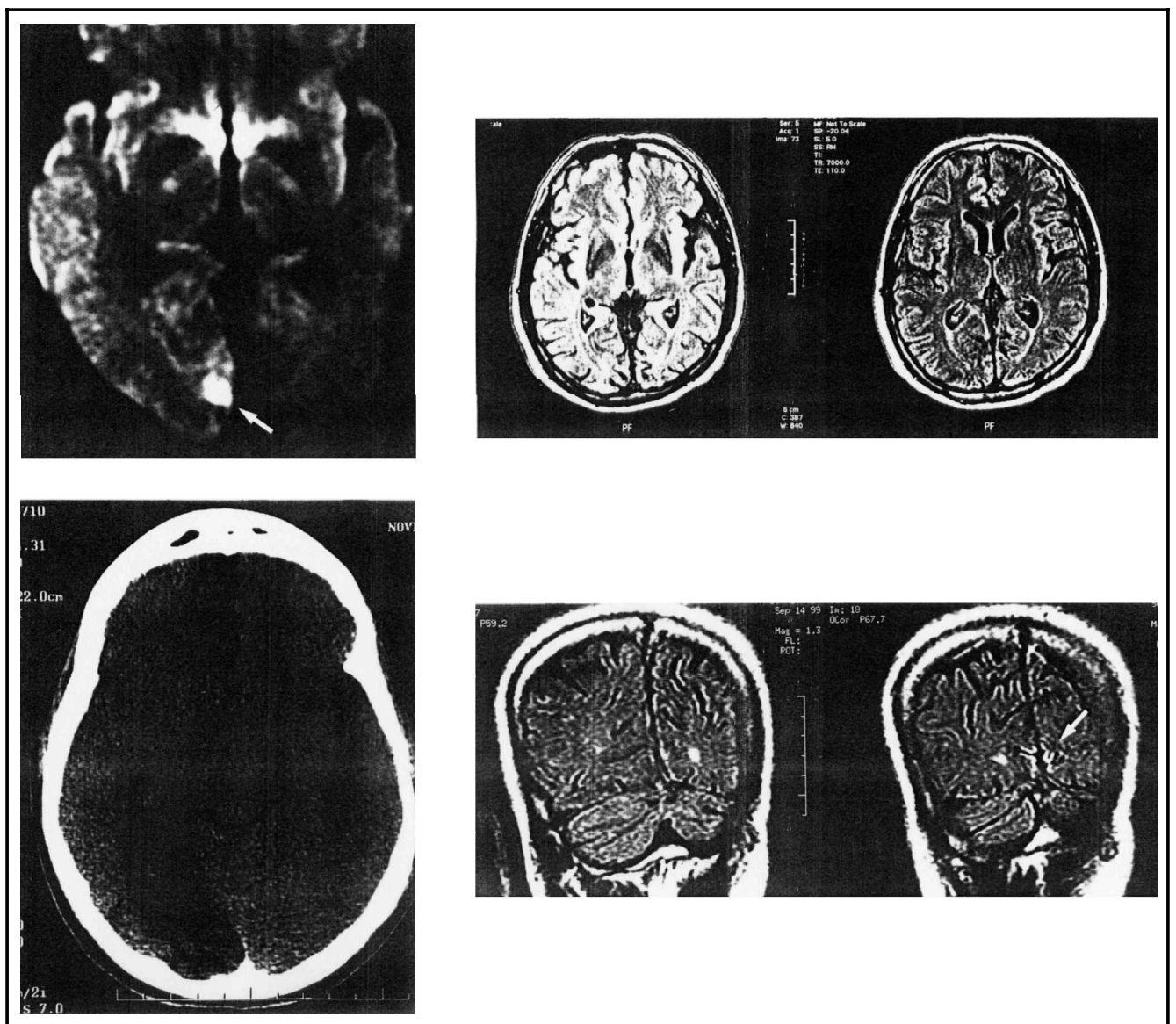


Figure 1. Lesions on imaging. JS (top left) has a right focal striate lesion (arrow) that showed up only on diffusion-weighted MR scans. Axial image is shown. (The prior left striate lesion does not appear as it is not acute at this stage.) NA (right top and bottom) has small occipital white matter lesions and bilateral occipital pole lesions (arrows), showing up as white on these axial (top) and coronal (bottom) FLAIR MR images. DNR (bottom) has an extensive medial occipito-temporal lesion on axial CT, consistent with a complete posterior cerebral arterial infarction.

Aglioti, 1990; Marzi, Tassinari, Agliotti, & Lutzemberger, 1986), and inhibition of return (Danziger, Fendrich, & Rafal, 1997). Regarding motion, Pizzamiglio, Antonucci, and Francia (1984) reported that, in 7 patients, rotating motion in both fields tilted the subjective visual vertical more than just motion in the seeing field. However, their hemifield stimuli contained inadvertent clues to the true vertical, and their trials were presented in a nonrandom fashion, limiting the interpretation of their results.

Here, we report the implementation of this modulatory strategy in 4 different tests. Two of these involved responses to stimulus motion. One studied whether optic flow perception could be augmented by flow information in the blind field. This was selected because optic-flow-responsive cells in the medial superior temporal area (MST, or V5a), a major projection zone of area MT, have large receptive fields spanning much of both contralateral and ipsilateral hemifields. The second measured ocular tracking responses to extrafoveal targets, where it is known that, in normal observers, smooth pursuit of two such targets is better than that of one (Wyatt, Pola, Fortune, & Posner, 1994). The question is whether a similar advantage could be found even if the second target was in the hemianopic field.

The last two tests measured nonmotion functions. One was response prompting, in which the reaction time to a seen stimuli is reduced when it is preceded by a prompt at another location. Studies of this phenomenon in blindsight have been reported by others (Tomaiuolo et al., 1997; Corbetta et al., 1990; Marzi et al., 1986). Lastly, we examined “crowding,” in which a target in the middle of a string of similar stimuli is more difficult to perceive than when it is presented in isolation or at the end position of a similar array, an effect sometimes referred to as lateral interference. The question is whether a target in the seeing field can be crowded by distracter stimuli within the blind hemifield.

RESULTS

Case JS

Our index case was JS, a 26-year-old man with focal sequential bilateral striate infarctions (Figure 1), which had caused previous small right hemifield scotomata and a more recent complete left hemianopia (Figure 2) that occurred 3 months before testing. Because age at onset (Moore, Rodman, Repp, Gross, & Mezrich, 1996; Payne, Lomber, Macneil, & Cornwell, 1996) and extent of extrastriate damage (Weizkrantz, 1990) may determine the likelihood of blindsight, his youth and his small lesions made him a good candidate. JS was available for intensive testing on these protocols over many days.

Temporal Response Prompting

In JS, a preceding stimulus in the blind hemifield caused a small but consistent average decrease of 10 msec in

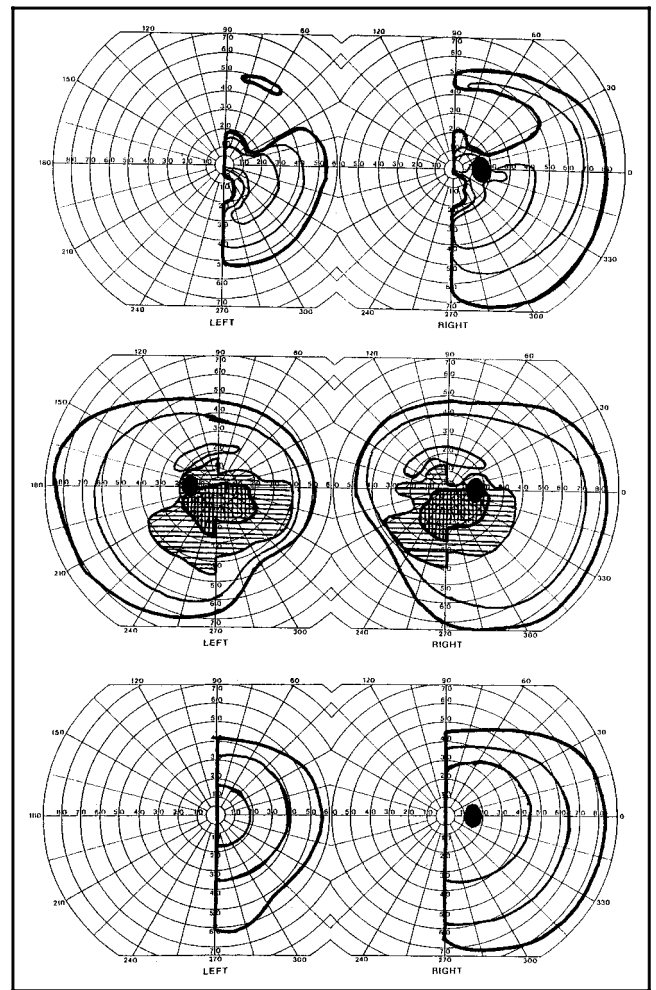


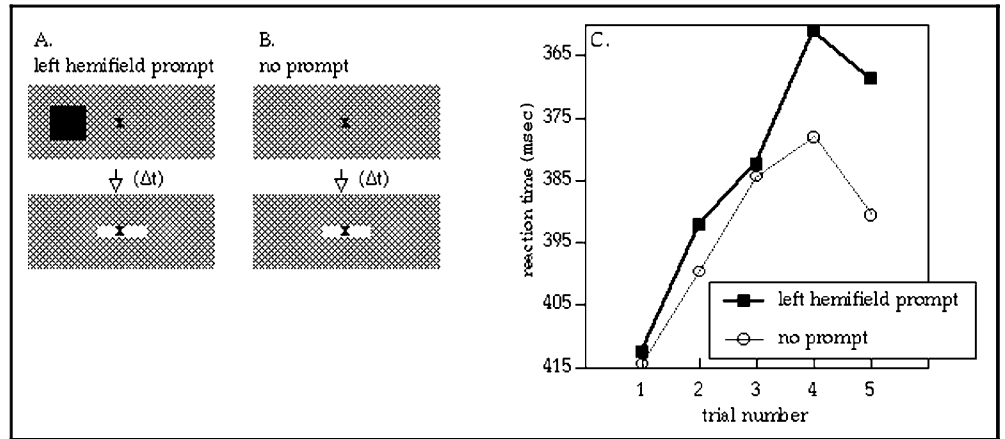
Figure 2. Goldmann perimetry. JS (top) has a complete left hemianopia and smaller right scotomata. NA (middle) has bilateral central scotomata, in which he can still consciously sense large bright target. In the horizontally striped area, he can sense the II4e but not the I4e target, and in the cross-hatched area, he can sense only targets equal to or larger than the III4e target. DNR (bottom) has a complete left homonymous hemianopia, without macular sparing.

reaction time to a central flash ($p < .04$, Figure 3). This compares with a 94-msec decrease with prompts in the seeing hemifield of JS, a value similar to that in the normal subject.

Crowding

Unilateral crowding by distractors in the blind left hemifield did not reduce discrimination when compared to a single uncrowded stimulus in the seeing right hemifield (Figure 4A). Second, unilateral crowding by distractors in the seeing right hemifield was not augmented in the bilateral crowding condition, when there were additional distractors in the blind left hemifield (Figure 4B). However, in these trials, the unilateral crowding from seeing right hemifield distractors was too effective, already reducing JS’s target discrimination to near chance. Hence, any additional effects from blind

Figure 3. Temporal response prompting. Subject presses a key when the central white rectangle appears. On some trials (A) a black square in the blind field appears 200 msec (Δt) before the white rectangle, while the subject maintains fixation at "x." Does this decrease reaction time, compared to when there is no blind-field prompt (B)? The results for JS in (C) show that, compared to the lack of a prompt, a blind-field prompt reduced reaction time consistently over five consecutive blocks (note inverted y-axis).



In this and all graphs, the dark thick lines with solid symbols indicate results with blind-field stimuli, and the thin lines with clear symbols are the results from control trials without blind-field stimuli. Graphs are arranged so that positive blindsight results are represented as a higher position of the dark line relative to the thin line.

hemifield distractors in bilateral crowding would not be detectable. Therefore, we performed additional experiments with reduced eccentricities of 6.1° and lower

spatial frequencies of 2.2 Hz. This successfully weakened the unilateral crowding from the visible distractors in the right hemifield (Figure 4B). Despite this, we still did

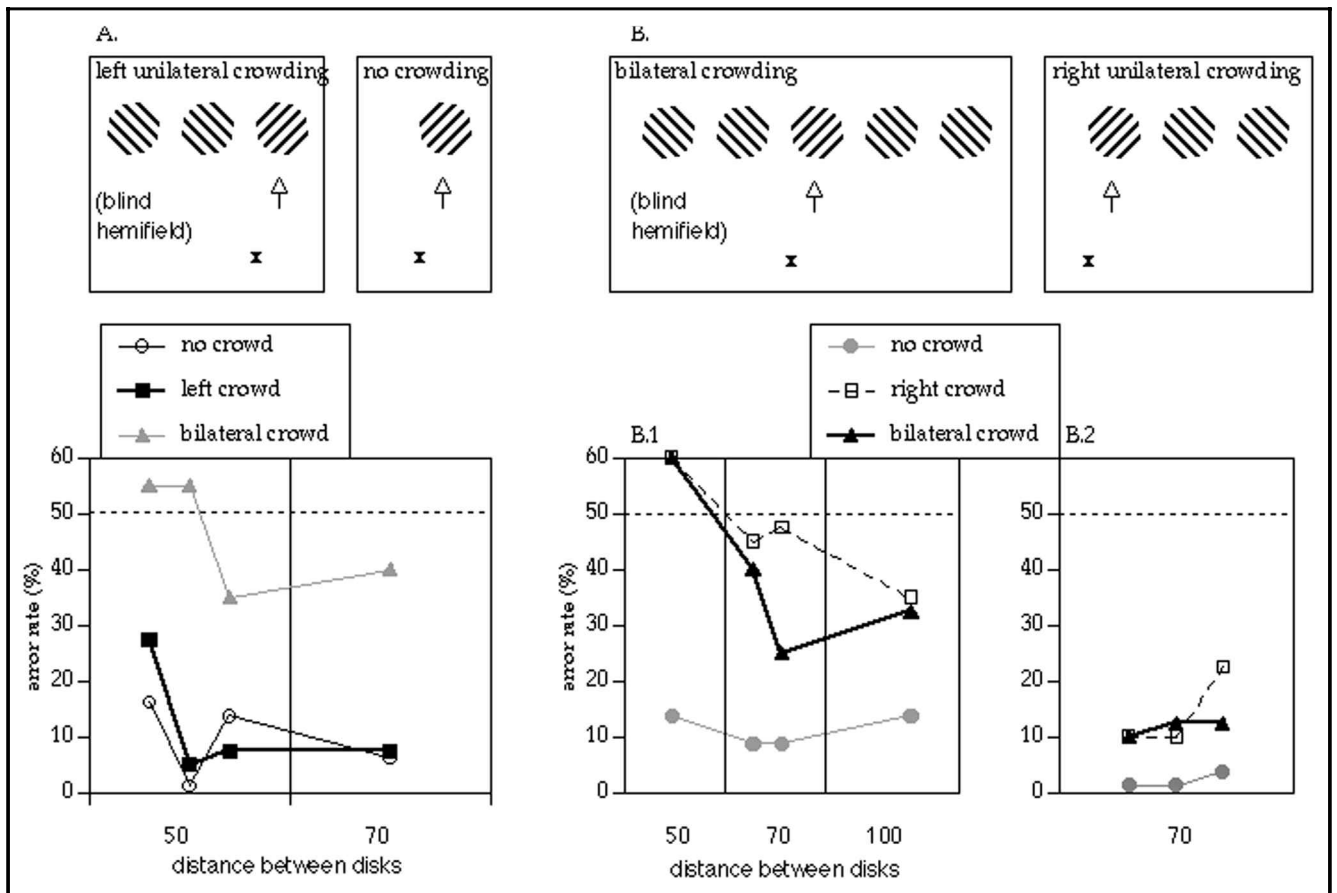


Figure 4. Crowding. The subject fixates at "x." Orientation discrimination of the target disk (arrow) is tested with or without flanking stimuli that decrease accuracy in normal subjects. Is discrimination of the disk seen alone better than when there are flanking disks in the blind left field? Is crowding increased if there are disks on both sides compared with just disks on the right seeing field? For JS, the left panel shows that unilateral crowding (squares) in the left blind field did not affect orientation discrimination, compared to no crowding (circles). Middle panel shows that bilateral crowding (triangles) was no worse than unilateral crowding (squares) in the right seeing field; however, the latter was already near chance. Weakening unilateral crowding in the seeing field by decreasing eccentricity and increasing grating frequency did not allow a bilateral crowding effect to emerge (right panel).

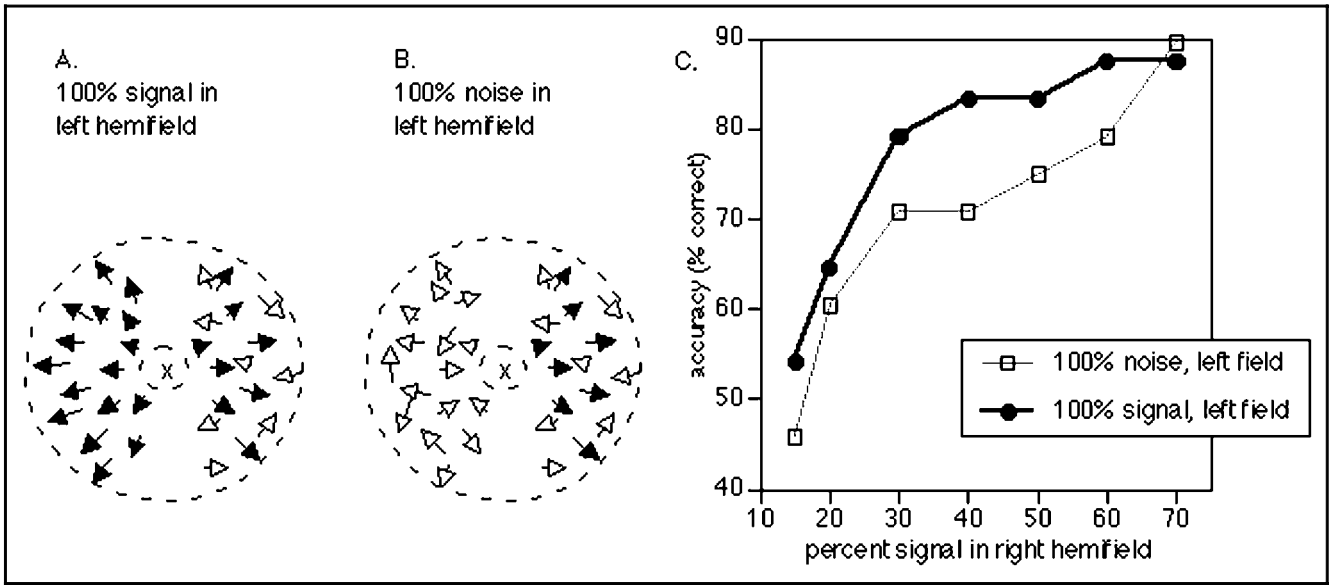


Figure 5. Optic flow. Subject discriminates direction of signal motion (black arrows) in the right seeing field in the presence of random motion noise (white arrows). Is discrimination more accurate if there is concomitant optic flow signal in the blind field (A), compared to when there is only random motion noise in the blind field (B)? Results for JS in C show that the accuracy of discriminating the optic flow signal increases with signal coherence, as plotted along the x-axis. Compared to stimuli with random dot motion in the blind field (clear squares), adding 100% optic flow signal to the blind field (solid circles) increased accuracy by 6% on the average.

not see any augmentation of this lesser effect by blind left hemifield distractors.

Optic Flow

JS's ability to perceive the noise-degraded optic flow signal in his right hemifield was consistently enhanced

by an average of nearly 7% ($p < .008$, paired t test) by a 100% optic flow signal in the blind hemifield, compared to trials where his blind left hemifield contained only random motion (Figure 5). In contrast, with "control" stimuli that presented a 100% flow signal in his blind left hemifield and no stimulus in his seeing right hemifield, accuracy was 52%, no different than

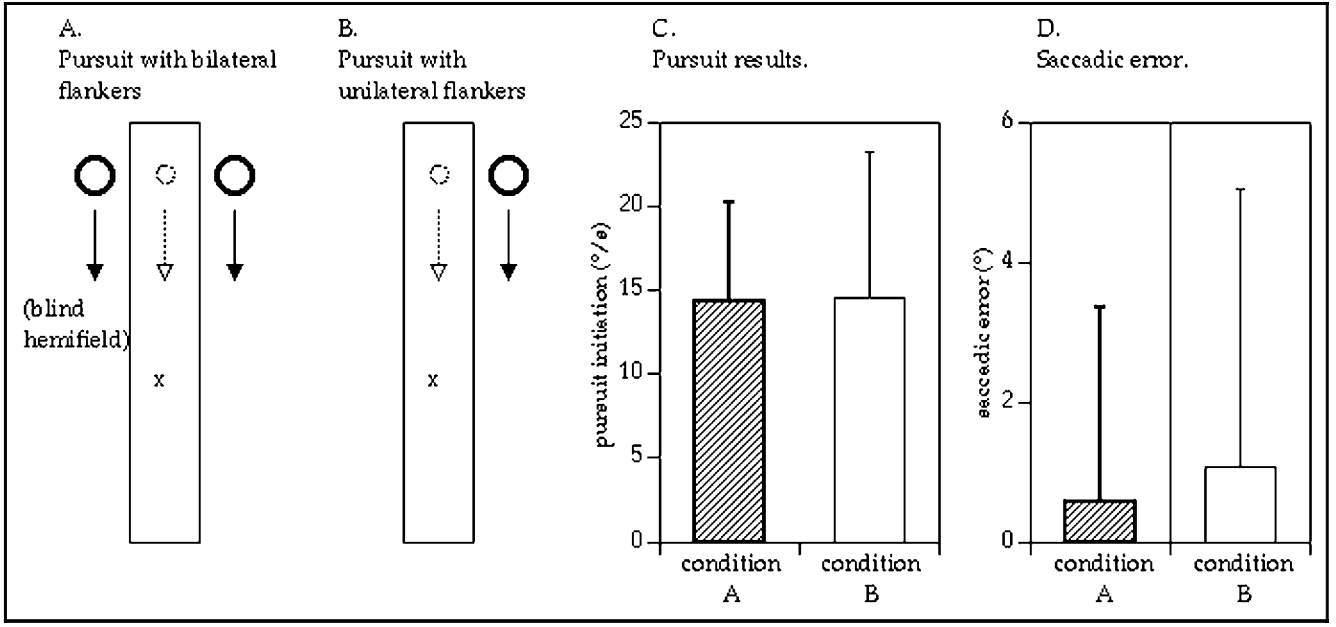


Figure 6. Pursuit. Subject imagines a target (dotted lines) moving within a track marked by the rectangle. The position of the imagined target is cued by flanking circular markers which move. Is ocular tracking better when there is an additional marker in the left blind field (A) compared to a single marker on the right seeing field (B)? (C) Results in JS. Means of tracking with two flanking markers are shown as striped bars (condition A) and those with a single marker as clear bars (condition B), with error bars indicating one standard deviation. There is no difference in the average postsaccadic pursuit velocity (C) or saccadic error (D), but the variances of both are reduced significantly.

Table 1. Test Result Comparison of the Three Subjects

Subject	Optic Flow				Response Prompting				
	Indirect Strategy			Direct Strategy	Blind Hemifield			Seeing Hemifield	
	Average Increase in Accuracy (%)	SD	<i>p</i> value	Correct Responses/Number of Trials	Average Decrease in Latency (msec)	SD	<i>p</i> value	Average Decrease in Latency (msec)	SD
JS	6.85	4.62	< .008	33/64	10.03	8.99	< .04	93.35	10.93
NA	10	14.79	< .04	24/60					
DNR	-1.40	10.63		39/66	2.71	11.39		43.29	15.36

chance ($p = .35$). This showed that our indirect strategy was more effective than the direct one, and also excluded scatter of the blind-field stimulus into the seeing field as an artifact.

Pursuit

As in our prior study (Barton & Sharpe, 1997b), with a single horizontal step-ramp stimulus that generated a vigorous pursuit response in his seeing right hemifield (slope = gain = .20, $r = .66$, $p < .0001$), there was no significant pursuit of stimuli confined to the blind left hemifield (slope = .03, $r = .14$, $p = .35$). With parafoveal markers to indicate the vertical position of an imaginary target (Wyatt et al., 1994), we then asked whether JS's ocular tracking was enhanced by two markers over one, even when one of the markers was in the blind left hemifield. We found that neither postsaccadic pursuit gain nor saccadic accuracy was increased by the second marker (Figure 6), in contrast to the findings in a normal subject. However, variances of both pursuit gain (F test, $p < .001$) and saccadic error (F test, $p < .004$) were significantly reduced by the presence of the second marker in the blind hemifield. This suggests that the blind-field stimuli made ocular responses more consistent even though they did not increase gain in the manner seen in the normal subject.

Cases NA and DNR

In addition to JS, we tested in a more limited fashion two other subjects with striate infarction (Figures 1 and 2). DNR is a 41-year-old woman who had a right posterior cerebral arterial infarction complicating streptococcal sepsis, 6 months prior to testing. She had a complete right homonymous hemianopia. A CT scan showed an extensive medial occipito-temporal lesion, extending beyond striate cortex, but without involvement of the human V5 area in lateral occipito-temporal cortex. NA is a 52-year-old man who developed sudden cortical blindness 5 days after a myocardial infarction. His vision gradually improved, leaving him with a dense relative central scotoma from small bilateral infarctions of the occipital poles and underlying white matter, as shown

on MRI. He also described palinopsia and release hallucinations. He was tested 26 months after onset.

We examined DNR and NA on the tests that gave the most interesting results in JS. With the optic flow stimuli, DNR and NA also did not show any discrimination better than chance with the direct strategy with stimuli solely present in their scotomata (Table 1). With the indirect strategy, NA showed a 10% augmentation of optic flow discrimination by coherent patterns in his blind scotomata, similar to that which occurred in JS. DNR, on the other hand, showed no significant effect, despite many repetitions over several days. DNR also performed the temporal response prompt experiment. There was no effect of a prompt in the blind hemifield upon reaction times in her (Table 1).

DISCUSSION

Our results show that a weak motion signal survives damage to striate cortex. This motion signal can augment optic flow discrimination amidst noise and it can reduce the variance of pursuit responses. In addition, there is a slight effect of visual transients in the blind field in prompting reaction times to seen stimuli. Visual transients are known to generate signals in motion-sensitive neurons (Petersen, Miezin, & Allman, 1988). The weak motion and pursuit responses that we observed were not detectable with conventional direct blindsight strategies but emerged only in their ability to modulate responses to visible stimuli. This is consistent with a prior claim of superiority of indirect over direct methodologies for demonstrating blindsight (Marcel, 1998). Apart from this work, prior studies that used indirect methods did not compare direct and indirect strategies to determine their relative efficacy.

These weak blind-field motion responses were observed in JS, where his lack of awareness of stimuli in his blind hemifield indicates that these effects do constitute blindsight. NA, on the other hand, does see very bright targets within his scotoma, and so has some residual conscious vision. His results would constitute residual vision and may reflect incomplete damage to V1, given the subtlety of his lesion on MRI compared to both his current scotoma and his initial presentation

with cortical blindness. Nevertheless, like JS, NA cannot discriminate optic flow when it is presented solely within the scotoma, but can use this information to augment responses to flow outside of the scotoma.

Thus, this indirect modulation is effective for both a case (JS) that conforms to the phenomenologic definition of blindsight and one (NA) that represents residual vision, both after focal striate damage. Whether these two phenomena share the same pathophysiology is unclear (Weiskrantz, 1998; Zeki & ffytche, 1998). Subject GY's awareness of blind-field stimuli can be made to vary by changing stimulus parameters (Weiskrantz, Barbur, & Sahraie, 1995), and these are said to be reflected in variations in regional patterns of activity on functional imaging (Sahraie et al., 1997). However, the ability to make GY unaware of stimuli is not surprising, as stimulus manipulations can alter the awareness of stimuli in normal subjects (Kolb & Braun, 1995; Meeres & Graves, 1990). More to the point would be comparisons between subjects like GY and NA, who have residual vision at some level, and other subjects who never manifest awareness of blind-field stimuli, and yet have true blindsight.

After striate resection or cooling, directional selectivity, topography, and receptive field size can remain unaltered in up to 60% of neurons in MT, though response magnitude is reduced and directional tuning broader (Girard et al., 1992; Rodman et al., 1989). Adding a lesion to the superior colliculus to the striate damage eliminates the residual visual activity in MT (Gross, 1991; Rodman et al., 1989), supporting the concept that at least some remnant visual input involves a retino-tecto-pulvino-cortical relay. Recent data (Rosa, Tweedale, & Elston, 2000) confirm that after a focal striate lesion about 20% of corresponding V5 neurons retain both motion sensitivity and receptive fields that represent the area of the scotoma, while the remainder shift their fields to areas represented by viable striate cortex.

Given these data and functional imaging and electrophysiologic data from GY that show blind-field signals in the human V5 region (Holliday, Anderson, & Harding, 1997; ffytche, Guy, & Zeki, 1996; Barbur et al., 1993), one might expect that the residual motion perception that we demonstrate in JS may originate in V5 also, even though we cannot exclude residual weak V1 activity in NA. Certainly, the V5 region is not affected by JS's lesions. However, this region in lateral occipito-temporal cortex (Barton, Sharpe, & Raymond, 1995; Barton et al., 1996) is also spared in DNR, who clearly does not demonstrate any blindsight motion perception with the same technique. There are two possible explanations. One is that some region in medial occipito-temporal cortex with either motion sensitivity or an interaction with a lateral motion-sensitive region is critical for blindsight motion perception. Functional imaging does show that many human cortical areas

besides V5 are activated during motion perception. It may be that a motion-sensitive dorsal parieto-occipital region was affected by DNR's lesion, for example. A second possibility is that the extensive lesion of DNR was also more complete in its ablation of V1 than the focal damage in JS. A requirement for very focal striate damage may be difficult to distinguish practically from a requirement for incomplete striate damage, as the smaller the lesion, the more likely that it is partial. In this regard, a number of demonstrations of surviving islands of probable striate vision in patients with apparent blindsight are important (Scharli, Harman, & Hogben, 1999a, 1999b; Fendrich, Wessinger, & Gazzaniga, 1992). It is not likely that functional imaging will soon settle this issue, as it is not yet known how sensitive this technique is in detecting weak surviving activity in partly damaged cortex, striate or otherwise. Rather, what is needed is a correlation of blindsight anatomy and function in a larger series of patients. Our results indicate that, to yield the most informative findings, indirect methodologies should be incorporated into any blindsight battery that is used in such a study.

METHODS

Apparatus

All four experiments used a Power Macintosh 9600/233, with programs written on the Vision Shell platform (www.kagi.com/visionshell). For the first three tests utilizing manual keyboard responses, stimuli were viewed on an Apple Multiscan monitor 57 cm away in a darkened room. The background of the screen, except where otherwise indicated, was black ($<0.3 \text{ cd/m}^2$). Fixation was monitored either visually or with on-line video. If fixation was lost in a trial, the trial was cancelled and presented again later in the trial sequence. To measure pursuit eye movements, we used a magnetic search coil technique (Crist Instruments, Bethesda MD), with stimuli back-projected by an Eiki LC-7000U projector (Eiki, Lake Forest, CA) onto a paper screen with minimal scatter and 80% transmission, mounted on a clear glass 81 cm from the subject.

Protocols

Temporal Response Prompting

We measured manual reaction times for a key press to the appearance of a white (20 cd/m^2) bar measuring 6.5° horizontally by 2.5° vertically, centered at fixation, and which appeared for 60 msec after a period randomly varying between 1 and 2 sec following trial onset. The background was a randomly stippled pattern of average luminance of 10 cd/m^2 . On a third of trials, the white bar was preceded 200 msec earlier by a black $6.1^\circ \times 6.1^\circ$ square lasting 45 msec and centered laterally at 8.2° in the blind left hemifield. On another third, there was a

black square in the right hemifield, and on the remaining third, there was no prompt (Figure 3). Ninety trials were given in each of the five blocks for JS. DNR underwent six blocks. The difference between the blind-field prompted trials and the no-prompt trials for each block was averaged, and these block results were subjected to a paired-difference *t* test.

In a normal subject aged 32, the peripheral prompt reduced average reaction times by about 100 msec.

Crowding

The probe was a 2°-diameter disk containing a Gabor patch, which is a sinusoidal luminant grating whose peak-to-trough contrast is spatially modulated perpendicular to the bars by a cosine envelope. The disk was surrounded by a bright ring of 0.2° thickness and 30 cd/m² luminance. The standard patch used in most trials had a spatial frequency of 4.1 Hz, 100% contrast at maximum, and lasted 165 msec. It was shown at 8.2° eccentricity either up or down from fixation, centered just right (85°) of the vertical meridian, so that it lay entirely within the right (seeing) hemifield. The grating was oriented either 45° left or 45° right, and the task was to discriminate this orientation. In each block, 80 trials presented the probe alone, 40 trials showed the probe flanked horizontally on one side only by two similar disks that varied solely in grating orientation, and 40 had four flanking disks, two on each side (i.e., two in the seeing and two in the blind hemifield). The side of the unilateral crowding disks differed between blocks.

This allowed us to address two questions. The first was whether unilateral crowding occurred from within the blind hemifield, that is, is discrimination impaired when the disk is the rightmost of an array of three disks, the other two being in the blind field, compared to when the disk is seen as a single element? The second was whether stimuli on both the blind and intact hemifield (bilateral crowding, from the array with five disks) produced more crowding than the unilateral crowding from two disks on the (seeing) right of the target (Figure 4).

In seven normal subjects, with disk spacings of 2° or 2.8°, discrimination was reduced from 89%, with no crowding, to 82%, with unilateral crowding (target is at one end of an array of three disk stimuli) to 68%, with bilateral crowding (target is the middle disk of an array of five disks).

Optic Flow Perception

Each hemifield contained 2000 black dots in an arc-shaped region extending between 3.2° and 9.8° of eccentricity and not including a 30° wedge straddling the vertical meridian. Background luminance was 30 cd/m². All dots had a limited lifetime of 150 msec (10 frames), and stimulus duration was 225 msec. In the seeing

hemifield, dots were divided into signal and noise pools. Signal dots moved in radially expanding or contracting patterns, that is, either away from or towards the central fixation point, creating an illusion of forwards or backwards self-motion respectively. Noise dots moved in random directions. Coherence, or the percent of dots belonging to the signal pool, was the independent variable: Each block contained 96 trials each of two signal coherences, presented in random order. Half the trials were control trials, in that the blind hemifield contained only random motion; the remainder were experimental trials with 100% signal, in the same expanding or contracting direction as the signal dots in the seeing hemifield (Figure 5). Control and experimental trials were mixed randomly. The task was to indicate whether the illusion was of forward or backward self-motion.

For each of the coherence levels, the difference between the experimental and control trials were measured, and these were subjected to a paired *t* test. For JS and NA, five blocks (10 levels) were given, and 960 trials total. The stimuli in NA had to be rotated by 90° to match the shape of his scotoma (Figure 2, middle). Thus, his seeing hemifield was considered to be his superior field, and his blind field to be his inferior field. Because DNR had negative results, we obtained many blocks (25 levels total) over several days, to guard against a Type II error.

As a control for light scatter and errant fixation, and for comparison with our prior study using random dot patterns within the blind hemifield alone, we also presented two blocks of 32 trials with 100% coherent motion in the blind hemifield only, and no dots in the seeing hemifield. These “control” trials are direct in strategy and similar to the experimental trials in another blindsight study of motion perception (Mestre, Brouchon, Ceccaldi, & Poncet, 1992).

Pursuit

The initial visual display contained a red fixation cross of 0.43° width in the center of a long vertical white rectangle of 1.6° width, always visible, and which flashed red if horizontal eye position strayed outside. Trials were only initiated when the subject's eye was within 0.6° of central fixation. The subject was first trained to follow a red target at the vertical meridian that, after a variable interval, stepped 7.5° up or down from fixation and then ramped up or down at a constant velocity of 29°/sec, with both step and ramp randomly intermixed. This red target was flanked horizontally by two white circles of 0.7° diameter and 20 cd/m² luminance, 7.6° away from the red target. Next the subject trained with half the trials omitting the red target at the vertical meridian. For these trials, they were told to imagine that the red target was still there, and that its position was given by the flanking white circles. Finally, the experiment itself was given, containing trials that only showed the white

flanking circles. Of the 256 trials, 128 had one marker in the seeing hemifield alone, and 128 had two markers, one in the blind hemifield and one in the seeing hemifield (Figure 6). We identified saccades as eye movements with velocities exceeding 46.9°/sec. The onset of a saccade was taken as a point at which the velocity of the eye first exceeded 31.3°/sec, and the end of a saccade as a point where the eye's velocity fell below this baseline. We measured average eye velocity in the 100-msec period after the initial saccade to the target. Pursuit gain was defined as this eye velocity divided by the target velocity. In a normal subject 39 years of age, adding the second marker increased pursuit gain by 43% ($p < .01$, $n = 32$ trials). We also measured the saccadic error (°), which was the subtraction between eye position and target position at the end of the saccade.

For comparison, we also measured the horizontal step-ramp pursuit to a single stimulus of similar luminance and size, stepped 16° eccentrically and angled 30° below the horizontal meridian, then ramping 0°/sec or 29°/sec left or right randomly, in 165 trials.

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