Cross-modal attention enhances perceived contrast

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In this issue of PNAS, Störmer, McDonald, and Hillyard (1) investigate the neurophysiological basis of phenomenological experience, probing a central question in perception: Does attention alter our subjective experience of the world? Their study is the first to show converging evidence from human electrophysiology and behavior indicating that attention alters appearance.

Visual Attention

Each time we open our eyes, we are confronted with an overwhelming amount of information. How is it possible, then, that we still have a strong impression that we understand what we see? Visual attention is the mechanism that turns looking into seeing, allowing us to select a certain location or aspect of a busy visual scene, and prioritize its processing. Such selection is necessary to mediate between the torrent of information in our visual world and our severely limited capacity to absorb visual information—a limitation imposed by the fixed amount of energy consumption available to the brain and by the high energy cost of cortical computation. Attention helps optimize the use of our system's limited resources by enhancing the representation of the relevant locations or features while diminishing the representation of irrelevant information in our visual environment (2–5).

Visual attention can be covertly deployed, without eye movements (2–6). Humans use covert attention routinely in everyday situations, when they search for objects, drive a car, cross the street, play sports, or dance, as well as in social situations—for example, when moving the eyes would provide a cue to intentions that one wishes to conceal. There are two types of covert attention: voluntary and involuntary. Voluntary attention refers to the sustained, endogenous directing of attention to a location in the visual field. Involuntary attention is the transient, exogenous capture of attention to a location, brought about by a sudden change in the environment (2–4). Attention improves performance on many detection, discrimination, and localization tasks that rely on basic dimensions of early vision such as contrast sensitivity and spatial resolution. Moreover, attention has been shown to increase neural activity in early visual areas in a retinotopically specific fashion (4, 5).

Does Attention Alter Appearance?

Psychologists, physiologists, and philosophers alike have debated the phenomenology of attention for over a century: Does attention alter our subjective experience of the visual world? Do we experience attended objects differently from unattended objects? Which aspects of our visual experience does attention affect? Can attention make a visual pattern seem more detailed, or a color more vivid? The phenomenology of selective attention was a subject of debate among pioneers in experimental psychology, such as Mach, Fechner, von Helmholtz, Wundt, and James (6–8). Much of the early work on this topic was introspective, and conflicting conclusions were often drawn from such subjective methods of investigation. For instance, whereas Fechner believed that attention does not alter sensory impressions, Helmholtz (6) and James (7) claimed that attention intensifies sensory impressions. On this disagreement, James concluded: "The subject is one which would well repay exact experiment, if methods could be devised" (ref. 7, p. 426).

Attention augments perception by optimizing our representation of sensory input.

Psychophysical Studies

Whether and how attention affects appearance is an issue that scientists have only just begun to investigate systematically. This may be due to the difficulty in objectively testing and quantifying the subjective experience of perceived stimuli and changes in such experience with attention. Recently, a psychophysical paradigm has been developed to assess the phenomenological correlate of involuntary attention (9), making it possible to study subjective experience more objectively and rigorously (10, 11). This paradigm quantifies the observer's subjective perception by using a task contingent upon a comparative judgment between two stimuli on a particular feature. To investigate the effects of attention on the perceived contrast of a stimulus, observers are presented with two tilted sinusoidal gratings, one to the left and one to the right of fixation, and asked to report the orientation of the grating of higher contrast. The critical manipulation is that observers are not asked to rate their subjective experience of the stimulus contrast, but to make a decision about the stimulus orientation. On each trial, one of the gratings is of a particular fixed contrast, whereas the contrast of the other grating varies. In some trials, an uninformative peripheral cue grabs involuntary attention toward one of the two stimuli. Observers are told that the peripheral cue has an equal probability of appearing either to the left or right of fixation and adjacent to the higher- or lower-contrast stimulus. This eliminates the possibility of observers giving more weight to the information at the cued location and hence a decisional explanation for an attentional effect. In addition, this procedure allows simultaneous measurement of the effects of attention on both performance and appearance. By computing the contrast that is necessary for the attended stimulus to match the apparent contrast of the unattended stimulus, this paradigm allows one to measure the change that attention effects on the perceived contrast of a stimulus. This paradigm, coupled with control experiments, has ruled out alternative cue bias and response bias explanations (9, 12–18).

Using this paradigm, studies have shown that exogenous attention alters our subjective impression of many dimensions of spatial and temporal vision: e.g., contrast (9, 12–14), spatial resolution (15), color saturation (16), size of moving patterns (17), and speed (18). However, the issue continues to be debated (19, 20). Schneider (19) reported that peripheral cues increase perceived brightness only at levels near detection threshold, more so for white than black cues. Based on the interaction of sensory factors, he predicted that reversing the cue's luminance polarity should lead to differential cueing effects on contrast. However, testing this prediction revealed that both black and white cues increased the apparent contrast to the same de-

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gree, thus confirming that the cue effect is due to attention, not to sensory factors (12).

Electrophysiological Evidence

Störmer et al. (1) modified this paradigm in two insightful and exciting ways to investigate the effect of attention on appearance with concurrent electrophysiological and behavioral measures. First, to eliminate any possibility of intramodal sensory interactions between the cue and the stimulus, they used a lateralized auditory cue rather than a visual cue. This modification enabled the authors to study the effects of cross-modal attention on appearance. Second, they recorded evoked electrical fields on the scalp—event-related potentials (ERPs)—from visual cortex in response to the cued target as observers judged the relative contrast of visual stimuli presented to the right and left visual fields. ERPs are electrophysiological responses that arise during sensory, cognitive, and motor processing, which provide precise information about the time course of information processing. In this study, they help pinpoint the level of processing at which attention exerts its effect on judgments of contrast appearance. Short-latency evoked responses, P1 (90–150 ms) and N1 (180–240 ms), reflect early sensory processes that can be modulated by selective attention; longer-latency components (250–500 ms) arise from multiple cortical generators and reflect postperceptual processing, including decision-making, working memory encoding, and response selection.

In the Störmer et al. study (1), cross-modal spatial cueing of attention increased perceived contrast of the stimulus at the attended location concurrent with an amplified neural response in the contralateral visual cortex. Specifically, cueing attention to one of two identical stimuli boosted early processing (100–140 ms) of the attended stimulus in the ventral occipitotemporal visual cortex. Moreover, the amplitude of the enhanced neural response correlated positively with the perceived contrast of the cued stimulus, which provides converging evidence that contrast appearance arises from early cortical processing of visual stimuli. Crucially, the cueing of attention enhanced neural processing in the same ventral regions of the visual cortex, which, as the authors confirm, are responsive to physical differences in contrast. These results are consistent with the proposal that attention increases perceived contrast by boosting early sensory processing in visual cortex (9, 12–14), and they contradict the hypothesis that the effect of attention is due to a decisional bias (20).

Attention Alters Appearance

The appeal of visual attention and the attraction toward its study might be related to the puzzling observation that changing an observer's internal attentional state while keeping the retinal image unchanged can have dramatic effects on "sensory" neurons throughout the visual cortex and on perceptual performance and appearance. Adding to the appeal is the enticing possibility that attention may provide a link with the constructs of awareness and consciousness.

Progress in understanding visual attention is undoubtedly due to the integration of information gained from various techniques—psychophysics, neurophysiology, neuroimaging, and computational modeling. The study by Störmer et al. (1) exemplifies how converging evidence from different approaches furthers our understanding of the mechanisms of visual attention. Their finding that attention concurrently increases early cortical processing of visual stimuli as well as perceived contrast provides evidence in support of the claim that changes in appearance attributable to attention are the consequence of the neural mechanisms underlying preferential processing. This idea has been advanced as a "linking hypothesis" stating that the increased neuronal firing attributable to attention is interpreted as if the attended stimulus is physically of higher contrast (5, 6, 11). This notion of sensory gain has been supported by evidence from neurophysiology, psychophysics, neuroimaging, and modeling.

Bridging Physiology and Perception

The visual system operates on the retinal image so as to maximize its usefulness to the perceiver, often producing nonveridical percepts. The visual system does not provide an internal one-to-one copy of the external visual world; rather, it optimizes processing resources. Attention is a pervasive example of this perceptual optimization: attention augments perception by optimizing our representation of sensory input and by emphasizing relevant details at the expense of a faithful representation (4, 11, 14). By providing converging evidence from human electrophysiology and behavior, Störmer et al. (1) demonstrate that the enhanced perceived contrast at the cued location is attributable to an effect of attention on early visual processing. They show how the biophysical machinery of the brain engenders our phenomenological experience of the world: attention, both intra-modal (9–18) and cross-modal (1), affects not only how we perform in a visual task but also what we see and experience.

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