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Ignition's glow: Ultra-fast spread of global cortical activity accompanying local "ignitions" in visual cortex during conscious visual perception

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ABSTRACT

Despite extensive research, the spatiotemporal span of neuronal activations associated with the emergence of a conscious percept is still debated. The debate can be formulated in the context of local vs. global models, emphasizing local activity in visual cortex vs. a global fronto-parietal "workspace" as the key mechanisms of conscious visual perception. These alternative models lead to differential predictions with regard to the precise magnitude, timing and anatomical spread of neuronal activity during conscious perception. Here we aimed to test a specific aspect of these predictions in which local and global models appear to differ – namely the extent to which fronto-parietal regions modulate their activity during task performance under similar perceptual states. So far the main experimental results relevant to this debate have been obtained from non-invasive methods and led to conflicting interpretations. Here we examined these alternative predictions through large-scale intracranial measurements (Electrocorticogram – ECoG) in 43 patients and 4445 recording sites. Both ERP and broadband high frequency (50–150 Hz – BHF) responses were examined through the entire cortex during a simple 1-back visual recognition memory task. Our results reveal short latency intense visual responses, localized first in early visual cortex followed (at ~200 ms) by higher order visual areas, but failed to show significant delayed (300 ms) visual activations. By contrast, oddball image repeat events, linked to overt motor responses, were associated with a significant increase in a delayed (300 ms) peak of BHF power in fronto-parietal cortex. Comparing BHF responses with ERP revealed an additional peak in the ERP response – having a similar latency to the well-studied P3 scalp EEG response. Posterior and temporal regions demonstrated robust visual category selectivity. An unexpected observation was that high-order visual cortex responses were essentially concurrent (at ~200 ms) with an ultra-fast spread of signals of lower magnitude that invaded selected sites throughout fronto-parietal cortical areas. Our results are compatible with local models in demonstrating a clear task-dependence of the 300 ms fronto-parietal activation. However, they also reveal a more global

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component of low-magnitude and poor content selectivity that rapidly spreads into fronto-parietal sites. The precise functional role of this global "glow" remains to be elucidated.

1. Introduction

The neuronal events associated with the emergence of a content-specific visual image in human consciousness are still poorly understood and a source of an ongoing debate. A central question in this research concerns the minimal group of neurons whose activity is both necessary and sufficient for visual awareness and the magnitude and dynamics of this activity. Despite extensive research this question is far from resolved.

A useful way to frame this issue more concretely is from the perspective of global vs. local models of visual perception. Local models point to activity confined to content-selective visual neurons as the central mechanism that gives rise to a conscious visual percept (Block, 2005, 2007; Fisch et al., 2009; Malach, 2007; Zeki, 2001, 2003; Zeki & Bartels, 1999). In contrast, according to global models, a wide-spread "global work-space" (GWS) activation, encompassing fronto-parietal cortex as well, is the critical mechanism (Baars, 1997; Dehaene & Changeux, 2011; Del Cul, Baillet, & Dehaene, 2007; Sergent, Baillet, & Dehaene, 2005).

Unfortunately the global vs. local formulation is still rather vague, making it difficult to formulate unequivocal predictions for specific experimental designs. We therefore present here two extreme alternatives, aimed to illustrate, in a highly schematic form, a specific instance where the local and global models make clearly distinguishable and testable predictions.

The two alternatives are depicted in Fig. 1 which outlines central neuronal activation events that are predicted under the local vs. global alternatives. Note that these are highly idealized illustrations – aimed to highlight the extreme end-points of the local–global spectrum. The figure illustrates the contrast in the predictions of the two models in regard to the difference between passive viewing conditions – in which no overt introspective or motor act is required (illustrated by an eye icon in Fig. 1) and active viewing conditions – in which participants are asked to explicitly decide and report the content of the visual stimulus (illustrated by a button press icon).

The common framework, based on ample EEG data, underlying both local and global models, entails a three stage process that is initiated when a person perceives a visual image (see, e.g., Del Cul et al., 2007). These stages include early bursts of high activity occurring at ~100 ms and associated with early, retinotopic, visual cortex activations (EVA, light blue[1] curves in Fig. 1). The activations are then followed by a high activity burst at ~200 ms localized to high order, content-specific visual areas (HVA, dark blue curves in Fig. 1). Finally, there is a third peak of activity, occurring at ~300 ms. This high activity peak has been termed "global ignition" (Del Cul et al., 2007) and is suggested to engage a wide-spread global network of fronto-parietal cortical areas – the so called "global work space" (GWS, Baars, 1997, 2002; Dehaene, Changeux, Naccache, Sackur, & Sergent, 2006).

Within this common framework the local and global models differ in two critical aspects. First, local models do not predict a mandatory late (~300 ms) fronto-parietal activation during the passive viewing condition, while global models predict a high magnitude and wide-spread activation during this time. This is not a mere technical point, the difference stems from a fundamental disagreement in assumptions. While according to local models, neural correlates of visual perception per se begin and end in the visual cortex, the global models' view is that the visual cortex activation is just a preparatory stage, and a second, separate, global event is necessary for a conscious visual percept to emerge.

It is important to clarify at this point that local models by no means preclude the possibility of fronto-parietal activation during passive viewing conditions; they only argue that this activity is not *mandatory* for the emergence of the content-specific visual percept. Thus, one can envision a quite likely scenario in which even when perceiving a visual stimulus under passive conditions, such percepts may elicit, even involuntarily, non-visual cognitive events such as working memory encoding, naming and other linguistic associations and attentional effects. Such processes may inevitably activate non visual representations, even under the strictest passive viewing conditions.

However, according to local models, these activations reflect a different subjective content from that of the visual percepts and should be viewed as consequences of it. This, potentially tight, link between visual perception and subsequent processes poses a serious methodological challenge when attempting to disentangle the representations of visual content from these post-processing stages (see Malach, 2007). Fortunately, as will be shown below, there are certain experimental conditions in which activations related to visual perception can be disentangled from those associated with post-perceptual cognitive events.

A second difference between local and global models concerns the change in signals associated with the addition of a report component to the visual percept. Local models predict a significant increase of activation in the global 300 ms component when moving from passive viewing to active report, while global models do not predict additional large scale increases. This difference stems from the assumption of local models that the subsequent (300 ms) fronto-parietal activation does not reflect the visual percept itself, but rather subsequent non-visual aspects such as semantic processing or motor preparation and hence should be selectively activated when such post-visual processes are recruited during active report.

[1] For interpretation of color in Fig. 1, the reader is referred to the web version of this article.