

An extension to the hypothesis of the asynchrony of visual consciousness

I. Aleksander* and B. Dunmall

Department of Electrical and Electronic Engineering, Imperial College, London SW7 2AZ, UK

An existing hypothesis states that visual consciousness is made up of ‘microconsciousnesses’ occurring asynchronously in several sites of the visual system of the brain with no need for direct means of binding. We extend this hypothesis to define what qualifies a neural activity for generating an element of consciousness to distinguish it from one that does not. We argue that, for these separate neural activities to represent elements of a compound sense of consciousness, they each need the support of sites that unconsciously process an important attentional referent and that it is the commonality of such referents in differing sites which bring the microconsciousnesses together. We consider the broader implications of this extended hypothesis for other sensory modalities and mental imagery.

Keywords: vision; consciousness; perception; binding; imagery

1. BACKGROUND AND OBJECTIVE

Using ‘facts about the visual brain revealed in the past quarter of a century’ (p.1583), Zeki & Bartels (1998) stated a hypothesis of asynchrony in visual consciousness (the Zeki and Bartels hypothesis or ZBH). This suggests that physically separate and functionally specialized sites of the visual system contribute independently to conscious visual sensation in a way which does not require neurally mediated binding or synchronization between these areas. Normally a subject is not conscious of this asynchrony, except during ‘sophisticated psychophysical experiments’. Such short-exposure experiments show that neural activity is initiated at different times, providing the grounds on which the hypothesis was founded. The ZBH overtly embraces a close relationship between conscious experience and neural events: it states that particular neural events are the ‘neural correlates of consciousness’, that such events have ‘correlates in consciousness’ and that conscious experience can be a compound of separate microconscious experiences occurring in different sites. In what follows below we use these principles to show that the ZBH has some theoretical consequences which we treat as an extended hypothesis. These refer to the nature of supporting unconscious, neural conditions which appear necessary for collating microconscious experiences into a unified sensation. Specifically, the extension aims to address four questions.

- (i) What is the functional distinction between sites which contribute to consciousness and those which do not?
- (ii) Given that we are satisfied with the answer to (i), it is still necessary to decide what it is which brings events in separate consciousness-qualified sites into a single conscious experience. That is, were a subject looking at a moving red beetle on a white wall, three separate neural sites would be stimulated to represent the shape of the beetle, its colour and its motion. What guarantees that we sense these as being the attributes of the same object rather than three separate (albeit somewhat peculiar) phenomena? In short, what are

the necessary conditions in the ZBH for neural event $N(\alpha)$ in site A resulting in a conscious event $C(\alpha)$ and an asynchronous neural event $N(\beta)$ in site B resulting in a conscious event $C(\beta)$ to contribute cumulatively to a single conscious experience, say $C(\alpha \bullet \beta)$? ($\alpha \bullet \beta$) is the notation we adopt to indicate that (α) and (β) are correctly sensed as separate features of the same world event.

- (iii) Why might there be a lack of awareness of timing discrepancies between specialized sites under normal conditions?
- (iv) What is the relationship of consciousness during perception to conscious mental imaging?

2. ASSUMPTIONS

In common with other neurophysiological discussions of consciousness (e.g. Crick & Koch 1995; Cotterill 1999; Ramachandran & Blakeslee 1999), the ZBH includes two explicit assumptions which relate to experimental investigations of the neural basis of conscious experience.

Any experiment which attempts to link a measured neural event to a conscious experience uses the verbal reports or physical actions of the subject as a measure of their conscious experience. These are assumed to be accurate accounts of or reliable reactions to conscious experience.

- (i) Any experiment which attempts to link a measured neural event to a conscious experience uses the verbal reports of physical actions of the subject as a measure of their conscious experience. These are assumed to be accurate accounts of or reliable reactions to conscious experience.
- (ii) Despite the fact that the word ‘correlate’ is used, a causal direction from neural activity to conscious experience appears to be implicitly assumed in the sense that excised or incapacitated neural structure is assumed to cause measurable changes in reported conscious experience. This also implies that there cannot be conscious experience not supported by neural activity.

*Author for correspondence (i.aleksander@ic.ac.uk).

These assumptions are common to more general sometimes introspective observations about vision. Four of these are important to our argument.

- (iii) Observers report that the focal point of their consciousness (visual and other) is localized at a point somewhere inside their heads (Velmans (1993) gives an account of the literature on this). This provides a sense of 'self' or 'I' in visual perception and it is with respect to this point that the observer is able to plan their actions and attempt to predict the results of such. This implies that conscious perceptual experience is derived from neural activity which internally replicates the frame of reference which is identical to that of the external world from the perspective of the localized point. We refer to this as the 'world embedded from the point of view of the observer' (WEPVO). The alternative would be a representation which builds an abstract map of the world (a bit like a map with a 'you are here' sign). There is no neurobiological evidence which favours either of these alternatives and our assumption for the existence of the WEPVO version is a result of introspection.
- (iv) The WEPVO must be sufficiently accurate for observers to interact competently with the world and to plan their actions in imagination. That is, any inaccuracy in the representation could not be retrieved and would lead to errors in muscular action (e.g. failing to position one's hand and fingers over a cup handle) and some plans that involve actions (for example, crossing a road). This accurate conscious experience must be reflected in some neural activity which is at least as accurate as the reported perception or imagination. That is, the accuracy of what is being perceived or imagined must have a correspondingly accurate neural representation.
- (v) The sites which provide this accuracy are likely to be supported by unconscious compensating neural activity, a feature stressed by Crick & Koch (1995). For example, activity in areas such as LGN or V1, being stimulated retinotopically, represent a partial and changing view of the visual world as the eyes move. Were we conscious of this activity it would be confusing and disorientating. However, this is not the case, so such activity does not qualify as being able to contribute directly to a coherent conscious experience. This does not deny that these early parts of the visual system are the major conduits to sites (the extrastriate cortex (?) according to Crick & Koch (1995)) where a reconstruction may be taking place, which does qualify as a correlate of experience. Nor are we conscious of neural activities which drive the eye muscles (e.g. firing activity in the superior colliculus) during eye movement where these again are clearly essential in our becoming conscious of more than single flashes of the sensed visual world. We refer to neural activity in these examples as being 'in support' of sites where consciousness may be generated.
- (vi) Visual memory or mental imagery has for some time been believed to involve the same neural sites as perception (Perky 1910; Biasiach *et al.* 1979; Kosslyn

1980). Most of the evidence for this has been collected from patients with brain damage showing that damage to specific cortical areas affects perception and imagery (Farah 1995).

3. DEFINITIONS

In common with others (e.g. Kosslyn 1980) we refer to what can be visually perceived as a visual cone S with its apex at the assumed point of 'self' in (iii) above. Then according to (i) we can define $C(S)$ as the total conscious perceptual experience of a visual scene which a subject can access and report. We note that $C(S)$ is S as mediated by the limitations of the perceptual system (e.g. S may contain ultraviolet elements which do not enter $C(S)$). Then, according to (iv), we can define $N(S)$ as the neural activity which is at least as accurate as $C(S)$. Note that this makes no assumptions about the evolution of $C(S)$ and $N(S)$ in time. In addition, according to (ii) the causal direction may be expressed as

$$N(S) \Rightarrow C(S). \quad (1)$$

As $C(S)$ and $N(S)$ are generally gathered in time, we now define $(\delta S)_j$ as a minimally perceptible momentary element of the visual cone which can be gathered in parallel. The referent j is neural activity as in (v) above, which, through muscular action, selects $(\delta S)_j$ in S . Assumption (ii) above suggests that $(\delta S)_j$ results in elemental neural activity $N(\delta S)_j$ and elemental conscious experience $C(\delta S)_j$. For example, in visual perception j is the vector of total neural activity which controls the positioning of the fovea, head position and the convergence of the eyes, etc. We stress that the definition of $C(S)$ is based on that which can be reported as an experience and from this we work back to some neural correlate $N(S)$. This means that $N(S)$ does not include neural activity which could be seen as being in support of what occurs in the ZBH sites (e.g. cell activity in the lateral geniculate nucleus or superior colliculus).

Further, we let $\{\alpha, \beta, \dots\}$ be the discernable attributes of S in the sense that it is known that such attributes can cause activity in neural areas with different specialized properties (e.g. colour, edge and brightness or changes in these). Similarly, $\{\delta\alpha, \delta\beta, \dots\}_j$ are the corresponding elements of $(\delta S)_j$. The essence of the ZBH is that $C(S) = C(\alpha) \bullet C(\beta) \bullet \dots = C(\alpha \bullet \beta \bullet \dots)$, where $C(\alpha) \bullet C(\beta) \bullet$ are 'microconsciousnesses' generated at differing sites and \bullet is the notation which we use to indicate both the coincident occurrence of the microconsciousnesses and the apparent coincidence of the attributes of S in the resulting sensation.

4. EXTENDED HYPOTHESIS

- (i) For a 'microconsciousness' site as identified in the ZBH to contribute to visual conscious sensation and, therefore, represent at least one attribute λ from the attribute set $\{\alpha, \beta, \dots\}$ of S , that site must be capable of elemental neural activity, say $N(\delta\lambda)_j$, uniquely for each j of $(\delta S)_j$ (e.g. the foveal capture of an edge or the colour of the element). That is, $N(\delta\lambda)_j$ refers to the state of a group of neurons which is selected by

referent \mathbf{j} in the site sensitive to λ and which is capable of encoding all the variants of λ . Hence, $\mathcal{N}(\delta\lambda)_m$ is physically distinct (but not necessarily non-overlapping) from $\mathcal{N}(\delta\lambda)_n$ for $n \neq m$. As the site must eventually reconstruct $\mathcal{N}(\lambda)$, it can only do so if it receives projections from neural areas which generate the referent vector \mathbf{j} . It is this \mathbf{j} which carries information about the position of $(\delta\lambda)_j$ in real space by coding the activity required to capture the element of S . Conversely, a site which does not receive such projections cannot qualify as correlating with conscious experience.

- (ii) Any two or more sites which specialize in different attributes receive elements such as, for example, $(\delta\alpha)_j$ in site A and $(\delta\beta)_j$ in site B. . . . Binding these in conscious experience these sites require referent \mathbf{j} to encode the coincidence in S of these events and, therefore, it is \mathbf{j} which is necessary for each site for the juxtaposition of the microconsciousnesses at specific sites to bind together in experience.
- (iii) As the $(\delta S)_j$ elements are produced in the function of a sequential attentional process of eye movement, the neural element $\mathcal{N}(\delta\lambda)_j$ must have a persistence of sufficient duration to contribute to a continuous reconstruction of $\mathcal{N}(S)$ consequently constructing consciousness $C(S)$. This suggests that it is this persistent activity (rather than its onset) which dominates conscious experience, bringing onset timing discrepancies into consciousness only during 'sophisticated psychophysical experiments'.
- (iv) In mental imagery (accepting (vi) above), the referent \mathbf{j} is not directly available from muscular tracking of sensory input, but may be indirectly generated as a memory state as is the imagery itself. For example, verbal input such as 'think of a horse in the distance' or 'think of grooming a horse' carries a call for a recall of some aspect of \mathbf{j} . In addition, planning activities such as imagining a new layout for the furniture in a room implies values of \mathbf{j} generated from within. That is, the learning of stable configurations (sometimes 'schemata' as in Arbib (1987), chapter 9 of Cotterill (1999) or 'state space attractor confluent' as in Aleksander (1996)) where long-routed feedback connections and reverse connections (Zeki & Shipp 1988) are found include a representation of \mathbf{j} as well as the imagery.

5. COMMENTARY

As with the ZBH, the purpose of the paper is to develop existing theory for its importance in future theorizing about the neural correlates of consciousness. In this short report we have not attempted to link our conclusions directly to detailed computational models of the visual system, even though our hypothesis is currently being incorporated and successfully tested in such models in our laboratory (Aleksander & Dunmall 1999; Aleksander *et al.* 1999).

Put as a logical statement the extended hypothesis states that

a neural site in the visual system can cause a conscious experience if and only if it receives projections both from sensory inputs and the attentional sites which allow

sensors to locate the positions of objects in the visual world. If this condition is satisfied in differently specialized sites for the same attentional referent, the related sensation will be a juxtaposition of the specialized sensations. When visual experience is recalled in imagination, it is implied that the attentional referent is included among the state variables which encode learned state trajectories in dynamic neural structures.

The ZBH implies that minimal elements of activity in 'microconscious' sites not only have a correspondence with one another but 'correlate' with what must be minimal elements of that which, after some integration, becomes 'conscious experience'. The thrust of the extended hypothesis in this paper is to identify the features which are necessary to enable neural activity to correlate with conscious experience and, indeed, be responsible for it. The key feature of such experience is that it is the WEPVO and we therefore specify the requirements for sites in which the neural firing patterns could reflect this property. Such sites require projections both from conduits of sensory stimulation and supporting attentional neural activity. We have called the latter 'referent \mathbf{j} '. This, broadly speaking, is a vector generated from the motor activity which physically focuses the attention of the sensory transducers on elements of the perceived external domain. In the visual domain this is largely derived from eye and head movements. Some neurophysiological support for this extension may be found in the discovery of gaze-locked cells in monkeys (Zeki (1993) gives a full account) and in Crick & Koch's (1995) suggestion that the primary visual cortex cannot correlate with conscious experience as it is too distant from motor signals.

In vision, if partial WEPVO neural representations occur in separate sites which are specialized in representing different attributes of sensory input (motion, colour, etc.), we have suggested that it is the commonality of the referent \mathbf{j} between them which satisfies 'coming into consciousness', taking into account the asynchrony in the ZBH. We have also argued that, in the generation of mental imagery, this referent is still at play embedded into the state structure of postulated loops which sustain the phenomenon (see Cotterill (1999, chapter 10) for an overview).

While this paper has focused on the visual modality, there are good examples of the way in which the hypothetical scheme might work in other sensory modalities. In the tactile domain there are several accurate somatotopic representations but these still need a referent which positions the sensation in space in addition to a particular position on the skin. Relieving an itch indicates the involvement of motor activity in another limb as creating the referent. Iwamura *et al.* (1981) provided evidence of somatosensory activation mediated by motor activity which supports this idea. Ramachandran & Blakeslee's (1999) work with amputees indicated the effect of false consciousness mediated both by phantom activity in the somatosensory cortex and the residual referent which allows the patient to point to a phantom tactile sensation. Audition too has the 'out-there-ness' where the referent is generated in part from phase differences between the ears and mediated by the effect of head motion and ear shape. Olfaction and taste may be

different in having a more direct neural representation leading to consciousness which is given by vectors of molecule presence and position coding on the tongue, respectively.

Are the ZBH and the extension reported here testable in terms of what can be measured in neuronal activity? In principle and as experimental techniques achieve greater accuracy the answer should be positive. This work predicts that a highly localized lesion in a microconsciousness site will lead to an attribute deficit (in the ZBH, not seeing a coloured dot for example) which always affects the same element of the visual cone (extended hypothesis). This would be a reversal of experiments which reveal gaze locking (mentioned earlier) where eye attention to a point in the visual cone predicated measured neuronal activity.

On the whole, the ZBH and extensions such as reported here point the way to reconciling older theories of neuromuscular support for consciousness (e.g. Sherrington 1940; Sperry 1959) with modern findings of the localization of sensory processing (Zeki *et al.* 1991). As also argued by Cotterill (1999, chapter 9), this type of reconciliation is essential in neuroscience if one is to understand consciousness as a systemic emergent property of the neural mechanics of the brain.

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