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The autonomy of the visual systems and the modularity of conscious vision

S. Zeki and A. Bartels

Wellcome Department of Cognitive Neurology, University College London, London WC1E 6BT, UK

Anatomical and physiological evidence shows that the primate visual brain consists of many distributed processing systems, acting in parallel. Psychophysical studies show that the activity in each of the parallel systems reaches its perceptual end-point at a different time, thus leading to a perceptual asynchrony in vision. This, together with clinical and human imaging evidence, suggests strongly that the processing systems are also perceptual systems and that the different processing–perceptual systems can act more or less autonomously. Moreover, activity in each can have a conscious correlate without necessarily involving activity in other visual systems. This leads us to conclude not only that visual consciousness is itself modular, reflecting the basic modular organization of the visual brain, but that the binding of cellular activity in the processing–perceptual systems is more properly thought of as a binding of the consciousnesses generated by each of them. It is this binding that gives us our integrated image of the visual world.

Keywords: consciousness; colour; binding; asynchrony; motion; cortex

1. SPATIALLY DISTRIBUTED, PARALLEL PROCESSING SYSTEMS IN THE VISUAL BRAIN

(i) The primate visual brain has been shown to consist of many separate visual areas (Zeki 1969, 1971; Allman & Kaas 1974) and the number of areas continues to grow (Felleman & Van Essen 1991). Central to the visual brain is area V1 of the primary visual cortex. This receives its input from the retina via the lateral geniculate nucleus and distributes specialized signals in parallel to the other visual areas that are situated in the cortex surrounding it (Zeki 1975; Livingstone & Hubel 1984; Felleman & Van Essen 1991).

(ii) The different visual areas in the cortex surrounding area V1 are specialized to process different attributes of the visual scene (Zeki 1978). Prominent among these are motion and colour.

(iii) It is generally accepted that the cortical components of both the motion and the colour processing systems are multistage, involving specialized and segregated groups of cells in areas V1 and V2, and the more specialized areas V5 and V4, respectively (DeYoe & Van Essen 1988; Livingstone & Hubel 1988; Shipp & Zeki 1989*a*,*b*; Zeki & Shipp 1989).

(iv) V5 represents but one aspect of a specialization for motion. There are several specialized areas surrounding V5, which receive a direct input from V5. Among the specializations of these areas are ones for rotatory motion, biological motion and optical flow, in both monkey (Sakata *et al.* 1986; Tanaka & Saito 1989; Wurtz *et al.* 1990) and man (Shipp *et al.* 1994; Howard *et al.* 1996).

(v) It follows from the above that one characteristic of the visual brain is the presence of spatially distributed, functionally specialized, processing systems that deal with different attributes of the visual scene. The visual brain is therefore modular in its organization.

2. TEMPORAL ASYNCHRONY IN VISUAL PERCEPTION

(i) The major characteristic of the visual brain, that of spatially distributed parallel processing systems, raises the question of how the results of the operations undertaken by the different processing systems are integrated to give us our unitary image of the visual world. Alternative suppositions for the processing systems are (i) terminate their tasks at the same time, or (ii) that they report the results of their operations in a convergent manner to a central integrator area or areas, or (iii) that a specialized form of communication between the areas—e.g. in the temporal domain—leads to an integrated percept. But anatomical experiments show that there is no single area that receives input from all the specialized areas and that when two specialized areas such as V4 and V5 project to the same, higher area, each largely maintains its territory within the higher area. We thus speak of *juxta-convergence* rather than overlapping inputs (Shipp & Zeki 1995).

(ii) Moreover, psychophysical experiments show that different processing systems do not complete their tasks at the same time (Moutoussis & Zeki 1997*a*). Different attributes of the visual scene are not perceived at the same time. Instead, colour is seen before orientation, and orientation is seen before motion (Moutoussis & Zeki 1997*a*,*b*; Zeki & Moutoussis 1997), the difference between perceptual times for colour and for motion being about 60–80 ms.

(iii) This extends functional specialization into the time domain and shows that another characteristic of the visual brain is a temporal asynchrony in perceiving different attributes. It leads us to conclude that a mutual integration of activity between different processing systems is not necessary for the creation of a conscious percept. Rather, it suggests strongly that the processing systems are also perceptual systems. Hence we speak of processing–perceptual systems (Zeki 1998).

(iv) The psychophysical evidence also shows that the brain does not necessarily bind together what happens in real time but may instead bind the results of the operations undertaken by its different processing systems which require different amounts of time to complete their tasks. In the sub-second window, the brain therefore misbinds in terms of real time (Moutoussis & Zeki 1997*a*,*b*).

(v) It follows that visual perception is also modular.

3. THE AUTONOMY OF THE VISUAL PROCESSING SYSTEMS

(i) The evidence given in §§ 1 and 2 suggests that the different processing–perceptual systems are fairly autonomous of one another and able to function more or less independently.

(ii) The absence of a central area to which all the specialized processing systems uniquely project (Shipp & Zeki 1995), and the temporal segregation of the perceptive systems, argue against the necessity for a central synthesizer or integrator mechanism, either in space or in time.

(iii) Human studies confirm that the different processing–perceptual systems are fairly autonomous. Thus specific damage to one system alone, such as colour, does not lead to a global deficit in vision; the most characteristic outcome of such a specific damage to the human colour centre (the V4 complex; see Bartels & Zeki 1998*a*) is a colour imperception, or cerebral achromatopsia (for a review, see Zeki (1990*a*)). But achromatopsic subjects are able to perceive motion normally. Equally, the characteristic result of damage to the motion centre (area V5) is a motion imperception or cerebral akinetopsia (for a review, see Zeki (1991)). But akinetopsic subjects are able to perceive colour normally (Zihl *et al.* 1983).

(iv) We conclude that the two systems are fairly autonomous of one another and that one can function more or less normally in the absence of the other.

4. THE CONSCIOUS CORRELATE OF ACTIVITY IN INDIVIDUAL PROCESSING–PERCEPTUAL SYSTEMS

(i) The relative autonomy of the visual areas in terms of processing and of perception raises the question of whether activity in each has a conscious correlate, without the mandatory participation of other visual areas or systems. It also raises the question not only of whether different processing systems create conscious correlates, but also whether activity at different stages within each can have a conscious correlate (Bartels & Zeki 1998*b*; Zeki & Bartels 1998). We have argued elsewhere on the basis of clinical and physiological evidence that activity at each level of a multistage system can be made perceptually explicit and does not necessarily require the participation of further stages within that system (Zeki 1990*b*, 1993; Bartels & Zeki 1998*a*). By perceptually explicit activity, we mean activity that does not require further processing.

(ii) It has now been shown conclusively that patients with a damaged area V1 and an intact area V5 can discriminate and experience consciously fast motion presented to their blind hemifields (Barbur *et al.* 1993; Weiskrantz 1995; Zeki & ffytche 1998). This capacity is almost certainly conferred on them by the direct retinal input to V5 that bypasses V1 which, apparently, is specialized to deliver signals from fast-moving stimuli (Beckers & Zeki 1995; ffytche *et al.* 1995). Imaging studies show that when such a patient experiences motion in his blind field, the activity is restricted to V5 and to the reticular activating system (Zeki & ffytche 1998). Thus a subdivision of the visual motion pathway can function more or less autonomously, if crudely, and activity within it has a conscious correlate.

(iii) There is evidence that activity in other specialized areas of the cortical motion system can result in a conscious perception of the attribute for which the relevant area(s) is specialized, without involving other visual areas or area V1, presumably reflecting the cortical specialization for visual motion (see § (iv) above). An interesting example comes from the patient of Ceccaldi (Ceccaldi *et al.* 1992) and Mestre (Mestre *et al.* 1992), blinded by a lesion in V1; he can perceive optical flow motion stimuli, which appear to be processed by distinct cortical areas (Shipp *et al.* 1994), without perceiving translational motion (M. Ceccaldi, D. Mestre and S. Zeki, unpublished data).

(iv) Carbon monoxide-poisoned patients who have lost the ability to see form and motion and depth can sometimes retain selectively the capacity to see in colour (Wechsler 1933; Humphrey *et al.* 1995; Zeki *et al.* 1998). They are conscious of seeing colours. This constitutes a further indication that the separate systems can act more or less autonomously and that activity in them can have a conscious correlate without the participation of the other areas.

(v) There is at least one report in the published literature of a patient blinded by a lesion in area V1 who is nevertheless able to see colour consciously in her blind field (Blythe *et al.* 1987), presumably through the direct input linking the lateral geniculate nucleus to V4 (Fries 1981; Yukie & Iwai 1981). If confirmed by further cases, this would suggest a parallel between the motion and the colour systems, in that activity within each can lead to a conscious if crude experience of the relevant attribute.

5. CONCLUSION

Taken together, the above evidence suggests that the processing, the perception, and the conscious experience of a visual attribute do not depend upon the healthy functioning of the entire brain, or even the entire visual brain, but only of the subsystem specialized for that attribute. There may therefore be many consciousnesses, reflecting activity in the separate parallel processing–perceptual systems that constitute the visual brain. Visual consciousness may itself therefore be modular, thus reflecting the basic modularity of the processing perceptual systems. We have hypothesized elsewhere that activity at each level of each processing–perceptual system may generate a conscious correlate, and that it is these micro-consciousnesses that have to be bound to generate the integrated image in the brain (Zeki & Bartels 1998). It is, we believe, a hypothesis that is worth considering and one that may have applicability to more than the visual brain.

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