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Research Focus

Perceptual enhancement of contrast by attention

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Allocating spatial attention to a visual stimulus or increasing stimulus contrast both enhance neuronal responses. In a recent study Carrasco *et al.* demonstrated that attention itself changes perceived contrast. Using an elegant experimental manipulation, they showed that the contrast of an attended stimulus was perceived to be higher than when the same stimulus was unattended. This provides evidence that the enhancement of stimulus salience observed in electrophysiological studies creates an enhanced perceptual representation of attended stimuli.

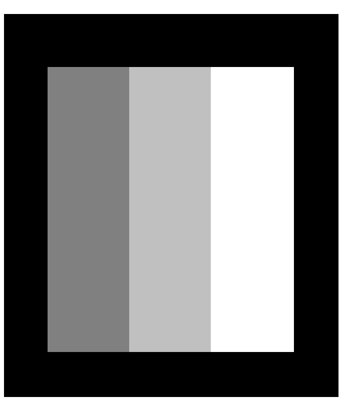
The visual system of humans and non-human primates is powerful. It endowes us with the ability to recover enormous details about our visual environment. Nevertheless, as a plethora of visual illusions demonstrates, it is far from accurate. Today we interpret many of these illusions not as an expression of the limits or failures of the visual system. Rather, they are the results of a highly developed and optimized representational process in which the visual system does not simply provide an internal one-to-one copy of the external visual world. Instead, the visual system is equipped with specific encoding mechanisms to optimize the use of precious processing resources by enhancing relevant features (e.g. see Figure 1) and providing only a sketchy representation of the less relevant aspects of our visual environment [1]. These sensory components of perception are augmented by attention, the process by which knowledge and assumptions about the world and the behavioral state of the organism influence the processing of sensory input.

A long history of psychophysical investigations of attention combined with a more recent surge of electrophysiological and brain-imaging studies have elucidated numerous such influences of attention [2], including enhanced neuronal [3,4] and behavioral sensitivity [5–7], improved discriminability [5] and spatial resolution [8,9], as well as accelerated information processing [10] and altered neuronal synchronization [11]. It is therefore quite surprising that virtually no hard data have been collected as to whether these attentional influences lead to a modified perceptual appearance of attended objects and aspects of the visual input.

Closing the gap between physiology and perception

This gap has now been closed by a recent study of Carrasco and her co-workers [12]. They used an elegantly simple design that avoided the limitations of previous attempts [13–15] to address this issue. Human subjects were presented with two gratings that appeared briefly (40 ms) and simultaneously on opposite sides of a central fixation point on a computer monitor. They were instructed to report which grating had the higher contrast and its orientation (tilted at either +45° or −45° from

(a)



(b)

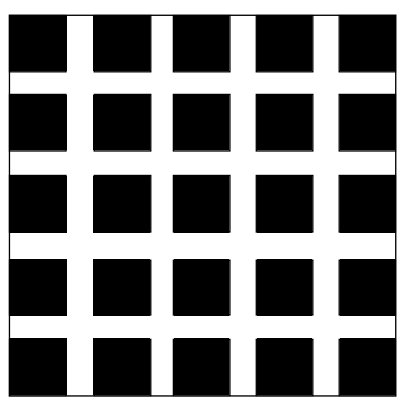


Figure 1. Illusions of apparent contrast: Mach bands and the Hermann grid. Two well-known examples of sensory effects on apparent contrast. **(a)** Mach bands: the apparent reduction in stimulus luminance at the dark side of an edge and the concomitant enhancement of apparent luminance on the bright side are thought to be the result of the antagonistic center–surround structure of the receptive fields of retinal ganglion cells. This mechanism serves to enhance the visibility of the edges, which are an inherently important component of all visual scenes. **(b)** The same explanation can be used to account for the appearance of small gray disks at the intersection of the white grid lines in the Hermann grid. These illusions are the sensory equivalents of the attentional illusion of enhanced apparent contrast observed by Carrasco *et al.* [12] (Figure 2). They probably reflect the visual system's effort to strengthen the representation or saliency of behaviorally relevant aspects of the visual environment. Both of these mechanisms achieve their goal by manipulating apparent contrast.

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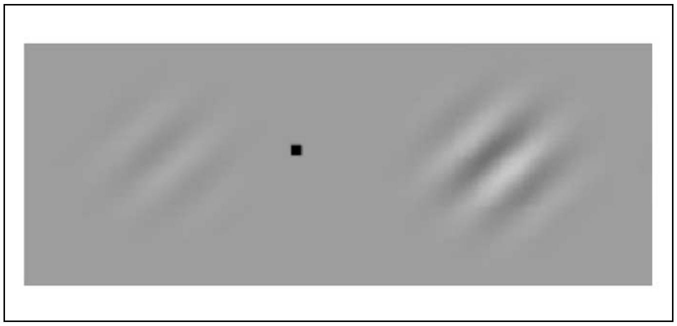

Figure 2. The contrast difference between the two gratings illustrates the effect of attention on apparent contrast. If subjects' attention is drawn to the left stimulus it appears to be of similar contrast as the (unattended) right stimulus. Note that this effect cannot be appreciated by inspecting the figure because any perceptual comparison between the two patterns will lead to equal allocation of attention to both of them. See text for details as to how Carrasco *et al.*'s [12] elegant design avoided this issue.

vertical), in a four-alternative forced-choice design. Before the appearance of the gratings a small dot (the 'cue') appeared and disappeared, either at the fixation point or at one of the sites of the upcoming gratings, although it was uninformative and subjects were told explicitly that the cue neither predicted the target location nor its orientation. Unbeknown to the subjects this cue provided the crucial manipulation to assess the influence of attention on stimulus appearance. The trials where the cue appeared at the fixation point provided the baseline measure of the subjects' contrast discrimination performance. The other trials served to draw the subjects' spatial attention reflexively towards the cued grating. If this allocation of attention enhances the perceived contrast of the cued grating then the subjects should report the orientation of this grating more frequently if both gratings had the same physical contrast. Similarly, at the point of subjective equality of the gratings, that is, when subjects reported each grating's orientation in exactly half of the trials, the uncued grating should be of (physically) higher contrast. This is exactly what Carrasco and her colleagues found. The allocation of attention boosted the apparent contrast of attended gratings of 3.5% and 16% contrast to that of unattended gratings of 8.5% and 28% contrast, respectively. Figure 2 illustrates this effect by showing a low-contrast grating on the left side that – if attended – would be perceived as having the same contrast as the stimulus on the right without attention.

With two control experiments the authors were able to rule out alternative accounts for their findings. In one control they increased the temporal separation between the cue and the gratings from 53 ms to 500 ms. This manipulation removed the contrast enhancement of the cued stimulus, an effect consistent with the quick decay of the involuntary allocation of attention to the cued location but inconstent with the possibility that subjects are simply biased to report the orientation of a cued stimulus *per se*. In the other control experiment subjects were asked to report which stimulus they judged to be of *lower* contrast. This manipulation caused subjects to select the cued stimulus less frequently if it was of the same contrast as the uncued stimulus, consistent with the enhanced apparent contrast of a cued stimulus observed in the main experiment. This control is important because it rules out the possibility that subjects simply report the orientation of a cued stimulus more often because they find its orientation easier to judge or are subject to some other type of cue bias.

Using sensory and attentional manipulations to generate an integrated saliency map

The study of Carrasco *et al.* completes a chain of findings providing important and far reaching insights concerning the interaction of attention and perception. This chain starts with data from neurophysiology indicating that varying levels of contrast create multiplicatively scaled tuning curves [16,17]. It continues with the recognition that attention similarly scales neuronal responses [3,4], that attention influences contrast gain mechanisms [18] and with further neurophysiological studies demonstrating that attentional modulation and changes in stimulus contrast create identical and therefore indistinguisheable modulations of firing rates ([19,20] and see [21] for review). Although these earlier findings are suggestive they provide no direct evidence that the tight integration, early interaction [22] and similarity between the sensory effect of stimulus contrast and the modulation by attention have immediate perceptual consequences. Carrasco *et al.* elegantly and convincingly provide this evidence. Together the available data support the hypothesis that sensory and attentional effects interact in the creation of an integrated saliency map [23].

This topographic representation of the visual input applies weights to stimuli by a combination of their local feature contrast and their behavioral significance – that is, their attentional modulation. The importance of creating this representation at the expense of accurately representing the visual input point-to-point is reflected in the multitude of neural mechanisms and processing stages that contribute to this actively constructed representation. An important and well-known example of the low-level mechanism contributing to this process are the center–surround receptive fields that enhance local contrast, thereby creating illusions such as those illustrated in Figure 1.

The saliency map is not just a tool for directing gaze to potentially relevant parts of the visual environment [24] but seems also to be the basis of perceptual judgments. This hypothesis is supported by the finding that the cue in Carrasco *et al.*'s study not only enhanced the cued stimulus' appearance but also improved the subjects' performance.

In summary, this study provides convincing support for an attentional enhancement of stimulus appearance. It completes a triangle of converging evidence from electrophysiology, functional brain imaging and now psychophysical findings, which argues that attention not only enhances the processing of attended sensory information but manipulates its very appearance. Just like sensory features of visual information processing, such as the center–surround organization of visual receptive fields that serves to manipulate the perceived contrast of luminance edges, attention turns out to be another tool at the visual system's disposal to provide an organism with an optimized representation of the sensory input that emphasizes relevant details, even at the expense of a faithful representation of the sensory input.

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Algebra and the adolescent brain

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New fMRI evidence suggests that adolescents could be at an advantage for learning algebra compared with adults. Qin and colleagues present findings indicating that after several days of practice adolescents rely on prefrontal regions to support the retrieval of algebraic rules to solve equations, as do adults. Unlike adults, however, after practice adolescents decrease their reliance on parietal regions, which assist in the transformation of the equations, suggesting an enhanced ability for learning algebra. These findings are discussed with regard to adolescent brain maturation.

Have you ever been stumped when helping your teenager with an algebra equation and then realize (with horror) that they actually understand it better than you do? Doesn't it seem odd that although adolescents seem limited in their ability to perform some mental tasks, such as assessing 'risky' behavior, they can be surprisingly adept at others, including complex reasoning such as that required in algebra? Using fMRI, Qin and colleagues [1] present intriguing evidence indicating that there may be a brain basis for adolescents' ability to implement the high-level logical reasoning required to perform algebraic equations.

Cognitive and brain development in adolescence

Adolescence is a period when the basic cognitive building blocks that have taken root during childhood are beginning to be refined. As such, the adolescent brain might have unique plasticity for learning. Although salient changes in mental abilities and brain maturation occur in infancy and childhood, there are significant improvements that continue through adolescence which are largely underappreciated (much like the parent of an adolescent). During adolescence scholarly demands increase dramatically as abstract thought and rule formation become essential to the ability to perform the math and reading required by school curriculums. Executive function, the abilities that include working memory and response inhibition, which allow us to have goal-directed

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