

Toward Unmasking the Dynamics of Visual Perception

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Fisch et al. report in this issue of *Neuron* the results of an investigation of the neural correlates of conscious perception. They find an early, dramatic, and long-lasting gamma response in high-level visual areas, when (and only when) a rapidly presented image is perceived.

Subjective feelings and percepts emerge from the activity of neuronal circuits in the brain. While most would agree with this statement, much less agreement can be reached regarding the mechanisms responsible for subjective sensations. The “where,” “when,” and particularly “how” of the so-called neuronal correlates of consciousness constitute an area of active research and passionate debate (Koch, 2005). Historically, many neuroscientists avoided research in this field as a topic too complex or too far removed from what we understood to be worth a serious investment of time and effort. In recent years, however, this has begun to change: while we are still very far from a solution, systematic and rigorous approaches guided by neuroscience knowledge are making progress toward understanding these most complex cognitive functions. In this issue, Fisch et al. (2009) report exciting results pertaining to the locus and timing of neural activity that may give rise to a conscious visual percept.

Due to practical reasons, the underpinnings of subjective perception have been particularly (but not exclusively) studied in the domain of vision. There have been several heroic efforts to study the neuronal correlates of visual perception using animal models (e.g., Leopold and Logothetis, 1999; Macknik, 2006, among many others). A prevalent experimental paradigm involves dissociating the visual input from perception. For example, in multistable percepts (such as the well-known Necker cube illusion), the same input can lead to two different percepts. Under these conditions, investigators ask which neuronal events correlate with the alternating subjective percepts. It has become clear that the firing of neurons in many parts of

the brain may not be correlated with perception. In a perhaps trivial example, activity in the retina is essential for seeing, but the perceptual experience does not arise until several synapses later, when activity reaches higher stages within visual cortex. Several neurophysiological studies suggest that there is an increase in the degree of correlation between neuronal activity and visual awareness at progressively higher levels of ventral visual cortex (Leopold and Logothetis, 1999; Macknik, 2006). Neurophysiological, neuroanatomical, and theoretical considerations suggest that subjective perception correlates with activity occurring after primary visual cortex (Koch, 2005; Leopold and Logothetis, 1999; Macknik, 2006). Investigators have similarly suggested an upper bound on the circuits involved in subjective perception. Lesions in the hippocampus and frontal cortex (which are thought to underlie memory and association) yield severe cognitive impairments, but these lesions seem to leave many aspects of visual perception largely intact. Thus, the neurophysiological and lesion studies seem to constrain the problem to the multiple stages involved in processing visual information along the ventral visual cortex.

To interrogate the neural circuits involved in visual perception, Fisch et al. used a technique called backward masking. Masking has been used to control the visibility of stimuli in behavioral studies since the early 20th century. The basic idea is that when two images are shown in rapid succession, one of the images may influence perception of the other image. In the case of backward masking, a mask is presented shortly after the stimulus under study. Depending on the nature of the mask and, in particular, on the time interval between stimulus and

mask, perception of the first stimulus may be severely impaired or even completely eliminated. The possibility of controlling perceptual visibility has interested several neurophysiologists in examining the neuronal responses during masking (for a review, see Macknik, 2006). Single-unit recordings in monkey inferotemporal cortex (IT) have shown that masked stimuli that are not perceived can still drive selective responses in high-level visual areas, though the duration and amount of information carried are both decreased (Kovács et al., 1995; Rolls et al., 1999).

It is possible to study neurophysiological activity at high spatiotemporal resolution in animal models, but it is not always easy to access the subjective state of the animals. While the subjective state of humans is comparatively easier to evaluate, current noninvasive tools offer poor spatial and/or temporal resolution. Patients who have electrodes implanted for clinical reasons offer a rare opportunity to study physiological activity in the human brain at high spatial and temporal resolution (Engel et al., 2005; Kreiman, 2007). Depth electrodes, as well as subdural grid and strip electrodes, are routinely implanted in patients with intractable epilepsy in preparation for surgical resection of epileptic foci. Neurophysiological recordings in awake patients offer a window of opportunity to localize and characterize the dynamics of the neural activity underlying cognitive events at millisecond resolution, the relevant timescale involved in visual perception.

The high temporal resolution of these recordings enables investigators to interrogate the different temporal rhythms observed in brain activity, some of which have been associated with cognitive processing. These rhythms were first noted

in scalp electroencephalograms, and have since been observed using a variety of electrophysiological techniques. One such example is the power in the gamma band of the frequency spectrum (typically defined as a band around 40 Hz). Several neurophysiological reports have observed gamma rhythms that are modulated by attentional demands and cognitive tasks (e.g., [Womelsdorf et al., 2006](#), among many others). Modulation in the gamma band of the spectrum has also been observed in recordings in epilepsy patients with implanted electrodes. For example, increases in gamma power over widespread regions of cortex were observed when patients performed a task in which they had to identify masked and unmasked words ([Gaillard et al., 2009](#)). These increases vanished quickly for masked words, but persisted for several hundred milliseconds when words were unmasked and therefore identifiable.

In this issue of *Neuron*, Fisch et al. used a backward masking paradigm to inquire about the timing, location, and nature of neural responses correlated with conscious perception. They presented subjects implanted with subdural electrodes with images of faces, houses, and man-made objects, followed by a mask. Subjects were asked to identify verbally which of those three categories described the image or to indicate that they could not tell. The delay between the image and the mask was in most trials set at a point where the subject's correct categorization performance was close to 50%. Under these conditions, Fisch et al. were able to compare neural responses to stimuli that were in every way very similar but gave rise to very different conscious perceptual experiences. As reported in other studies, they found many visually responsive electrodes over visual cortex ([McCarthy et al., 1999](#); [Liu et al., 2009](#)). In addition to changes in the overall power of the response, they observed that these electrodes recorded significant increases in gamma power (defined in this study as the band between 30 and 70 Hz) within 250 ms of stimulus onset. They restricted the bulk of their analyses to electrodes that showed significantly higher gamma power in response to at least one of the three stimulus categories as compared with the response to control trials in which only a mask was shown. This allowed them to focus on the visual

responses to the experimental stimuli rather than responses to the masks. All of these category-selective electrodes were located over brain regions known to be important for high-level vision.

The key comparison in terms of correlating the neural responses with subjective perception involved comparing trials with the same stimulus category but different recognition performance—that is, comparing those trials that yielded recognition versus those trials that failed to elicit recognition. While the stimuli were not identical in these two conditions, the category-selective electrodes tended to show similar responses to the different exemplars of a given category. The majority of target-selective electrodes showed increases in gamma power in recognized trials when compared with unrecognized trials. Interestingly, these differences started early: they were detected in the population analysis as early as 90 ms after stimulus onset. This rapid onset is as fast as the earliest visually selective responses in macaque IT neurons (e.g., [Logothetis and Sheinberg, 1996](#)) or human temporal lobe recordings ([Liu et al., 2009](#)). The increase in gamma power in recognized versus unrecognized trials lasted several hundred milliseconds.

Fisch et al. describe these results as consistent with a model in which visual input leads to reverberatory activity in higher-level visual areas. This reverberatory activity “ignites” after a short buildup into a prolonged period of strong neural activation, giving rise to the observed increase in gamma power. The authors propose that this change in gamma band power could underlie conscious visual perception. A mask shortly after stimulus presentation could interrupt that reverberatory process and prevent ignition, and thus perception. In those trials where the mask failed to interrupt the information flow, areas downstream from these late visual areas would receive the message of what was seen, then process and interpret those messages—perhaps giving rise to the late gamma activity noted in many brain regions by [Gaillard et al. \(2009\)](#) in their masked word-recognition task.

This study highlights a variety of important questions. What are the neuronal circuits, neuronal cell types, and mechanisms underlying these gamma oscillations? What are the minimal conditions that are necessary and sufficient to trigger

the type of reverberatory activity described in this study? Are the observed gamma oscillations necessary for perception? To examine further the role of gamma band frequencies, it would be of interest to disrupt the gamma activity patterns (without affecting the rest of the network, to the extent that this is possible). Exciting new developments using a combination of high-resolution imaging, electrophysiology, and molecular biology promise to make progress in this direction ([Cardin et al., 2009](#); [Han et al., 2009](#)). The elegant work of Fisch et al. provides concrete and testable hypotheses about the spatial and temporal location of neural events involved in perception. As our knowledge and our tool sets grow, we grow ever closer to a basic understanding of the nature of subjective human experience.

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