

Parameters affecting conscious versus unconscious visual discrimination with damage to the visual cortex (V1)

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ABSTRACT When the visual (striate) cortex (V1) is damaged in human subjects, cortical blindness results in the contralateral visual half field. Nevertheless, under some experimental conditions, subjects demonstrate a capacity to make visual discriminations in the blind hemifield (blindsight), even though they have no phenomenal experience of seeing. This capacity must, therefore, be mediated by parallel projections to other brain areas. It is also the case that some subjects have conscious residual vision in response to fast moving stimuli or sudden changes in light flux level presented to the blind hemifield, characterized by a contentless kind of awareness, a feeling of something happening, albeit not normal seeing. The relationship between these two modes of discrimination has never been studied systematically. We examine, in the same experiment, both the unconscious discrimination and the conscious visual awareness of moving stimuli in a subject with unilateral damage to V1. The results demonstrate an excellent capacity to discriminate motion direction and orientation in the absence of acknowledged perceptual awareness. Discrimination of the stimulus parameters for acknowledged awareness apparently follows a different functional relationship with respect to stimulus speed, displacement, and stimulus contrast. As performance in the two modes can be quantitatively matched, the findings suggest that it should be possible to image brain activity and to identify the active areas involved in the same subject performing the same discrimination task, both with and without conscious awareness, and hence to determine whether any structures contribute uniquely to conscious perception.

G.Y. is a 39-year-old subject who has been investigated extensively in several studies (1–6). His left visual cortex was damaged at 8 years of age in a head injury, and his right half field remains clinically blind, with the exception of a small zone ($<3^\circ$) of macular sparing. Magnetic resonance imaging scans reveal no intact striate cortex (V1) except for tissue at the occipital pole that would correspond to his macular sparing (7). All studies have used stimuli outside the spared macular zone, and it is presumed, therefore, that residual visual capacity is mediated by pathways of retinal origin that by-pass the striate cortex (8). The various investigations carried out on this subject have focused largely on his residual visual capacity for detection and localization of rapid changes of retinal illuminance and for fast moving stimuli. In the majority of those studies, the subject had, or could be assumed to have had, conscious residual vision—i.e., some sort of awareness of the visual event even though he could not describe its content. This stands in contrast to blindsight (9, 10)—i.e., significant visual discrimination in the absence of any acknowledged awareness in some subjects with damage to the striate cortex.

The object of the present study was to determine whether there were conditions under which G.Y. had blindsight (i.e., could discriminate between different directions and orienta-

tions of motion in the absence of awareness) and, if so, to compare the stimulus parameters that define both the conscious and unconscious modes of discrimination. A key question is whether the two modes of discrimination are just different portions of the same psychometric function or whether they reflect different and possibly independent processes. We investigated how stimulus parameters such as speed, stimulus contrast, orientation of motion trajectory, and length of excursion affected the subject's conscious awareness of the visual stimulus and also the probability of correct discrimination.

MATERIALS AND METHODS

The method used was the commentary key paradigm (10). The subject was presented with stimuli in a two-alternative forced-choice procedure (2AFC) or a two-alternative forced-response procedure (FR). The subject's task was to choose (by guessing, if necessary) in which of two successive intervals the target stimulus (e.g., horizontal motion) had occurred or in a single-interval FR to choose to which of two alternatives (e.g., horizontal or vertical motion) the single presented stimulus belonged. In all trials, the subject signaled his choice by pressing one of two response keys.

In addition to making a choice between the two stimulus alternatives, G.Y. was asked to signal whether he was aware of the stimulus in each trial. He was insistently instructed, and frequently reminded, that he was to signal unaware only when he had absolutely no sensation or feeling or experience of the visual event, and he repeatedly confirmed his conformance with this instruction. Thus, in each condition he was provided with four keys, two keys to signal his choice of which of two stimulus alternatives that had been presented (even if only by guessing) and two keys to signal aware or not aware of any visual aspect of the stimulus presentation on every trial. It was thus possible to analyze performance for aware and unaware modes separately. In blocks of 50 or 100 trials, the stimulus movement parameters (i.e., speed, displacement, and contrast) were held constant, and he was required to discriminate between horizontal and nonhorizontal movement of the spot or, in another condition, between a horizontal movement in one direction or the opposite direction along the same trajectory. Replications were given in sequences to counter effects due to fatigue or other order effects.

Fig. 1 shows schematically the stimulus configuration employed for discrimination of the direction of a moving spot. The point O (located 15° into the blind hemifield and 12° above the horizontal meridian) was always the midpoint for any stimulus excursion length, direction of motion, or orientation studied. The screen was viewed from a distance of 80 cm and subtended a visual angle of $108^\circ \times 60^\circ$. The fixation target was positioned 3.5° into the bright field (shown on the left) and subtended a visual angle of $\approx 30'$. To eliminate the detection

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Abbreviations: 2AFC, two-alternative forced-choice procedure; FR, forced-response procedure.

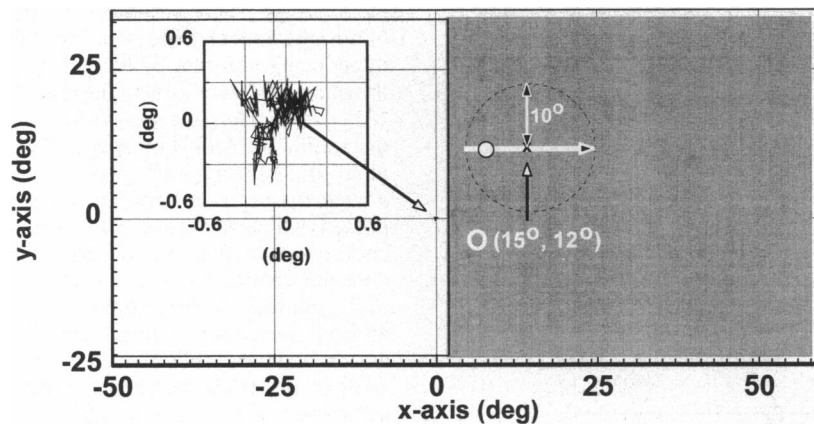


FIG. 1. Stimulus configuration employed for discrimination of the direction of a moving spot. (*Inset*) Expanded view of the fixation spot, and the subject's typical eye fixation record. The point O (15° into the blind hemifield and 12° above the horizontal meridian) was always the midpoint for any stimulus excursion length, direction, motion, or orientation studied.

of scattered light into the sighted hemifield, the area on the left was flooded with light from a Kodak Carousel S-3AV projector fitted with a 36-mm f/2.8 lens. The edge of the flooding field also extended 3.5° into the right field along its entire vertical extent. The average luminance of the bright field on the left was 90 cd/m^2 and that of the darker field on the right was 4.3 cd/m^2 . The moving test target was generated from a He/Ne laser [Rofin-Sinar (Egham, Surrey, U.K.), model RSI 20, 2 mW, 632.8 nm], and its direction was controlled by an x - y servo-drive mirror system [McLennan Engineering (Camberley, Surrey, U.K.), model PM121] to generate smooth continuous movement of the laser beam at any constant speed in the range $0.3^\circ/\text{s}$ to $22^\circ/\text{s}$. The speed setting error was $<1\%$ and the positioning accuracy was better than $\pm 5'$. The luminance of the moving disc target followed a Gaussian profile and subtended $\approx 40'$ over ± 2 standard deviations. The mean luminance of the disc target was 1600 cd/m^2 . Although the luminance of the stimulus is high, the light flux it generates toward the eye, and hence the illuminance level in the plane of the pupil, is small because of its small size. The amount of scattered light in the eye is also small since it is proportional to the illuminance level generated by the scatter source in the pupil plane (11).

An earlier investigation with G.Y. measured the minimum background luminance required to eliminate the detection of scattered light when the scatter source generated at least 12 times more light in the plane of the pupil (and hence forward scatter in the eye) than the stimulus employed in this study (6). The results showed that the subject was unable to detect scattered light at an eccentricity of 3.5° when the luminance of the uniform background was $>8 \text{ cd/m}^2$. In this investigation, the luminance of the uniform background in the sighted field was 90 cd/m^2 , and the smallest test stimulus eccentricity was 5° . The detection of light from the test stimulus that is scattered in the eye and ends up in the sighted hemifield can, therefore, be ruled out. We also tested the detection of any stray light directly from the optical system that might be scattered onto the sighted field on the large screen. None of the five subjects that took part in this test could detect the moving stimulus and were unaware of its presentation when a small rectangular occluder was placed a few centimeters from the eye so as to block the region of the field that corresponded to the trajectory of the moving stimulus. These observations suggest that discrimination cannot be based on the detection of scattered light. In some experiments the luminance of the test target was reduced to 131 cd/m^2 by means of a neutral density filter.

The subject was required to maintain strict fixation during presentation of the stimulus. Fig. 1 *Inset* shows an expanded view of the small spot at the origin and a typical record of

G.Y.'s fixation stability measured with the P_SCAN system (12) during the presentation of the moving stimulus to the blind hemifield. The results show that G.Y.'s fixation stability was well within $\pm 30'$.

RESULTS

The results demonstrate that outside a range of critical values, the subject has no visual awareness of the stimulus but performed well above chance. The parameters that most affect the subject's visual awareness in these experiments are speed of movement and the luminance contrast of the stimulus.

Luminance contrast can be altered by changing background luminance while keeping stimulus luminance constant. Reducing contrast was found to be very effective in switching off the

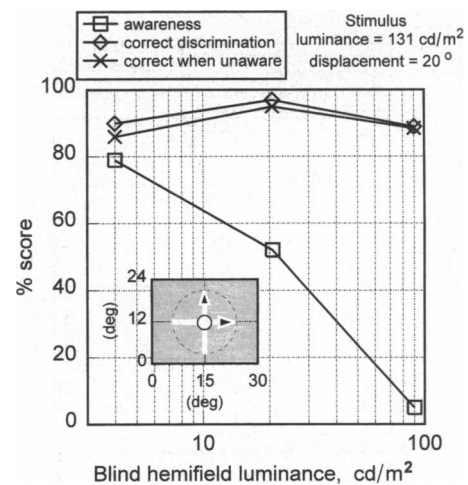


FIG. 2. Discrimination of horizontal vs. vertical movement (FR paradigm), as a function of stimulus contrast. The subject had to indicate (by guessing if necessary) whether the presented stimulus was moving horizontally or vertically by pressing the appropriate response key. He also had two commentary keys to use on every trial. Awareness refers to the percentage of trials on which the subject pressed the aware key. Correct when unaware refers to performance during those trials when the subject pressed the unaware key. The luminance of the test stimulus was held constant at 131 cd/m^2 , and background luminance in the blind hemifield was altered systematically thus changing the contrast of the stimulus. Speed was $15^\circ/\text{s}$, and displacement was 20° . Note the relative stability of the high level of performance independent of contrast but with a steep decline in percentage of aware responses at high background luminance level when the contrast decreased.

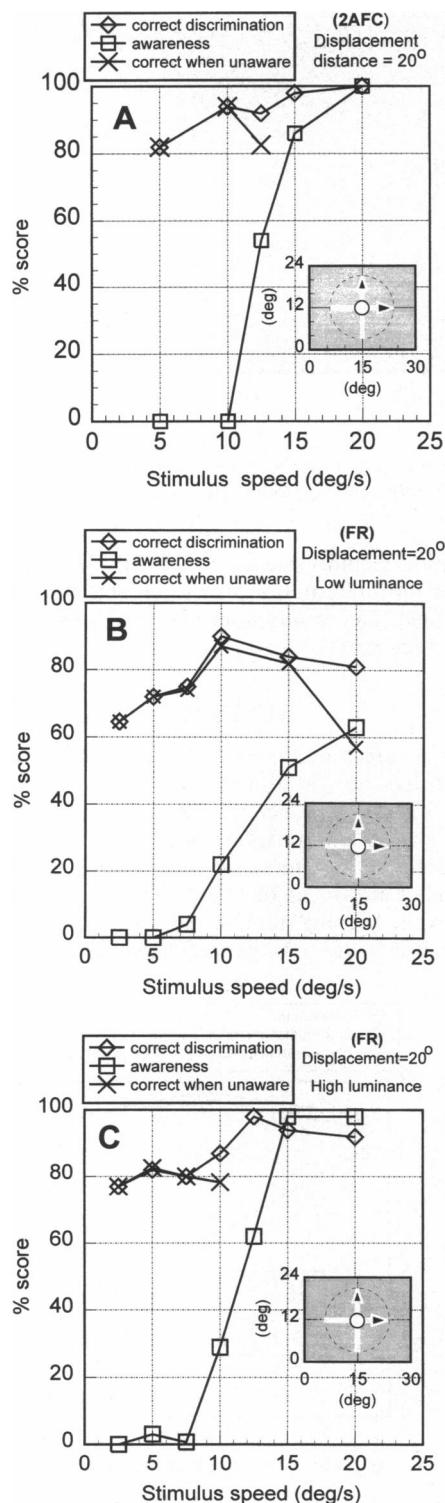


FIG. 3. (A) Awareness and discrimination performance for a horizontal vs. a vertical movement, as a function of stimulus speed, the low-stimulus luminance condition. 2AFC was used. Horizontal movement was presented in either the first or second of two intervals selected randomly, and a vertical movement in the other, and the subject had to indicate (by guessing if necessary) the correct interval of stimulus presentation by pressing the appropriate response key. He also had two commentary keys to use on every trial. Awareness refers to the percentage of trials on which the subject pressed the aware response key. Correct when unaware refers to performance during those trials when the subject pressed the unaware key. Note high levels of discriminative performance at speeds at which subject reported no awareness. (B) The same discrimination and same luminance, but with a FR paradigm (see Fig. 2). On any trial, a horizontal or a vertical

incidence of aware responses in an early study with another blindsight subject, D.B. (10). Fig. 2 shows the results with G.Y. of reducing contrast by increasing background luminance of the blind field and holding the stimulus luminance constant (at 131 cd/m^2). The task was the horizontal vs. vertical movement discrimination (constant speed of $15^\circ/\text{s}$ and constant displacement of 20°) using a FR psychophysical paradigm. There was a clear dissociation between the level of aware responses reported, which falls from 80% to almost zero with increasing background luminance, and discriminative performance, which does not change and remains impressively high—90% correct in the unaware mode in the lowest contrast condition. (In this and all subsequent figures, percentage correct data for unaware trials are only plotted when these constituted at least 40% of the trials, to reduce random statistical fluctuations associated with a small number of trials).

By holding stimulus contrast constant but varying speed or displacement, the results revealed that with a small moving disc whose speed and displacement extended well below the range of particular critical values, the subject reported no visual awareness of the stimuli. Nevertheless, he displayed high levels of accuracy, well above chance, reaching $>90\%$ correct. The subject's awareness shows a rapid increase for speeds above $12^\circ/\text{s}$ (with displacement of 20°). In contrast, his discrimination accuracy shows only a marginal increase.

This pattern of results is shown in Fig. 3A for discrimination of horizontal vs. vertical movement as a function of speed, with displacement excursion held constant by using the low luminance target and the 2AFC psychophysical paradigm. Fig. 3B shows the results with the same stimulus conditions as in Fig. 3A but with the FR paradigm. As is apparent from a comparison of Fig. 3A and B, the FR paradigm was slightly less sensitive than the 2AFC paradigm, as expected, but the same pattern emerges. Because the FR paradigm results in shorter experimental sessions and is, therefore, less tiring for the subject, FR was used in all other experiments. It is noteworthy in Fig. 3B that at the highest velocity, when numbers of awareness trials increase, unaware performance diminishes somewhat. Finally, in Fig. 3C, the high luminance target was used with FR, again demonstrating good performance at low speeds.

Because speed emerged as a very important stimulus variable, it was more difficult to find particular conditions of constant speed under which to examine the effects of varying displacement or orientation to obtain a smooth transition between the unaware and aware modes. At speeds of $10^\circ/\text{s}$, most trials yielded unaware responses, and at $20^\circ/\text{s}$ most responses were aware. Time did not always permit an examination of other intermediate values. These two constant speeds are plotted separately for displacement excursion and for orientation differences, yielding unaware responses and aware responses, respectively. Fig. 4 shows the results for varying displacements of a horizontal movement toward or away from the vertical midline and Fig. 5 shows the results for discrimination between horizontal and varying oblique directions of movement, with equal displacements. It is evident that for the particular values of constant speeds in Figs. 4 and 5, discrimination performance when aware is slightly better than when unaware. But a strong point that emerges is that it is possible to find stimulus values of the aware and unaware modes for which performance can be quantitatively closely matched. Thus it can be seen that a value of $\approx 20^\circ$ displacement in the unaware mode at $10^\circ/\text{s}$ is roughly equivalent to 10° displacement at $20^\circ/\text{s}$ in the aware mode (Fig. 3A and B,

movement was presented, and the subject had to indicate (by guessing if necessary) which it was by pressing the appropriate key. Commentary keys were also used. (C) The same discrimination, with high luminance target, with a FR paradigm.

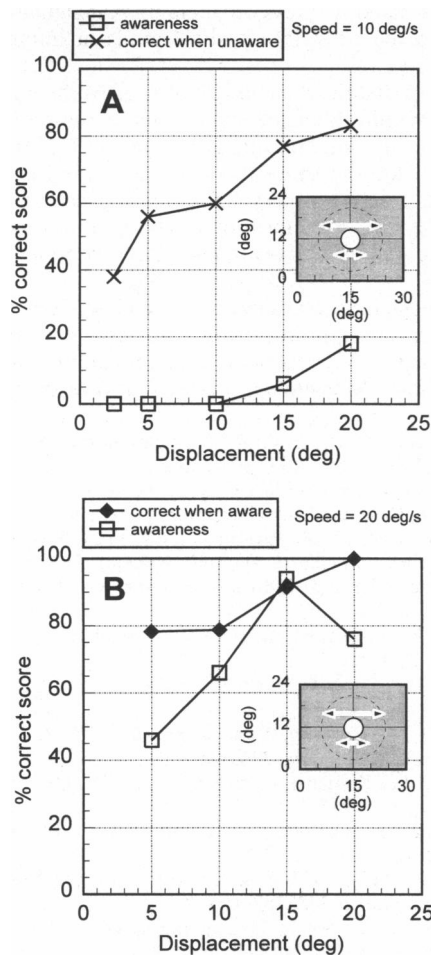


FIG. 4. (A) Discrimination of direction of horizontal movement away or toward the vertical meridian, as a function of the size of the displacement of the moving target. FR paradigm was used. Speed was $10^\circ/\text{s}$, which yielded mainly unaware responses. (B) The same as in A, but with speed of $20^\circ/\text{s}$, which yielded mainly aware responses. Values in A and B can be found that have equal quantitative levels of performance.

respectively). In Fig. 5, in fact, the aware and unaware modes converge on a performance value of close to 100%.

DISCUSSION

Five points emerging from the results deserve discussion. (i) A remarkable finding is that high levels of discrimination can be demonstrated by G.Y. when unaware of the stimulus, with stimulus speeds as low as $2.5^\circ/\text{s}$ (Fig. 3B), and with contrast as low as 0.16 under photopic adaptation conditions (Fig. 2). It is very unusual in psychophysical determinations with normal subjects to find such high performance levels as reached here, 90% or better, when they have no awareness of the stimuli.

(ii) For the stimulus parameters employed, high discrimination scores when G.Y. is aware of something presented to the blind hemifield can only be reliably demonstrated in the high speed range (Fig. 3) and with high contrast (Fig. 2) and large displacements. Judging from the literature, aware responses to stimuli in the blind field appear to be restricted to stimuli that contain fast on/off transients, and/or rapid movement, and given stimuli of high contrast. It is possible that the aware mode, when activated, may well affect the sensitivity of the unaware mode, as suggested by the results in Fig. 3B for speed, but no such suggestion was found for stimulus contrast. There may also be some reciprocal interactions between the two modes. In another blindsight subject, D.B., when condi-

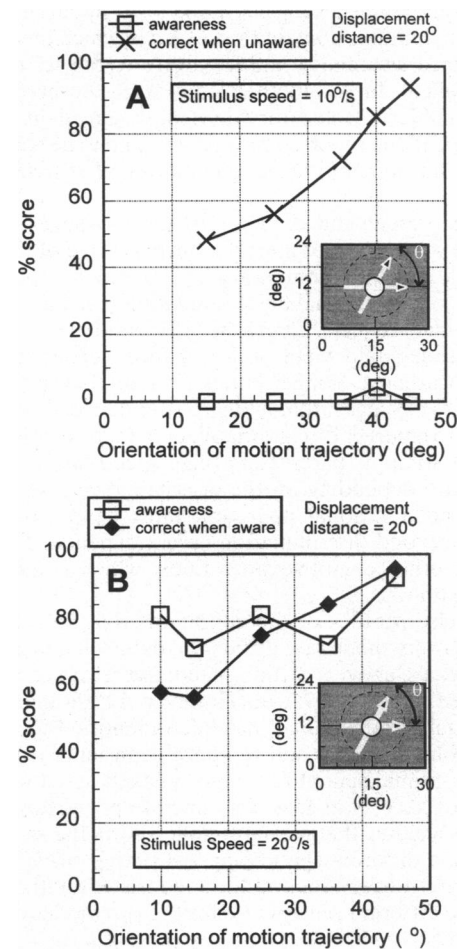


FIG. 5. (A) Discrimination of horizontal from nonhorizontal orientation of movement, as a function of angular difference. Fixed displacement was 20° . Speed was $10^\circ/\text{s}$, which yielded mainly unaware responses. (B) Same as in A, but with speed of $20^\circ/\text{s}$, which yielded mainly aware responses. Values in A and B can be found that have equal quantitative levels of performance.

tions were arranged to eliminate aware responses, his overall performance in certain situations actually improved (10). In addition to controllable stimulus parameters such as speed, size, contrast, and level of background adaptation, the limiting conditions under which discrimination when aware can be demonstrated are also affected by other factors that are more difficult to control such as the psychophysical method and the requirements of the task involved, as well as the level of alertness of the subject, etc., but speed and luminance still retain their relative importance for aware vs. unaware responses.

(iii) Given that the capacity of subjects like G.Y. evidently extends well beyond the stimulus conditions that typically yield above-chance performance accompanied by some form of conscious residual awareness, the region of unaware discrimination has tended to be understudied in most subjects, and also in G.Y., with a few exceptions (1, 13). It is also the case that many negative patients might have been dropped prematurely because the parameters were either outside the limits of the awareness domain of those patients or, more understandably, because unaware discrimination was not even tackled. In general, it has been intuitively more attractive and easier for both the subject and the experimenter to investigate conscious residual vision than to study discrimination performance when the subject is unaware of the stimulus presented and is forced to guess. It still remains unknown, however, whether all subjects who have awareness of moving or transient stimuli also have an unaware capacity, or vice versa. One of the most

systematically studied subjects, D.B. (10), apparently had a much larger stimulus domain than G.Y., in which there was no acknowledged awareness, and his aware responses tended to be nonveridical. In yet another study with another group of blindsight subjects tested for wavelength sensitivity and discrimination, all the reported results were said to be without any awareness throughout the lengthy series of discriminations (14).

(iv) The present and earlier (10) results suggest that the unaware sensitivity is not merely a mirror image of the aware. By using a similar commentary key paradigm for sensory experience of ventral thalamic stimulation (for the control of pain) in human subjects, Libet *et al.* (15) found that short bursts of stimulation could yield above chance detection without reported awareness. Longer bursts generated awareness, and Libet *et al.* (15) suggest that a longer stimulation is needed for awareness to emerge. But alternatives are that specific changes in relevant stimulus parameters (e.g., speed and luminance) are necessary depending on the discriminative task or that a separate and additional operation must be performed for awareness beyond discrimination *per se*, depending on attentional and other cognitive operations, which could involve different pathways.

The precise profiles of the conditions that define the unaware and aware modes are difficult to determine with moving stimuli, because above a certain speed, awareness continues to be obtained without reversal. However, in another study a tuned spatial aware channel has been identified for G.Y. by using stationary stimuli and temporal transients (6). In that study, the optimal spatial frequency peaked at 1.1 cycles per degree. Hence, it is at least in principle practicable also to determine whether the unaware mode shows the same or, as we suspect, a different spatiotemporal tuning curve from the known aware mode. This would be consistent with the existence of the different sensitivities for the two modes measured in this study.

(v) Positron emission tomography (PET) studies may also help to answer comparative questions about the blindsight vs. aware modes, but, to our knowledge, no study has been reported that was designed to investigate blindsight. A recent PET study in G.Y. revealed several identifiable areas of the cortex that showed a significant change in neural activity when he was aware of something moving in the blind hemifield and was able to discriminate correctly the direction of movement in all presentations (7). At least three of the cortical areas that were activated in that experiment also show significant levels of activation in normal subjects (16) when comparison is made between moving and equivalent stationary stimuli (i.e., V5, putative V3, and Brodman area 7). Although this PET study does not provide information about the pattern of cortical activity when discrimination without awareness is involved, it

nevertheless demonstrates convincingly that signals of retinal origin can reach prestriate cortical areas in humans in the absence of V1.

It is evident that the present results suggest the possibility of comparing, within the same subject, the activity of the brain when the two stimulus conditions are matched at high levels of performance for the same type of discrimination, with and without conscious awareness. Subtraction of the two averaged images might reveal the location of those neural mechanisms that mediate perceptual awareness of the stimulus attributes involved.

Thus, blindsight, the discovery of which was unexpected (it emerged from attempts to bridge the results of animal and clinical findings), may offer a unique possibility of uncovering neural mechanisms involved in conscious awareness.

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