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The High and Low of Visual Awareness

What specific network of neural activity mediates awareness? In this issue of *Neuron*, Wilke et al. report psychophysical results showing that perturbations of early topographic visual areas can lead to all-or-none image disappearance, demonstrating the importance and versatility of low-level visual processing in controlling visual awareness.

Suppose a bright red disc appears near fixation. What does it take to see it? When this question is restated in terms of what neural activity is essential for seeing the disc, the answer becomes elusive. Certainly, the light pattern from the red disc must sufficiently stimulate retinal cells so that their activity is raised significantly above baseline. What else is required?

Cells in the primary visual cortex (V1) may be particularly important—individuals with V1 lesions assert that they do not see anything when objects stimulate retinal regions corresponding to the lesioned parts of V1. Some inputs bypass V1, sending direct signals to higher visual areas such as V3, V4, IT (inferotemporal cortex), and MT (middle temporal area). Though these connections may allow V1 lesioned individuals to respond appropriately to “unseen” stimuli and perform above chance on forced-choice pattern discriminations (“blindsight”), they do not support normal experiences of seeing (see Lamme, 2001, for a review).

Sufficient activation of V1 might thus be necessary for visual awareness. V1 lesions substantially decrease activity in the ventral visual pathway (e.g., V2, V4, and IT) thought to mediate object perception. Thus, activation of higher areas through connections bypassing V1 might be too weak to enter visual awareness. Would sufficient activation of higher visual areas support awareness in the absence of V1 activity? Ideally, an isolated contribution from each area should be assessed by brain stimulation studies in which normal feedforward inputs to each area are simulated without concurrent activation of lower areas. At present, neuropsychological results (from humans and monkeys with lesions in different

brain areas) suggest that no single visual area is both necessary and sufficient for visual awareness (see Lamme et al., 2000, for a review).

An alternative to seeking “the locus” of visual awareness is to characterize visual awareness as a global state of neural activation. Intuitively, it seems that attended stimuli that induce strong feedforward activations in multiple visual areas should enter awareness. Apparently, when the sensory activation of the visual system is diminished by reducing image contrast, the pattern becomes less perceptually salient and eventually disappears at sufficiently low contrasts. Interestingly, however, recent results by Wilke et al. (in this issue of *Neuron*) and Bonnef et al. (2001) suggest that (1) strong retinal stimulation does not necessarily translate to visibility and (2) substantial contributions to awareness come from low-level codings that are dissociated from activation strengths.

Bonnef et al. demonstrated that attended salient shapes spontaneously and intermittently disappeared, for several seconds at a time, when presented against a background of moving dots (which never overlapped the shapes)—termed motion-induced blindness (MIB). Rather than gradual dimming and brightening, disappearances and appearances of the shapes were all-or-none. Crucially, reducing the luminance contrast of the shapes, thereby reducing neural responses to the shapes in low-level visual areas, did not increase their disappearance. Disappearance of multiple shapes was also influenced by similarity-based grouping. Bonnef et al. thus concluded that MIB was mediated by neural suppression in high-level visual areas. They attributed the potency of moving dots in extinguishing high-contrast shapes to “sensory dissociation” induced within the visual inputs (due to the co-existence of static and dynamic patterns), which shifted the visual system into an all-or-none competition mode. They noted that this idea was consistent with binocular rivalry, in which sensory dissociation induced by presenting a dissimilar image to each eye causes the percept to alternate exclusively between the two images (see Blake and Logothetis, 2001, for a review).

Wilke et al. discovered that when a target shape was presented first and then followed (a fraction of a second to seconds later) by the addition of background dots, the onset of the background dots caused the attended salient shape to disappear. Though an onset of moving dots was the most potent in extinguishing the target, an onset of static dots or a color change of the pre-existing dots were also effective. Because a disappearance could be attributed to the stimulus manipulation in each trial, this new paradigm, which Wilke et al. termed “generalized flash suppression (GFS),” allowed detailed psychophysical investigations of the stimulus factors that influenced perceptual disappearance of a salient shape. Whereas the properties of MIB implicated suppression in high-level processing as the primary cause of pattern disappearance, Wilke et al. demonstrated that subtle perturbations of early topographic visual areas contributed substantially to the disappearance.

For example, presenting the target in both eyes rather than in only one eye reduced target disappearance, whereas presenting the background dots in both eyes increased target disappearance. Apparent contrast should

have been greater with the both-eye presentation due to binocular summation. However, because contrast reduction did not facilitate target disappearance in MIB (not reported for GFS), the both-eye benefit is unlikely to be due to increased activation in low-level visual areas, but rather due to an alternative means of emphasizing coherent signals from both eyes as "reliable." Furthermore, when both the target and background dots were presented in one eye, target disappearance was much greater when they were presented in different eyes, consistent with Bonnef et al.'s speculation that sensory dissociation facilitates pattern disappearance.

By using concentric rings as the target, Wilke et al. also showed that the delay of disappearance of an inner ring (relative to disappearance of an outer ring) was monotonically related to the difference in diameter between the two rings. This indicated that disappearance progressed in a wave-like manner, implicating neural interactions in early topographic visual areas.

Finally, target disappearance depended on (at least) several hundred milliseconds of adaptation to the target shape prior to presentation of the background dots. Significantly, this adaptation was position and orientation specific, demonstrating that brief adaptation in low-level topographic visual areas was crucial for target disappearance. Because such brief adaptation minimally influences apparent contrast and reduced contrast did not facilitate target disappearance in MIB, these brief adaptation effects are unlikely to be due to reduced activation in low-level visual areas, but rather due to an alternative means of de-emphasizing outputs of the adapted cells as "already seen and to be ignored."

Wilke et al.'s results are significant because they imply that processes in high-level visual areas such as IT where neural responses reflect perceived shape (e.g., Baylis and Driver, 2001) and where strengths of activity tend to mirror subjective pattern visibility (at least during binocular rivalry; e.g., Sheinberg and Logothetis, 1997) can be substantially influenced by low-level processes in ways other than by the strengths of low-level neural activity. The latter point was verified by Wilke et al.'s neurophysiological finding that many V1 neurons responded to perceptually extinguished targets in the GFS paradigm. An intriguing possibility is that early visual areas might tag various incoming visual inputs according to their reliability (e.g., coming from only one eye or from both eyes), history (e.g., old or new), and other yet-to-be-discovered principles, substantially influencing competitive interactions occurring in high-level processing (e.g., Wang et al., 2000). Such tagging might be based on temporal patterns of neural activity (e.g., Lumer, 1998; Suzuki and Grabowecky, 2002). Because activity strength in V1 is correlated with image contrast and perceived brightness (e.g., Rossi et al., 1996), the ability of early visual areas to influence visual awareness independently of their activation strengths might be behaviorally significant. For example, it may allow (1) selection of potentially important portions of a scene into awareness regardless of contrast, (2) selection of novel features independently of contrast (activation strength can reduce due to lowered contrast or due to adaptation, confounding contrast level and old-new status), and (3) control of the content of visual awareness without distorting brightness perception.

The richness of visual awareness should also be considered beyond seeing or not seeing. For example, when looking at a gray disc, one is aware of its shape as well as its shade of gray. Because low-level neural activity is correlated with perceived brightness whereas high-level activity (such as activity of form-tuned cells in IT) is relatively independent of image contrast, the full visual awareness of the gray disc should depend on neural activity at both levels. Wilke et al.'s results suggest that losing the high-level activity makes the continuing low-level activity (still signaling the shade of gray) unavailable to awareness. When relevant visual areas are nonhierarchical (e.g., ventral and dorsal pathways), however, their processes can be extinguished from awareness independently. For example, when the form of a moving pattern was extinguished from awareness (in binocular rivalry), its motion still entered awareness (Andrews and Blakemore, 1999). Therefore, it is likely that multiple visual areas make unique contributions to the richness of visual awareness and that reentrant neural activity from higher to lower visual areas makes an important contribution (e.g., Lamme et al., 2000; Lamme, 2001).

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