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Why is “blindsight” blind? A new perspective on primary visual cortex, recurrent activity and visual awareness

Juha Silvanto

University of Westminster, Faculty of Science and Technology, Department of Psychology, 309 Regent Street, W1B 2HW London, UK
Brain Research Unit, O.V. Lounasmaa Laboratory, School of Science, Aalto University, PO BOX 15100, 00076 Aalto, Finland

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ABSTRACT

The neuropsychological phenomenon of blindsight has been taken to suggest that the primary visual cortex (V1) plays a unique role in visual awareness, and that extrastriate activation needs to be fed back to V1 in order for the content of that activation to be consciously perceived. The aim of this review is to evaluate this theoretical framework and to revisit its key tenets. Firstly, is blindsight truly a dissociation of awareness and visual detection? Secondly, is there sufficient evidence to rule out the possibility that the loss of awareness resulting from a V1 lesion simply reflects reduced extrastriate responsiveness, rather than a unique role of V1 in conscious experience? Evaluation of these arguments and the empirical evidence leads to the conclusion that the loss of phenomenal awareness in blindsight may not be due to feedback activity in V1 being the hallmark awareness. On the basis of existing literature, an alternative explanation of blindsight is proposed. In this view, visual awareness is a “global” cognitive function as its hallmark is the availability of information to a large number of perceptual and cognitive systems; this requires inter-areal long-range synchronous oscillatory activity. For these oscillations to arise, a specific temporal profile of neuronal activity is required, which is established through recurrent feedback activity involving V1 and the extrastriate cortex. When V1 is lesioned, the loss of recurrent activity prevents inter-areal networks on the basis of oscillatory activity. However, as limited amount of input can reach extrastriate cortex and some extrastriate neuronal selectivity is preserved, computations involving comparison of neural firing rates within a cortical area remain possible. This enables “local” read-out from specific brain regions, allowing for the detection and discrimination of basic visual attributes. Thus blindsight is blind due to lack of “global” long-range synchrony, and it functions via “local” neural readout from extrastriate areas.

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1. Introduction

Investigations into the effect of posterior occipital lesions on human visual perception have concluded that the induced field defects are absolute (Holmes, 1918; Horton & Hoyt, 1991).¹ However, when assessed through forced choice paradigms, some patients with V1 damage are able to detect stimuli presented in their blind field, despite reporting a complete lack of

E-mail address: j.silvanto@westminster.ac.uk

¹ Riddoch (1917) argued that awareness of motion information may be selectively preserved. However, this observation may have been due to V1 lesion being incomplete in many of the patients, and motion processing being less susceptible to impairment (Cowey, 2004). In well-known blindsight patients in whom complete absence of V1 has been confirmed, motion awareness is not preserved (e.g. Weiskrantz, 1997; Stoerig & Cowey, 1995).

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conscious visual experience. This phenomenon was first reported by Pöppel et al. (1973), whose sample of cortically blind patients was able to localize visual stimuli presented in their blind field with eye movements. Subsequently it was shown that patients with V1 damage can localize unseen stimuli also by pointing, even more accurately so than by eye movements (see Cowey, 2004, 2010 for reviews). This detection and discrimination ability in the absence of visual experience is known as blindsight (Weiskrantz, Warrington, Sanders, & Marshall, 1974). Intriguingly, blindsight is not merely a subcortical phenomenon, as extrastriate regions in the damaged hemisphere can be activated by blind field stimuli (e.g. Goebel, Muckli, Zanella, Singer, & Stoerig, 2001; Rodman, Gross, & Albright, 1989a; Schmid, Panagiotaropoulos, Augath, Logothetis, & Smirnakis, 2009), and these activations are functionally significant, as their disruption by transcranial magnetic stimulation (TMS) impairs blindsight performance (Alexander & Cowey, 2009). Blindsight is likely to be mediated by pathways projecting directly to extrastriate cortex, bypassing V1 (Cowey & Stoerig, 1989; Rodman, Gross, & Albright, 1989b; Schmid et al., 2010).

The failure of extrastriate activation to reach awareness when V1 is lesioned, despite the ability of this activation to guide visual detection, appeared to suggest unique role for V1 in visual awareness. Blindsight thus challenged, together with a number of electrophysiological findings, the strictly hierarchical feedforward models of visual processing in which V1 was viewed as merely a source of extrastriate input (e.g. Crick & Koch, 1995). This led to a shift towards models emphasizing the role of recurrent processing in visual awareness, a view which gained substantial support primarily from brain stimulation studies carried out in both blindsight patients as well as in neurologically normal observers. However, the picture has recently been complicated by demonstrations of conscious experience in blindsight, as well as by evidence implicating feedback activity in V1 in *all* visual processing, whether conscious or not.

The aim of the present manuscript is to review these developments. Firstly, I will discuss the origins of the hierarchical feedforward model, its inability to explain various neurophysiological phenomena, and how feedback activity involving V1 took center stage in theories of awareness. Secondly, I will review the key evidence in favor of these views, as well as recent results which have challenged them. Thirdly I will evaluate two key arguments of the feedback model: is blindsight a true dissociation of awareness and visual detection? Are extrastriate responses relatively normal in the absence of V1, ruling out an explanation in terms of impoverished extrastriate responses? Finally, I will offer an explanation of blindsight in terms of “local” computations and “global” inter-areal neural synchrony.

2. Hierarchical and feedback models of visual processing and awareness

2.1. The hierarchical view of visual awareness

Two characteristics of the visual cortex strongly contributed to the conventional view that visual information processing giving rise to conscious perception is fundamentally hierarchical in nature (e.g. Crick & Koch, 1995). One of these is anatomical hierarchy, based on the principle that connections between visual areas are normally reciprocal in nature, and that within a reciprocal pair of connections, there are differences in the laminar distribution of cells of origin and axonal termination (Rockland & Pandya, 1979, 1981; Maunsell & Van Essen, 1983; Felleman & Van Essen, 1991). One type of projection arises primarily from cells in supragranular layers, with a small contribution of 10–15% from infragranular layers, and terminates in the granular layer; this type of pathway was named *feedforward* (or ascending) projection, and it provides the excitatory drive of neuronal activity (e.g. Orban, 1984; Maunsell & Van Essen, 1987; Stone, Dreher, & Leventhal, 1979). A second type of projection arises from cells in both supra- and infragranular layers and terminates most densely in layer I and/or VI. This type of pathway was named the *feedback* or descending projection and it has a modulatory influence on the activity induced by feedforward activity (e.g. Dreher, 1986; Van Essen & Maunsell, 1983). The model of cortical hierarchy was constructed such that each area was assigned just below the highest area to which it provides ascending input; visual areas sharing intermediate projections were placed on the same level of the hierarchy. In this hierarchy (see Fig. 1), V1 is at the bottom, and regions in the parietal, temporal and frontal regions at the top.

The second feature of the visual system contributing to the hierarchical view was functional specialization, which is a key feature of the extrastriate cortex (Zeki, 1974, 1978). For example, nearly all neurons in the upper part of the posterior bank of the superior temporal sulcus, now known as V5 or MT, respond to visual motion but not to other attributes such as wavelength (Zeki, 1974), a finding later confirmed by other studies (Albright, 1984; Van Essen, Maunsell, & Bixby, 1981). The motion selectivity of V5/MT has also been demonstrated in the human visual cortex (Zeki et al., 1991). The existence of a color-selective visual area, V4, has also been proposed (Zeki, 1973, 1977), although the precise location of a “color – center” in both the monkey and human cortex is still a matter of controversy (Heywood, Gadotti, & Cowey, 1992; Tootell, Nelissen, Vanduffel, & Orban, 2004; Hadjikhani et al., 1998). At higher levels of the ventral cortical hierarchy, neurons display an even higher level of specialization, for example, cells in the inferotemporal (IT) cortex are tuned to complex geometrical figures (e.g. Tanaka, 1993) and faces (Perrett et al., 1982). In contrast, regions (such as V1 and V2) at the bottom of the cortical hierarchy act as filters for a range of low-level stimulus attributes that fall within its receptive field (e.g. Van Essen et al., 1992).

Anatomical hierarchy coupled with functional specialization contributed to the view that visual processing proceeds in a feedforward fashion, with the role of lower-level areas such as V1 to merely provide input to regions at the top of the hierarchy where high-level visual perception and awareness arise (Crick & Koch, 1995; Felleman & Van Essen, 1991). This was, to an extent, consistent with Barlow's (1972) view that “perception corresponds to the activity of a small selection from the very numerous high-level neurons, each of which corresponds to a pattern of external events of the order of complexity

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