REVIEW

Parallel Processing, Asynchronous Perception, and a Distributed System of Consciousness in Vision

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The primate visual brain is characterized by a set of parallel, multistage systems that are specialized to process different attributes of the visual scene. They occupy spatially distinct positions in the visual brain and do not project to a unique common area. These processing systems are also perceptual systems, because the result of activity in each leads to the perception of the relevant visual attribute. But the different processing-perceptual systems require different times to complete their tasks, thus leading to another characteristic of the visual brain, a temporal hierarchy for perception. Together, these two characteristics—of parallel processing and temporal hierarchy— suggest that each processing-perceptual system can act with fair autonomy. Studies of the diseased human brain show that activity in separate processing-perceptual systems—especially those concerned with color and motion— can lead to the perception of the relevant attribute even when the other processing systems are inactive and that activity in individual processing perceptual systems has a conscious experience as a correlate, which suggests that consciousness itself is a modular, distributed system. NEUROSCIENTIST 4:365—372, 1998

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The problem of consciousness imposes itself on any study that seeks to comprehend the workings of the visual brain in any profound sense. This follows imme- diately from the single most important question about the visual brain that one can ask: why do we see at all? The only plausible answer is: to acquire knowledge about the world (1). But such an answer plunges one into a deeply philosophical world, of learning on the one hand something about the nature of the knowledge that the brain seeks to acquire and something about the strategy that it has developed to acquire that knowledge. And because no significant knowledge can be acquired save in the conscious state, the study of consciousness itself becomes an integral part of a study of the visual brain. That study thus becomes largely a philosophical inquiry, though one conducted with neurological means.

A Knowledge of Unchanging Properties in the Face of Changing Information

The only visual knowledge that the brain is concerned with relates to those permanent, essential, or character- istic properties of objects and surfaces that allows the brain to categorize them. But the information reaching the brain from these surfaces and objects is in continual

flux; an object may have to be categorized according to color (as when judging the state of ripeness of an edible fruit). But the wavelength composition of the light re- flected from it changes, depending upon the time of day, without entailing a substantial shift in its color (color constancy). Or a face may be categorized as a sad one, thus giving the brain knowledge about a person, in spite of the continual changes in individual features or in viewing angle; or the destination of an object may have to be decided by its direction of motion, regardless of speed. Vision must therefore be an active process re- quiring the brain to discount the continual changes and extract from them only that which is necessary for it to categorize objects. How the brain does this is a puzzle. Indeed the question has only been seriously addressed in the last 30 years, which have witnessed a prolific output of work on the visual brain. Among the chief discoveries is that it is comp6sed of many visual areas (2-4) that are distributed in the cortex surrounding VI (the "visuo- sensory'" cortex), which, to distinguish it from VI, was previously known as the "visuo-psychic" cortex. Because V1 was thought for a long time to be the only cortical stage to receive a direct input from the retina though the lateral geniculate nucleus and because lesions in it lead to blindness (the position and extent of which is in precise correspondence to the position and extent of the lesion), V1 was considered to be responsible for seeing and the surrounding "visuo-psychic"

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cortex for "understanding" what is seen, a view that divides seeing from understanding and assigns a separate cortical seat to each. The more recent evidence shows that V1 is but the essential first cortical step in an elaborate cortical machinery designed to acquire knowledge about the visual world. It connects, directly or indirectly, to many of the visual areas surrounding it, distributing specialized visual signals to them (5). Because the visual areas surrounding V1 receive specialized signals, it is not surprising to find that lesions in them lead to more selective defects, rather than total blindness. A lesion in the color center, for example, leads to color imperception (achromatopsia) (6) and in the motion center (V5) to motion imperception (akinetopsia) (7). Yet other specific lesions lead to specific recognition defects, such as an incapacity to recognize familiar faces (8), or to more vaguely defined syndromes such as agnosia, in which the patient may be unable to recognize certain objects or only recognize them on some occasions or if they are in motion (1).

In this essay, I put forward the proposition that the reality of many different visual areas, each group having its own specialization, reflects another reality—that there are different visual systems for acquiring different kinds of knowledge about the visual scene. Activity in each leads to both the seeing and the understanding of a particular visual attribute, say motion or color, without the mandatory participation of the other systems; each, in other words, has a certain autonomy. As a corollary, activity in each has its own separate conscious correlate. Visual consciousness is thus not a unitary entity; instead, it is a distributed, modular system; when one of the subsystems composing it is compromised, the other visual consciousnesses, resulting from activity in other autonomous visual processing-perceptual systems, need not be so; they may instead remain more or less intact. There is, in other words, no central unique area for conscious experience of the visual world.

The Separate Systems for Processing Different Attributes

Although there is no unanimity of views about the extent of functional specialization within the visual brain, most would agree that it is an important feature of its organization. This is especially so for color and motion, the two attributes that T used to propound the doctrine of functional specialization in the visual brain a quarter of a century ago (3, 9) and that today continue to give us insights into the separation of visual perceptions (Fig. 1). More recently, imaging techniques have provided a direct demonstration of functional specialization in the human visual brain (10). The human evidence shows a greater degree of parcelation (11—13) than has been achieved in the monkey, perhaps because such faculties as the recognition of familiar faces or color naming or object naming are easier to study in the human. Although T shall not consider these other specializations in

any detail here, the conclusions derived from a study of the color and motion systems may well in the end apply to them too, although with modifications. Collectively, this evidence shows that one characteristic of the visual brain is the presence of spatially distributed processing systems, ones that process different attributes of the visual scene in parallel. This reflects, T believe, the strategy that the brain has evolved for acquiring knowledge about different attributes of the visual world by discounting different kinds of information—for color, it is the precise wavelength composition of the light coming from a surface that has to be discounted, whereas for size, it is the precise viewing distance, and so on.

A Processing-Perceptual System?

It is worth addressing the question of whether activity in the processing systems themselves leads to percepts, and whether, therefore, the processing systems are equivalent to the perceptual systems. It is, after all, entirely possible that a given processing system (say, for example, the motion one based on area V5 and its connections; Fig. 1) may report the results of its operations to yet further areas to which it projects, of which there are many (14, 15); area V5 may, in other words, contribute to the perception of motion without being itself a perceptual site. The perceptual site may be located elsewhere and, given the wholeness and unity of the visual image, one could even suppose that the site is an integrator zone, receiving input from many different specialized areas. My preference is to equate the processing system with the perceptual system, for a number of reasons. First, anatomical studies show that there is no cortical area to which all the antecedent visual areas uniquely project; there is also no cortical area that is recipient only (1), which implies that there is no terminal station in the brain. Next, in showing that even a decision that depends upon a percept is enshrined to some extent at least in an area such as V5 (16), physiological experiments tend to favor the equation of the processing systems with the perceptual systems. Moreover, human lesion studies, although always open to differences in interpretation, are at least consistent with the notion that damage to one processing system, say. the motion one, results in a profound motion imperception (7) without an accompanying color imperception (6), whereas lesions in the color system have the reverse effect, a demonstration that none has succeeded in challenging. This argues for an independence of these two perceptual systems at least.

Multistage Perceptual-Processing Systems

Striking as well is the perceptual consequence of damage to one stage of a given processing system outside of VI. The result is not a total perceptual incapacity in the submodality for which the damaged system is specialized. The color system and the motion system, each of which
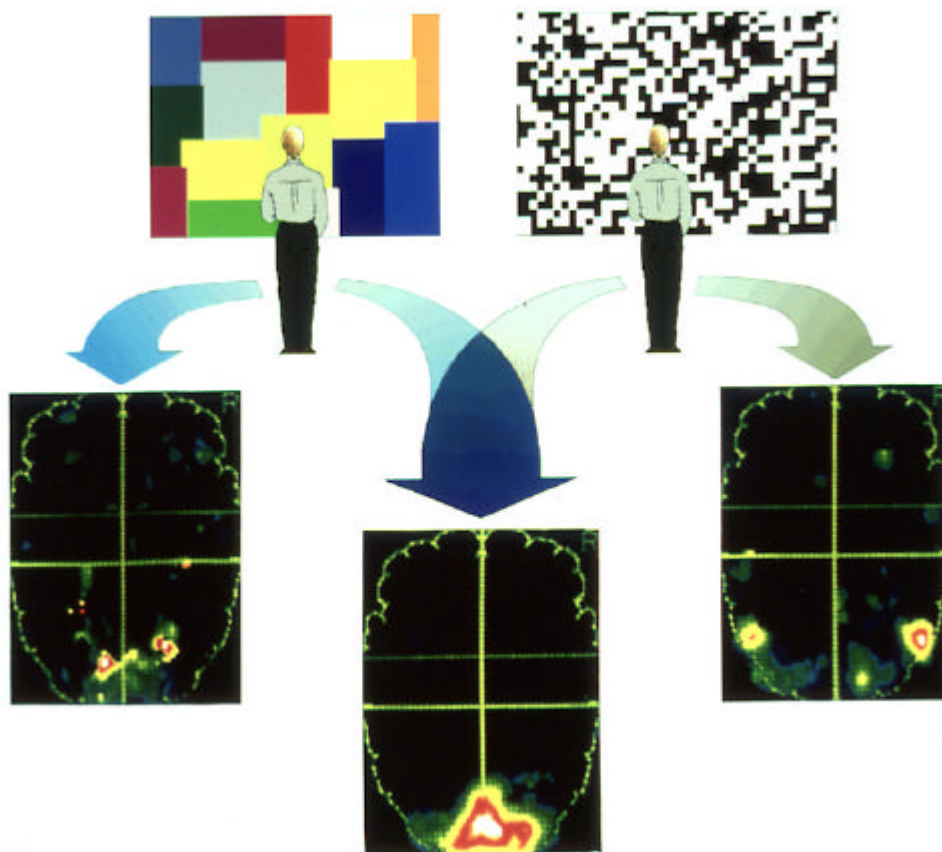
Fig. 1. The changes in regional cerebral blood flow when subjects view an abstract multicolored scene *(left)* and a pattern of black and white squares that move and change their direction of motion. The changes are shown in the horizontal sections through the brain *(bottom).* Both stimuli activate area VI *(bottom centre):* additionally, the colored stimulus activates the color center (V4. *left)* and the motion stimulus activates a separate area, V5 *(right).* Modified and reprinted from ref. 47 with permission.

are commonly accepted to have several cortical stages (Fig. 2), provide good examples. I have argued elsewhere (17, 18) that the visual image is constructed, not analyzed, by the brain; each level of a given, specialized, pathway contributes to that construction at a certain level of complexity. Damage to one level may leave the antecedent levels intact, enabling the brain to perceive according to the physiological capacities of the parts that are left intact but unable to construct the final attribute, which requires more extensive comparisons across larger parts of the field of view. In other words, activity at each level can become perceptually explicit without requiring further processing; where there is a lesion and further processing is not possible, the perceptual capacity of the individual reflects the capacity of cells at the levels untouched by the lesion. In the color system, patients rendered achromatopsic by a lesion in the color center can nevertheless discriminate different wavelengths from one another (19) (Fries W and Zeki S, unpublished observations), a function of the wavelength-selective cells of VI; but they are not able to attribute colors to them,

a capacity that depends upon the ability to compare the wavelength composition of the light coming from large parts of the field of view (20). This also seems to be true of monkeys with V4 lesions (21, 22) who, like human patients with lesions in the color center, lose the capacity for maintaining the constancy of colors (23). Equally, although lesions that include V5 render a human patient akinetopsic, the imperception is only for fast moving objects, in excess of 5^0/sec; the capacity to discriminate very slow motion is far less compromised (24, 25), probably reflecting the capacities of the parts of the system that are left intact by the lesion (1). This in itself argues in favor of a perceptual capacity for each level of a processing-perceptual system. We note that the perceptual capacities of such patients, and the knowledge that it gives them, are fully conscious. Thus achromatopsic patients can distinguish verbally between different wavelengths and a patient with a lesion that includes V5 can report verbally the presence of slow motion (25, 26). I shall therefore speak of processing-perceptual systems.
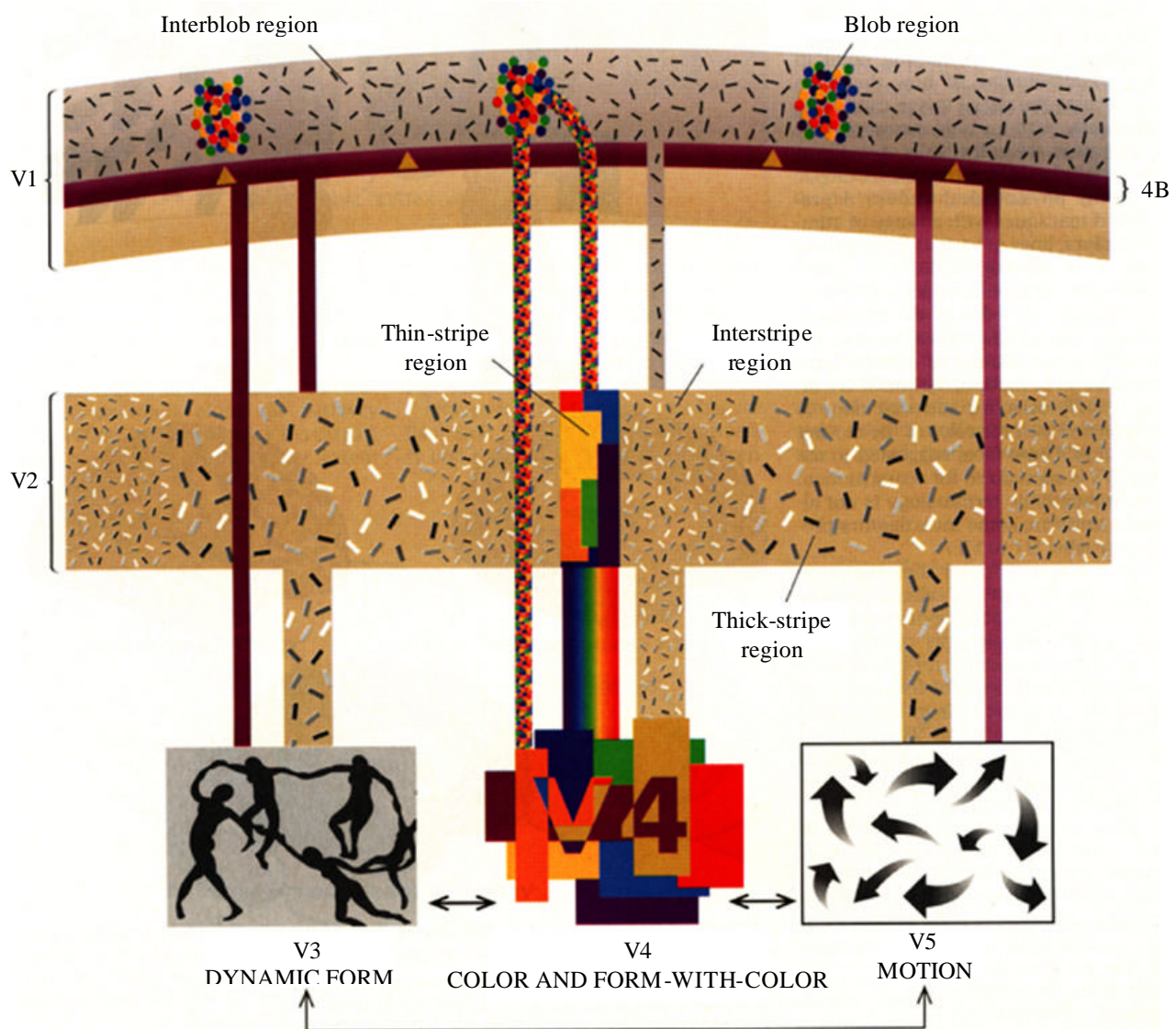
Fig. 2. A schematic representation of four processing perceptual pathways within the visual cortex. Color is seen when wavelength-selective cells in V1, concentrated in the metabolically rich 'blob' regions, send signals to specialized area V4 and also to the wavelength selective cells of V2, an area of cortex surrounding V1, which in turn connect with V4. Form in association with color depends on connections between form-detecting cells of V1, located in the zones between the 'blob' regions, and their counterparts in the 'interstripes' of V2 and in area V4 Cells in layer 4B of Vi send signals to specialized area V3 and V5 directly and also through motion selective cells in the Thick stripes' of V2; these connections give rise to the perception of motion and dynamic form. Other processing-perceptual pathways, yet to be uncovered, are suspected to exist. Reprinted from ref. 48 by permission.

Criss-Crossing Processing-Perceptual Systems

A processing-perceptual system may share a common neurological substratum with other processing-perceptual systems belonging to the same sub-modality of vision, before branching out (Fig. 3). Recent imaging studies show that, as in the monkey (25, 27, 28), there is a specialization for different types of motion in the visual areas surrounding human area V5 (25, 27): one subdivision emphasizes optical flow whereas another subdivision is especially active when humans view biological (Johanssen) motion (i.e., motion from which human figures can be discerned). But the subspecialized areas do not constitute parts of separate processing systems, totally distinct from V5. Indeed, the anatomical evidence shows that many of the satellite areas surrounding V5 do not receive an independent input from V1; rather, the input from V1 is funneled to them through V5 (15), although each also receives a retinal input that bypasses VI and reaches it directly through a subcortical relay, giving them a certain autonomy from VI and V5. The areas specialized for different kinds of motion may thus share a common conical processing system up to the point of divergence, VS in this case, but the conical processing-perceptual systems beyond divergence may be separate and more or less independent. This conjecture receives fair support from the presently available
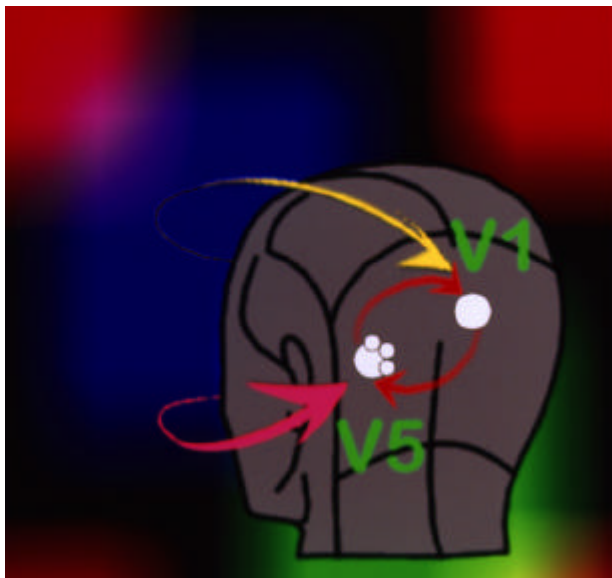
Fig. 3. The pathway that a motion related signal can follow can take either of two routes to area V5. One of these is a direct route to V5. which bypasses V1; signals in it reach V5 at the highest speeds, when the motion is fast *(>5º/sec)*. The other, which goes via Vi. is activated first during slower motion. V5 and V1 are interconnected and it is probable that the signals are reciprocated between them. Surrounding area V5. and constituting part of the V5 complex, are a number of satellite areas, shown here as small circles: these are specialized for different kinds of motion; optic flow, circular motion, biological motion, etc.

clinical evidence, (for example, that which shows that the perception of coherent two-dimensional motion but not biological motion can be compromised with a given conical lesion invading the V5 complex but leaving V1 [and presumably the output from it] intact [29]). The anatomical basis for the sparing is possibly the direct subcortical input that bypasses both V1 and V5. A direct subcortical input is in fact also the likely explanation for the motion vision of subjects blinded by lesions in V1 (see below).

Equally, two processing-perceptual systems dealing with different attributes of a submodality of vision (for example, fast and slow motion) may be independent from one another until they reach a given area (for example V5). Recent work has distinguished two components in motion vision, one dealing with fast and the other with slow motion (30). Fast motion signals ($> 5º/$sec) arrive in V5 first through the direct subcortical pathway, with latencies as short as 30—35 msec, consistent with the observation that the shortest latency signals recorded in monkey have been from V5 (31). By contrast, signals from slowly moving stimuli take a cortical route and reach V5 through V1, This provides a dynamically parallel system dealing with two sub-divisions of the motion system, both of which converge on V5. The point is that the fast-motion system is itself a processing-perceptual system, activity in which leads to conscious

knowledge of certain events in the external world related to fast motion only, without the participation of V1 or of the slow-motion system. Thus a patient with a damaged V1 but an intact V5 can discriminate the direction of fast, but not slow, motion consciously. On the other hand, a patient with a damaged V5 but an intact V1 can only discriminate slow, but not fast motion, presumably reflecting the capacities of the remaining parts of a multi-stage motion system, whose capacities are unaffected by the lesion. Neural damage that affects the slow motion system need not affect the fast motion system or at least not affect it to the same extent.

Perceptual Asynchrony

Although the evidence thus suggests that a processing system also doubles as a perceptual system, it does not prove that in the intact human brain the separate attributes of the visual world are perceived separately. Even if they are, it does not follow that there is no central synchronizer, capable of binding the results of the operations performed by the different processing systems, and thus giving us our unitary image of the visual world, where all the different attributes of the visual scene are apparently seen in precise spatio-temporal registration. The absence of a unique cortical area (or areas) to which all the specialized visual areas project convergently and the rarity of cells with dual or multiple selectivities to different attributes of the visual scene, at least in our experience, led Konstantinos Moutoussis and me to inquire whether there is a central synchronizer, capable of setting to 'time zero" the perceptual results of the activity in the different processing systems (32). Our psychophysical studies showed that there is not; color, orientation and motion are not perceived at the same exact time, that color has an advantage of some 60—80 msec over motion. That color is perceived before motion, even though motion signals arrive in the cortex first, suggests that the longer perceptual time of motion necessitates a faster conduction system. When confronted with very brief periods of time, in the subsecond range, the brain is not able to bind what occurs veridically in real time but only the results of activity in its own processing systems, the time taken by each processing-perceptual system to complete its task differing from the others. Because color and motion are processed separately and therefore perceived at significantly different times, what the brain does is to bind the color that occurs at time t with the motion that occurred at time $t—1$. Hence a second characteristic of the visual brain is a temporal hierarchy in perception, different attributes of the visual scene being perceived at different times. Because the brain integrates the results of activity in its separate processing-perceptual systems, and because each processing-perceptual system is multi-stage, I conjecture that, in the lesioned brain in which the remaining intact pails become the final perceptual site for a given attribute, the relative perceptual times will differ from
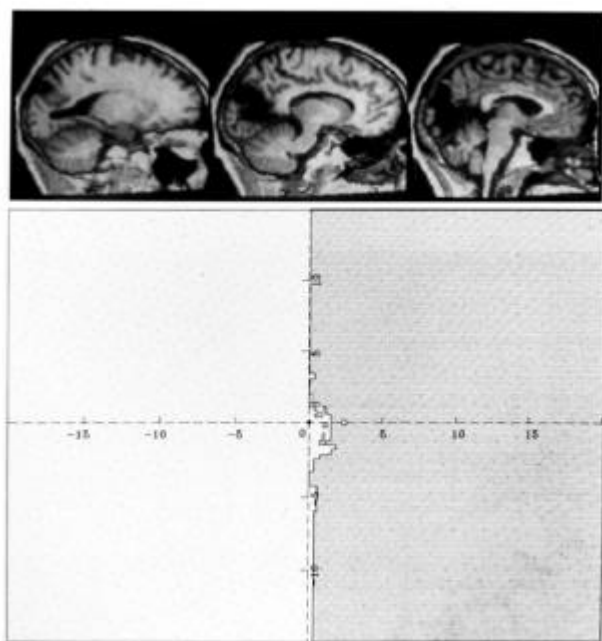
Fig, 4. *Top,* Magnetic resonance images (MRI) of the brain of patient GY seen in sagittal sections. The damage is quite extensive, with nearly complete destruction of medial occipital cortex and the underlying optic radiation, but sparing of the occipital pole. *Bottom,* Plot of fly's visual field, showing his 'blind' hemifield in *grey.* Note the area of spared vision around his fovea.

that found in normal brains, with further departures from real time but without leading to a failure in integration.

The Conscious Experience of Visual Motion in the Blind Field

These two characteristics—parallelism and temporal hierarchy—allow us to test the general proposition that activity in an individual processing-perceptual system or at a given level of a processing-perceptual system also has consciousness as a correlate, without necessarily entailing activity in the whole set of parallel systems, and that individual processing-perceptual systems do not have to report the results of their activities to a central area (or areas) of the brain that alone are capable of endowing the systems with a conscious component. It allows us, in brief, to test the proposition that visual consciousness is not a unitary state but a distributed, modular one. Area V5, specialized for motion, is a good one to begin with. It is obvious that, with V1 gone, it is the fast motion system alone, which inputs into V5 without passing through V1, that remains operational. This provides an experimental paradigm to test our general proposition, especially because studies in monkeys with an inactivated V1 have shown that the characteristic of V5, directional selectivity to motion, is maintained even m the absence of V1(33, 34).

George Riddoch (35), a rarely acknowledged English neurologist, first described during the Great War the phenomenon that later came to be called "residual vision" (36). He had studied patients rendered partially blind by bullet wounds in their brain and found that they could consciously distinguish motion, but not much else,

in their blind fields. A modem counterpart to Riddoch's patients is patient GY, whom a car accident had rendered hemi-blind at the age of 8 after damage to his occipital lobe that spared much of the cortex surrounding V1, including the territory of area V5 (Fig. 4). Even though such a disconnected system is a much degraded one, it allows us to test the proposition that seeing and understanding are inseparable and the consequence of activity in each of the parallel systems. Our studies of GY (37), since confirmed (38, 39), give a picture that is consistent with the account given by Riddoch. GY cannot detect or discriminate the direction of slow motion, which in the normal is dependent upon V1; at best he can detect (and shows some conscious awareness) of the onset only of slowly moving stimuli. By contrast, he has a good capacity to discriminate fast motion consciously. Electroencephalographic studies have shown that the activity evoked from his brain is comparable with that of normal brains when he consciously sees fast motion; on the other hand, with a range of control stimuli that he could not discriminate and of which he had no conscious awareness the evoked activity was largely absent or highly abnormal (40) (Fig. 5). Imaging studies of his brain while he was discriminating consciously showed activity in V5 and the two areas that we (41) and others (42) had previously found to be co-activated with it in normal brains, obviously with no activation of V1.
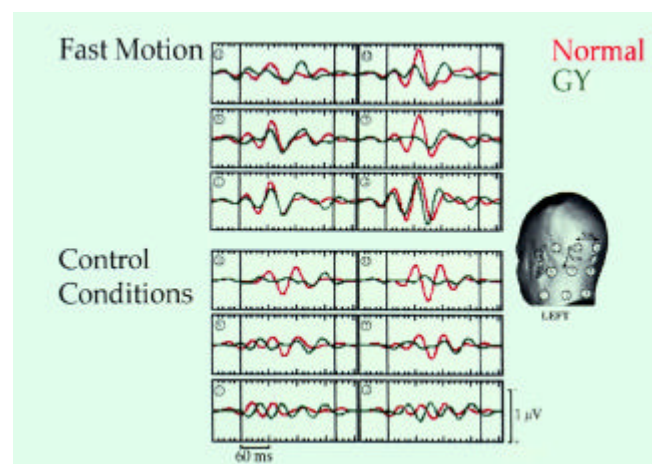

Fig. 5. The evoked EEG activity elicited by last motion and control stimuli at six electrodes placed over the occipital cortex in patient GY *(green)* and two control subjects *(red).* When stimulated with fast motion, which GY could see and of which he was consciously aware, the activity recorded over the ventral occipital cortex (electrodes 1, 2 and 6) in the control subjects matches the activity elicited in GY. In the control conditions, pattern offset and slow motion, of which GY was unaware and could not see, the activity elicited in the control subjects is located at different electrodes (11 and 12) and is absent in GY. Modified and reprinted from ref. 40 by permission of Oxford University Press.

When he was shown slow-moving stimuli that he could not detect consciously, there was still some activity in his *V5,* but to detect this required a considerable relaxation of thresholds, which suggests that conscious awareness requires the mobilization of a certain threshold level of activity in a specific specialized area (or set of areas) in the visual brain, but not in the whole of the visual brain (49).

An especially interesting insight into the modularity of conscious visual experience is provided in the contrast between GY and patient MM (43, 44), also rendered hemianopic by a lesion largely confined to the calcarine sulcus, where most of V1 is located. T have recently examined MM with my French colleagues and confirm his remarkable capacity to see consciously optical flow stimuli in his blind field, especially when these are peripherally presented. What further examination has shown is that this capacity is actually rather specific: Unlike GY, MM is not able to detect or discriminate fast-moving coherent two-dimensional motion, which is so effortlessly detected by GY; he cannot detect biological motion either. This specificity must be viewed in the context of specializations for different kinds of motion within motion-related visual cortex; activity channeled to each one can seemingly result in the capacity to see and understand the relevant attribute and does not generalize to other types of visual motion.

Construction and Conscious Awareness of Color When the Color System Alone Is Intact

That the color system, too, is able to function more or less autonomously and yield a conscious experience is shown by the perceptual capacities of' subjects rendered blind by vascular insufficiency. The first description of this was given by Wechsler (45) and, like Riddoch's evidence, relegated to oblivion. His 13-year-old subject, rendered completely blind in a hypoxic episode, could nevertheless recognize all primary colors as well as their shades, which he picked out "on command." This led Wechsler to suppose that "color vision and visual acuity can be dissociated in such a way that the former is preserved while the latter is impaired." It has in turn led me to hypothesize that the metabolically rich color pathways are more resistant to the effects of hypoxia (1). A recent example of this is the patient PB (46), whom I have examined with Salvatore Aglioti and Giovanni Berlucchi. He had become blind because of a severe electric shock that led to cardiac insufficiency and prolonged unconsciousness. But he was nevertheless left with a surprisingly good capacity to discriminate colors. He reported spontaneously the colors of brightly lit objects in the room, though he could not, in both informal and formal tests, attach forms to the objects, thus providing the most remarkable evidence for a dissociation of' color and form that I have encountered. But his conscious color vision is nevertheless abnormal; it is very much wavelength-based and he is in general (though not always) unable to effect the comparisons that are needed to compensate for changes in wavelength composition. His color vision, in brief, obeys better the physiology of wavelength selective cells in V1 than elsewhere. Not surprisingly, and quite unlike normal brains, imaging the

activity in his brain when he viewed large, colored squares resulted in activity in V1, the activity in his color center being very low and requiring a relaxation of thresholds to demonstrate. It would thus seem that a preserved but degraded color system can function more or less autonomously, leading to both seeing and understanding, as well as a conscious correlate. Taken in conjunction with the evidence derived from the motion system, this strongly suggests that consciousness itself us a distributed and possibly even a multi-stage system, not dependent upon one central station.

We have evidently come a long way since the pioneering days of Henschen, Flechsig, Holmes, Inouye, and others. The conclusions that they reached about the visual brain and about vision as a process were ineluctable, given the anatomical and pathological knowledge at their disposal. Our present evidence, richer in anatomy, supplanted by physiology, and fortified by human imaging and pathological studies, leads us, also ineluctably, in a different direction. Above all, it promises us profound insights into that most elusive but most fundamental properties of' the human brain-consciousness.

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