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Investigating Neural Correlates of Consciousness with Ambiguous Stimuli: Commentary by Jeffrey D. Schall (Nashville, TN)

In the target article Crick and Koch explore the premise that a neural correlate of consciousness can be discovered by finding neural activity related to high level (Marr's 2½D or 3D sketch) representations of stimuli. While this is certainly important information, it is not self-evident that this approach provides the necessary leverage on the question. Neurons can respond to complex stimulus properties and arrangements and still have nothing at all to do (directly) with awareness of that stimulus. Evidence for this is the fact that neurons responding to faces are still active and selective under anesthesia (e.g., Gross, Rocha-Miranda, and Bender, 1972). The logical link that a sufficiently high level neural representation correlates with consciousness—or more precisely visual aware-

ness—depends on the premise that it is that level of representation of which we seem to be aware. This may be true and skepticism should not prohibit further investigation along these lines. But I would like to review briefly a more direct path to neural correlates of consciousness, of which Crick and Koch are certainly already aware (e.g., Crick and Koch, 1998).

Determining how the activity of neurons relates to behavior and inferred cognitive states requires an experimental strategy of dissociations. For example, separating in time the presentation of a stimulus from the time of a motor response allows a neurophysiologist to distinguish neural processes related to sensory processing from neural processes related to response production. To investigate neural correlates of consciousness—or more particularly visual awareness—one needs to dissociate the presentation or appearance of a stimulus from awareness of that stimulus. In other words, the neural correlates of visual

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Acknowledgments. Research support provided by the National Eye Institute and the McKnight Endowment Fund for Neuroscience.

awareness can be discovered by creating the condition of “now you see it, now you don’t.”

Nikos Logothetis and I employed that strategy in our original investigation of the neural responses in the middle temporal (MT) visual area associated with visual awareness (Logothetis and Schall, 1989). Macaque monkeys viewed stimuli that induced binocular rivalry. Binocular rivalry is a perceptual alternation that happens when the stimuli presented to the two eyes are so different that they cannot be fused (reviewed by Blake, 1989). We found that many neurons responded according to the properties of the stimuli and had no unique relation to the perceptual state inferred from the behavioral report. These neurons appeared to be coding the stimulus on the retina. However, we observed a fraction of neurons that discharged according to what the monkeys reported seeing. These neurons represent not just the properties of the stimuli on the retina but the properties of the stimulus perceived by the monkey. This finding was the first explicit demonstration of neural activity related to visual awareness as opposed to stimulus properties.

In subsequent work Logothetis and his colleagues have investigated the responses of neurons in other visual areas. In visual area V4, which represents an intermediate level of processing like area MT, they found a similar fraction of neurons as we found in area MT related to the monkeys’ perceptual report. However, a much smaller fraction of neurons correlated with monkeys’ perceptual report was observed in primary visual cortex (Leopold and Logothetis, 1996). In contrast, effectively all of the neurons in the high level areas of the temporal lobe that represent complex objects like faces were correlated with monkeys’ perceptual report (Sheinberg and Logothetis, 1997). This body of results is generally consistent with the premise of the target article, neurons at a level of the visual pathway that represent complex objects are more likely to be correlated with visual awareness than are neurons at lower levels of the visual pathway that represent more elementary features of visual objects. In fact, Crick and Koch (1995) have argued that no activity in primary visual cortex is correlated with visual awareness. Recent data from an fMRI study of binocular rivalry indicate that this conclusion may require reconsideration (Polonsky, Blake, Braun, and Heeger, 1999). Whatever the outcome, though, this level of inquiry represents the kind of advanced empirical discussion of neural correlates of consciousness that has been absent until the last 10 years.

Now, binocular rivalry is just one way of dissociating stimulus presentation from awareness, and it is important to learn whether these conclusions about the relations of neurons to visual awareness are not unique to the conditions of binocular rivalry. Another method that can dissociate perception from presentation of a stimulus is masking (reviewing by Breitmeyer, 1984). Kirk Thompson and I have employed backward masking to investigate neural activity related to the perception during backward masking (Thompson and Schall, 1999, 2000). We carried out our study in an area of prefrontal cortex called the frontal eye field that converts the outcome of visual processing into a command to move the eyes (reviewed by Schall, 1997).

In the backward masking paradigm the ability to detect a dim target stimulus, which is perfectly visible if presented alone, is impaired when the target is immediately followed by a bright masking stimulus. The strength and timing of the target and mask stimuli can be adjusted so that a particular physical stimulus condition can result in mutually exclusive perceptual reports, either the presence or the absence of the target. A human observer in a backward masking experiment will report that on some trials the masked stimulus was seen (referred to as Hits) and on others it was not seen (referred to as Misses). As an experimenter we know that the physical conditions on both sets of trials were not measurably different. So the different perception and performance arises from difference in the brain.

Thus, it appears that masking provides the same dissociation as binocular rivalry. However, previous studies with masked stimuli have concluded that motor responses can be directed to stimuli without visual awareness (Merikle, 1992) or that awareness indexed by verbal reports arises after a manual movement is initiated (Castiello, Paulignan, and Jeannerod, 1991; MacIntyre and McComas, 1996). However, it is important to understand that the design of our experiment was fundamentally different from that of earlier studies that reported localization without detection in three key ways. First, we provided feedback after every trial. Second, the inclusion of trials on which no target appeared provided the option of reporting the absence of a target. Third, the interval between the target and the mask was continuously adjusted in a staircase procedure. These procedures led to an elevated response criterion because feedback was given, guessing was discouraged, and the difficulty of the task was adjusted according to performance. Accordingly, for monkeys to respond that the target was present, the sensory

evidence had to reach higher levels. Our conclusion is that under the conditions we employed, the behavioral report was a reliable indicator that the monkeys had some kind of more or less distinct perceptual experience related to target detection.

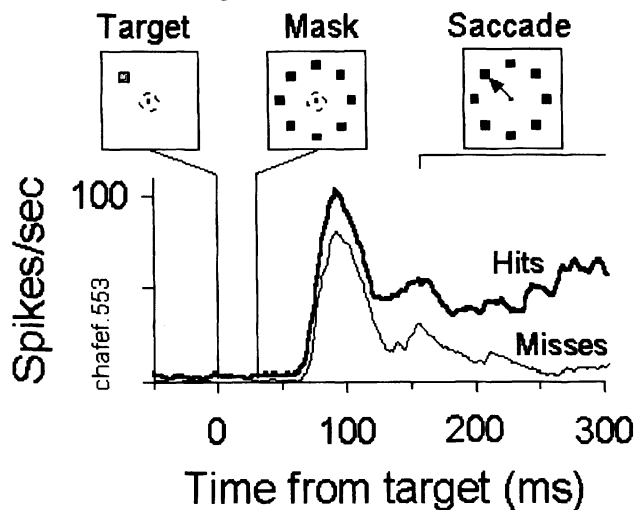


Figure 1. FEF visual selection during visual backward masking. The average firing rate obtained from one visually responsive frontal eye field neuron during hits (thick) and misses (thin).

Figure 1 illustrates one of our findings. The figure shows the average activity of a visually responsive neuron in the frontal eye field on trials when the target was presented and the monkeys reported detecting it (Hits) and on trials when the target was presented but the monkeys did not report it (Misses). Two differences are evident. First, the initial visual response was slightly higher when the masked target was detected. Second, the activity when the target was detected was elevated after the response to the mask until the behavioral response. Several lines of evidence indicate that the selective prolonged activation observed in these neurons in frontal eye field should not be regarded as a motor command (Thompson and Schall, 2000).

In the target article Crick and Koch write that the neural correlate of consciousness “involves a very specific set of neurons that are active in some special way . . . distinguished from all other neurons by . . . particular strong type of synaptic interconnection, unique cellular morphology . . . some privileged cellular property.” The neurophysiological experiments I have reviewed suggest that such unique properties may not be necessary. The only privilege neurons correlated with visual awareness need have is that they stand in a particular relation through functional connections to other parts of the brain such as sensory and motor structures. The reconstructions we have done of physiological recording sites in FEF indicate that vi-

sual neurons that participate in visual selection are located in upper and lower layers (see Thompson, Hanes, Bichot, and Schall, 1996). It is possible if not likely that the visual neurons with the selective post-mask response are the pyramidal cells that project to visual areas.

Several lines of research have suggested that neural activity must be of a sufficient magnitude and duration to be related to awareness (e.g., Libet et al., 1991; Ray et al., 1999). If we accept that there is such a thing as visual awareness and that it requires a sufficient magnitude and duration of activation, then we may ask whether the different phases of activation observed in frontal eye field meet the criteria. The difference in the initial visual response is too small and too brief to be a neural correlate of awareness according to these criteria. However, the prolonged activity before the saccade in Hit trials does meet the criteria; it is long enough (~100 msec) and large enough (at least large enough to correlate strongly with behavioral report/eye movement).

The data from visual cortex during binocular rivalry show a neural correlate of the awareness of a particular stimulus—we may say that the neural activity corresponds to the contents of awareness. But another question is how does a particular representation in visual cortex that can be the contents of awareness gain that explicit level of representation? This forces us to distinguish the neural correlate of the contents of awareness from the neural process by which the representation enters awareness. The data I have reviewed invite the speculation that activity in prefrontal cortex feeding back onto extrastriate visual areas may be a critical step in raising the level of activation of one of the competing interpretations of the image sufficient to make that representation the interpretation that will guide action and be the contents of awareness. In other words, the hypothesis is that some small difference in activation arising from an ambiguous stimulus is amplified by frontal cortex through reciprocal connections with extrastriate visual cortex in relation to generating a response.

The goal of this commentary was to indicate the kind of empirical data that can provide rich, new insights into neural correlates of consciousness. To make progress on this question, we must accept the premise that there is such a thing as visual awareness. However, we should recognize that such a concept is not required by present models to explain the behavioral detection of signals. If this is so, then the concept of awareness may succumb to Occam’s razor. Nevertheless, we should remember William James’s adage:

“Occam’s razor, though a very good rule of method, is certainly no law of nature.”

The continued use of experimental dissociations like binocular rivalry and masking is certain to put neural flesh on philosophical bones, but it is not a one-way street. The intelligent interpretation of the neurophysiological data will require more sophisticated and self-consistent concepts which philosophers can help provide. Nothing but time and research resources prevent us from learning more about where neurons correlated with consciousness are located, how they are connected, and how they are active in an extended variety of conditions. Such information should permit us to translate philosophical speculations into scientific hypotheses.

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