

The disunity of consciousness

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Attempts to decode what has become known as the (singular) neural correlate of consciousness (NCC) suppose that consciousness is a single unified entity, a belief that finds expression in the term ‘unity of consciousness’. Here, I propose that the quest for the NCC will remain elusive until we acknowledge that consciousness is not a unity, and that there are instead many consciousnesses that are distributed in time and space.

In this article, I propose that there are multiple consciousnesses which constitute a hierarchy [1,2], with what Kant [3] called the ‘synthetic, transcendental’ unified consciousness (that of myself as the perceiving person) sitting at the apex. Here, I restrict myself to writing about visual consciousness and, within vision, mainly about the colour and the visual motion systems, about which we know relatively more. For if it can be shown that we are conscious of these two attributes at different times, because of spatially and temporally different mechanisms, then the statement that there is a single, unified consciousness cannot be true.

Functional specialization in the visual brain

The foundation stone for my argument rests on the fact of functional specialization in the visual brain [4–6], from which several consequences follow. By general agreement, this functional specialization is especially true of the colour and the visual motion systems, which occupy geographically distinct locations in the visual cortex (Fig. 1). A pivotal area for the colour system is the V4 complex, and for the visual motion system the V5 complex [5,7]. There is substantial agreement that the two systems have distinct, and characteristic, anatomical inputs, despite the many anatomical opportunities for them to interact. The geographical separation of the two systems constitutes the cornerstone of a ‘theory of multiple consciousnesses’.

Further support comes from the generally accepted clinical evidence that lesions of V4 and of V5 lead to different visual disabilities, the former resulting in an achromatopsia (acquired colour blindness) [8,9] and the latter in an akinetopsia [10,11] (acquired visual motion blindness) (Fig. 1). Crucially, a lesion in one area does not invade and disable the perceptual territory of the other. Thus an akinetopsic patient sees colours consciously even though unable to perceive and be conscious of (fast) motion. By contrast, an achromatopsic patient is unable to perceive and be conscious of colours but is able to see and

be conscious of visual motion effortlessly. Hence consciousness of these elementary visual attributes are distinct from one another and I speak of them as ‘micro-consciousnesses’ [2]. Of course, to perceive something is to be conscious of it and thus to say ‘perceiving consciously’ is to be tautologous, but the tautology serves to emphasize a point that is not always clearly made.

Processing sites are also perceptual sites

One conclusion from the clinical evidence is that a micro-consciousness for colour or visual motion is generated through activity at a distinct processing site, and therefore that a processing site is also a perceptual site. Such a conclusion is reinforced by studies of the visual motion centre, area V5, which receives a direct visual input that bypasses the primary visual cortex (area V1) (Fig. 2) [12–15]. The perceptual consequences of this anatomical arrangement have been well studied in patient GY, blinded in one hemifield in childhood by damage to V1. Our psychophysical and imaging experiments [16,17], independently confirmed [18], have shown that, in spite of his blindness, this direct visual input to V5 [19–21] is sufficient to give GY a crude but conscious vision for fast moving, high contrast stimuli, the perception of which is mediated by V5 [17] (Fig. 2). It has also been shown that his consciousness, when visually stimulated, is visual [22]. These findings suggest that, contrary to previous

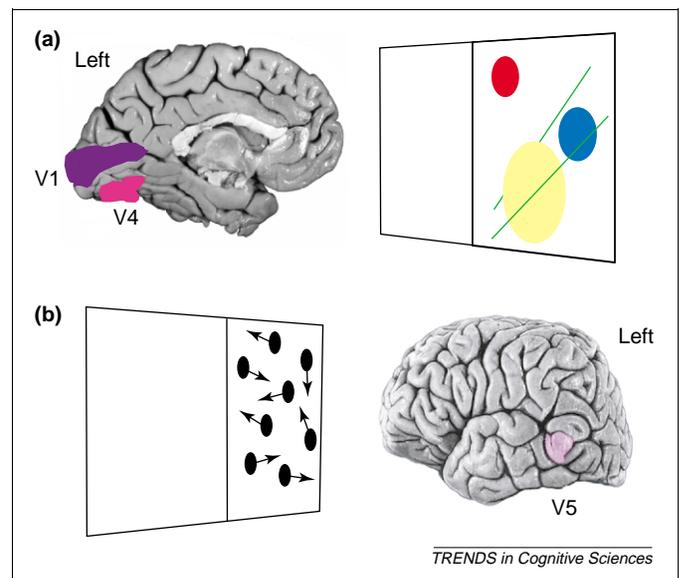


Fig. 1. Visual areas V4 (a) and V5 (b) of the human brain, specialized for colour and motion, respectively. Each receives inputs from the primary visual cortex (V1) and registers the relevant activity in the contralateral hemifield. Lesions in V4 produce achromatopsia – the inability to see colours; motion vision remains intact. Lesions in V5 produce akinetopsia, the inability to see motion; colour vision is unaffected.

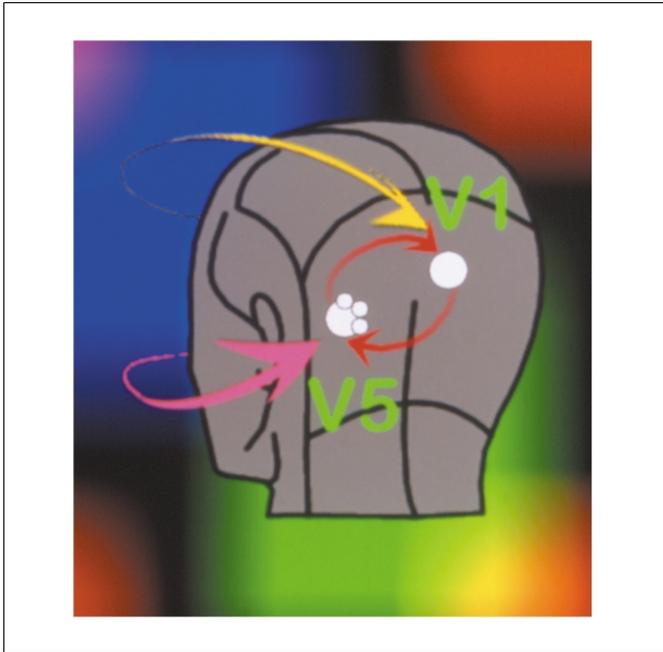


Fig. 2. The flow of visual information from the retina to V1 and V5. Notice that V5 receives a dual input from the retina, one through V1 and another that bypasses V1.

assumptions [23–25], conscious vision is possible without V1 and also that, if one can channel an appropriate visual input to a specialized visual area, then activity in it can result in a conscious correlate even if it is deprived of one of its major sources of visual input. It is thus incorrect to think of prestriate cortex as being not ‘conscious’ cortex [26]. Moreover, the switch from a state when GY is not conscious of visual stimuli and cannot therefore discriminate them correctly to the state when he is conscious of them and can therefore discriminate them correctly is accompanied by a significant increase in activity in area V5, not elsewhere [17]. This has led us to propose that it is heightened activity within a specialized cortical area that leads to conscious vision and that its absence (or lower activity) in the same area correlates with a lack of conscious experience, a proposal that has been confirmed in other systems, not related to visual motion [27] or even exclusively to vision [28].

Direct evidence that cortical processing sites are also perceptual sites comes from combined psychophysical–imaging experiments in humans [29]. Using dichoptic stimulation, where identical visual stimuli are presented for brief periods to the two eyes separately, thus leading to binocular fusion, one finds that when the two stimuli are identical in every respect (for example, an outline red house, or face, against a green background), subjects are able to identify (i.e. perceive) the stimulus correctly. But when the stimuli presented to the two eyes are of reverse colour contrast (for example, outline red house against a green background to the right eye and outline green house against a red background to the left eye), subjects report seeing only yellow. Under these conditions, imaging experiments show that the same specific areas of the brain, specialized for the processing and seeing of houses (or faces), are active, regardless of whether the subjects saw the stimulus (were conscious of it) or not (see Box 1).

The difference between the two states is that, in the former, the activity is higher than in the latter, although we do not know yet whether this is owing to the recruitment of previously inactive cells, to an increased discharge of already active cells, or to an increase in synaptic input without an increase in firing rate [30]. This direct evidence obviates the need to postulate separate cortical area(s) necessary for perception, as opposed to non-conscious processing. Of course, processing–perceptual sites are not sufficient on their own in generating a conscious correlate but depend upon enabling systems in the brain stem [18] and possibly additional uncharted cortical systems.

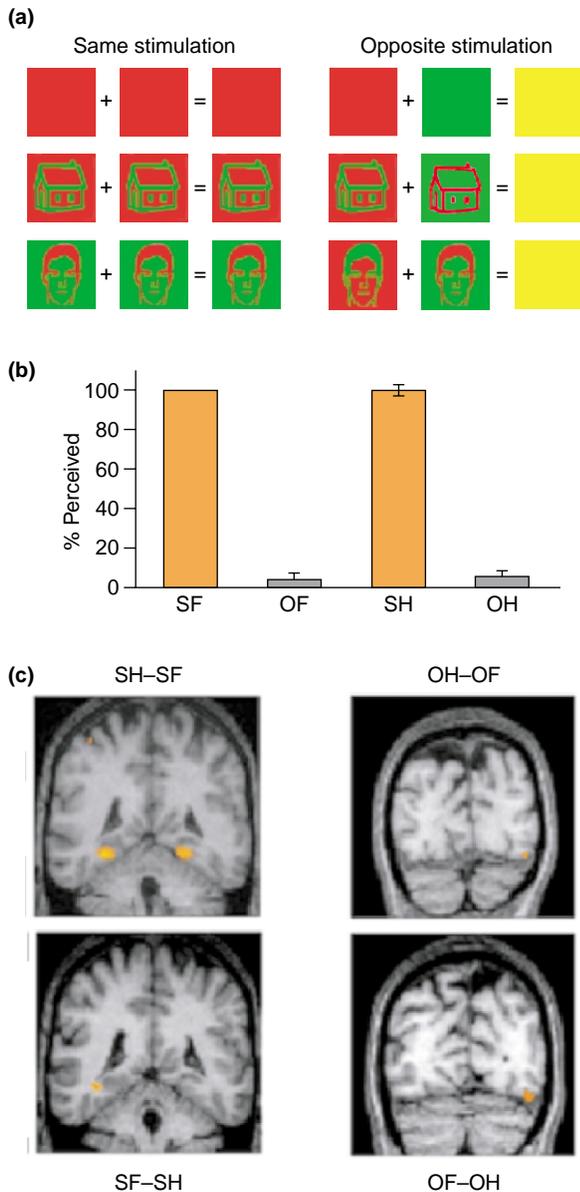
The asynchrony and temporal hierarchy of visual perception

Much has been written about the ability of so intricate a system as the visual brain, with its many parts and distributed parallel pathways, to process all attributes of the visual world simultaneously and thus provide a visual image in which all the different attributes are seen in perfect spatial and temporal registration. Our direct psychophysical results [31,32], now confirmed [33,34], show that this is not true over brief time windows. In particular, it has been shown that colour is perceived before motion by ~ 80 ms. Nor is the perceptual asynchrony limited to colour and motion, because it has also been shown that locations are perceived before colours [35], which are perceived before orientations [31]. The perceptual delay between colour and orientation (both first-order changes) makes it difficult to accept an alternative interpretation of our results [36], which suggests that the asynchrony is the result of comparisons between a first-order (colour) and a second-order (motion direction) change. We had assumed [2] that this asynchrony is due to differences in processing time between visual attributes and this assumption has been elegantly supported by recent experiments [37].

Because we become conscious of colour before we become conscious of motion, it follows that the micro-consciousnesses generated by activity at two distinct cortical sites are distributed in time as well. From this it follows that micro-consciousnesses are distributed in time and space, and that there is a temporal hierarchy of micro-consciousnesses, that for colour preceding that for motion. Of course, it is also true that over longer periods of time, in excess of 500 ms, we do see different attributes in perfect temporal and spatial registration (the attributes are ‘bound’ together). This raises questions that binding studies have so far not addressed, mainly whether one area ‘waits’ for the other to finish its processing, and whether a time buffer is part of the physiological mechanism for this waiting period.

Binding and macro-consciousnesses

The issue of binding between different attributes has not been systematically addressed to date by physiological studies; rather, the principal concern has been how activity of cells in a single area is bound to the activity of other cells in the same area to signal, for example, a continuous straight line [38]. This has led to the conclusion

Box 1. Combining psychophysics and imaging to demonstrate cortical processing–perceptual sites.


In the experiment of Moutoussiss and Zeki [29], subjects viewed pictures of houses, faces, and uniformly-coloured control squares dichoptically. When the stimuli presented to the two eyes were of reverse colour contrast (for example, an outline green house against a red background to the left eye and an outline red house against a green background to the right eye; Fig. 1a), subjects reported seeing no object but only a uniform yellow field, as in the case when uniform red and green fields were presented.

The group results from the concurrent fMRI recording revealed that brain activation was correlated with both perceived and not-perceived conditions (Fig. 1c), but the level of activation was higher in the perceived condition. The contrast same houses minus same faces (SH–SF) shows bilateral stimulus-specific activation in the parahippocampal gyrus (Talairach coordinates: $-30, -44, -12$ and $26, -44, -10$). The contrast opposite houses minus opposite faces (OH–OF) shows unilateral stimulus-specific activation in the same region ($-38, -42, -10$). The contrast SF–SH reveals stimulus-specific activation in a region of the fusiform gyrus ($42, -82, -12$), and the contrast OF–OH reveals stimulus-specific activation in the same brain region ($44, -74, -14$). This experiment provides direct evidence that cortical processing sites are also perceptual sites.

Fig. 1. The stimulation method and results from the experiment in Ref. [29]. (a) The input to the two eyes and the expected perceptual output. Dichoptic stimuli of opposite colour contrast (Opposite stimulation) between the two eyes were invisible, whereas identical stimuli of the same color contrast (Same stimulation) were easily perceived. Continuous fusion of the stimuli was achieved by using repetitive brief presentations. (b) The averaged performance of the seven subjects in the discrimination task (face or house stimuli vs. uniform yellow). The averaged percentage of the number of stimuli perceived (of a total of 448 per subject per stimulus category), shown with the standard error between subjects. SF, same faces; OF, opposite faces; SH, same houses; OH, opposite houses. (c) Group fMRI results: brain regions showing stimulus-specific activation under conditions of same and opposite stimulation, revealing that such activation correlates with perceived and not-perceived conditions (see text for details). (Modified from Ref. [29].)

that it is the binding itself that leads to the conscious experience [39,40]. Whatever its merits, this proposal cannot be accepted as being necessarily true of binding the activity between two specialized areas. The most compelling evidence for doubting this lies in the anatomy, which shows that there are few, if any, direct connections between V4 and V5 in the monkey. Correspondingly, chronoarchitectonic maps of human cerebral cortex [41], generated when subjects view complex scenes, show that the time courses of activity in human V4 and V5 are significantly uncorrelated, from which we can infer that there are no direct anatomical links between them. On the other hand, anatomical evidence from monkey shows that V4 and V5 project in a juxta-convergent manner to further

areas, in both the parietal and temporal areas [42]. This raises two inter-related questions: (1) whether binding of activity between two specialized areas such as V4 and V5 involves further area(s), and (2) whether binding occurs during the processing stage or is post-conscious, occurring only after a conscious correlate is generated in each of the two areas.

One indication that binding may be post-conscious comes from our current psychophysical experiments that demonstrate that the binding of colour to motion occurs after the binding of colour to colour or motion to motion [43]. Thus subjects become conscious of the bound percept *after* they become conscious of the attributes that are bound, again suggesting a temporal hierarchy in perception.

I refer to consciousness of a stimulus or of a percept that is compound, in the sense that it consists of more than one attribute, as a ‘macro-consciousness’, to distinguish it from consciousness of a single attribute alone (e.g. colour). Consistent with a theory of micro-consciousnesses, it is interesting to note that a macro-consciousness may be the result of false binding, as when the veridically ‘wrong’ colour is bound to the ‘right’ motion or form [44]. We have argued that this results from the brain’s binding what it has already processed [29].

A macro-consciousness need not, of course, be limited to a bound visual percept. It could equally signify consciousness of a percept that includes a visual and an auditory component, or of several visual components that, together, constitute a distinct new entity, for example a moving red bus.

Three levels of hierarchies in consciousness

It thus becomes possible to distinguish three hierarchical levels of consciousness: the levels of micro-consciousness, of macro-consciousness, and of the unified consciousness. Of necessity, one level depends upon the presence of the previous one. Within each level, one can postulate a temporal hierarchy. This has been demonstrated for the level of micro-consciousness, because colour and motion are perceived at different times. It has also been demonstrated for the level of the macro-consciousnesses, because binding between attributes takes longer than binding within attributes. This in turn leads one to postulate a set of temporal hierarchies, in which the binding of one set of attributes leading to a given macro-consciousness would take longer than the binding of another set of attributes leading to another macro-consciousness, and the binding of several attributes would take longer still. The experiment has not been conducted yet, but such a result seems likely.

Micro- and macro-consciousnesses, with their individual temporal hierarchies, lead to the final, unified consciousness, that of myself as the perceiving person. This and this alone qualifies as the unified consciousness, and this alone can be described in the singular. Kant probably saw, hesitatingly, the relation between the micro-consciousness (his ‘empirical consciousness’) and the unified consciousness. He wrote: ‘All presentations have a necessary reference to a *possible* empirical consciousness. For if they did not have this reference, and becoming conscious of them were entirely impossible, then this would be tantamount to saying that they do not exist at all. But all empirical consciousness has a necessary reference to a transcendental consciousness (a consciousness that precedes all particular experience), viz., the consciousness of myself as original apperception’ (original emphasis). Here, I disagree only with the suggestion that the ‘empirical’ (micro) consciousness has a *necessary* reference to the unified, transcendental consciousness.

Kant also suspected that the various attributes must themselves be synthesized first before being synthesized into the ‘pure consciousness’, although he could not have been aware of the principles of functional specialization. He continues: ‘But because every appearance contains a manifold, so that different perceptions are in themselves

encountered in the mind sporadically and individually, these perceptions need to be given a combination that in sense itself they cannot have. Hence there is in us an active power to synthesize this manifold’ (which he calls ‘imagination’) [3].

Kant supposed that the ‘transcendental’ consciousness is present *a priori*, before any experience is acquired. It is hard to be conclusive in this regard, but it is worth pointing out that consciousness of oneself as the perceiving person amounts to being aware of being aware, and I believe that this requires communication with others and, especially, the use of language. The cortical programs to construct visual attributes must also be present before any experience is acquired and all experience must therefore be read into them. It seems more likely that, ontogenetically, the micro-consciousnesses precede the unified consciousness and that the programs for them are also present at birth. Hence, even though in adult life the unified consciousness sits at the apex of the hierarchy of consciousnesses, ontogenetically it is the micro-consciousnesses that occupy this position.

I believe that the search for the neural correlates of consciousness will be elusive until we acknowledge the many components of consciousness and their temporally hierarchical relationship to one another. The transition from the singular neural correlate of consciousness to the plural neural correlates of the consciousnesses is a small step on paper but may yet prove to be a very important one in understanding consciousness.

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