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Attention, Adaptation, and the Motion Aftereffect

Activation of the human visual motion area V5/MT was previously thought to be the basis of the motion aftereffect. New findings suggest that previous observations were confounded by attention and arousal, providing evidence that adaptation of directionally selective neurons in area V5/MT represents the fundamental substrate for the motion aftereffect.

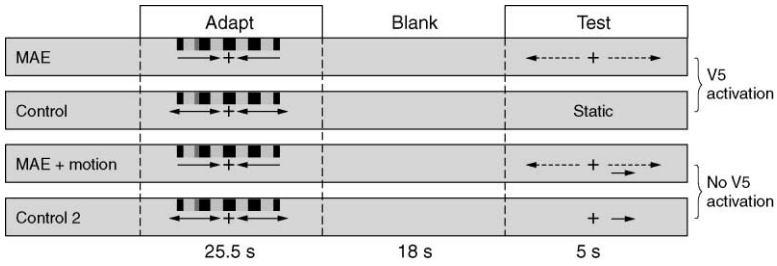
Many striking visual illusions result from disturbances of the equilibrium of the visual system caused by brief periods of intense activation. For example, prolonged viewing of a stimulus moving in one direction causes a motion aftereffect (MAE); a stationary stimulus viewed subsequently appears to move in the opposite direction (Wolgemuth, 1911). This is often known as the "waterfall illusion," referring to the MAE experienced when looking at adjacent static rocks after gazing at a waterfall for a prolonged period. The physiological substrate and neural locus of MAEs is under active investigation. Traditionally, MAEs have been attributed to fatigue or adaptation of units in visual cortex selective for particular directions of motion. Attention has therefore focused on cortical area V5/MT, an area in visual cortex that responds well to visual motion, and whose homolog in monkey contains a high proportion of directionally selective neurons.

Recent functional imaging studies in humans have examined cortical activity when subjects are presented with a static stimulus following adaptation to unidirectional motion, and either asked to passively view or actively judge the duration of the ensuing motion aftereffect (Culham et al., 1999; Hautzel et al., 2001; He et al., 1998; Taylor et al., 2000; Tootell et al., 1996). Typically, under these conditions, V5/MT activity is found to be elevated relative to a control condition when no motion aftereffect is perceived, such as following adaptation to alternating direction motion. This V5/MT activation has been interpreted as the neural correlate of the perceptual motion aftereffect. However, in this issue of *Neuron*, Huk and colleagues (Huk et al., 2001) present provocative new findings that will force a reconsideration of this interpretation. Their new findings suggest that V5/MT activation during the MAE may be entirely accounted for by the subjects' enhanced attention or arousal during perception of illusory motion.

First, the authors replicated earlier findings. Subjects adapted to two moving gratings placed on either side of fixation, and brain activity was measured with functional MRI (fMRI) in a delayed test phase when two static gratings were presented (Figure). Activity in V5/MT was elevated when an MAE was perceived (after adaptation to unidirectional motion), compared to a control condition when no MAE was perceived (after adaptation to alternating direction motion). However, Huk and colleagues then show that V5/MT activation no longer occurred if subjects were instead engaged in a psychophysical task of equivalent difficulty in the test phases of both the MAE and control trials. This suggests that the V5/MT activation previously attributed to the perceptual MAE may instead reflect the additional demands on attention or arousal associated with viewing a moving visual illusion compared to a static stimulus.

These results were obtained by making a slight modification to the test stimulus. One of the test gratings moved very slowly outward, approximately an order of magnitude slower than the psychophysically estimated speed of the MAE. Thus, on both MAE and control trials, one of the two test gratings moved very slightly faster than the other (and either with or without a superimposed MAE). Subjects viewed a short series of these test stimuli, and for both MAE and control trials, were asked to judge which grating moved faster. The task proved difficult for subjects because the added motion was close to the psychophysical threshold, but performance was equivalent in MAE and control conditions. Equating performance in this way, as a proxy for equating attention, led to a dramatic change in V5/MT activation. The previously strong activation during passive viewing was abolished when attention was controlled, with equal activation on MAE and control trials. Importantly, a vivid MAE was perceived on MAE trials even though there was no significant V5/MT activation compared to control trials (without MAE). The physical differences in the stimulus presented in the test phase in the second experiment appear not to account for the differences in V5/MT activation. A control experiment shows that V5/MT responses were not saturated by the presence of the slowly drifting test grating, as responses increased when the contrast of the grating was increased. However, in certain circumstances, dynamic and static test stimuli can produce dissociated MAEs (Culham et al., 2000), suggesting an alternate (if less likely) possibility, that the slowly drifting test grating tapped a different level of motion adaptation.

These findings indicate that a large proportion (perhaps all) of the elevated signal in V5/MT during passive viewing of the MAE may be due to effects of attention. Consistent with this, it is well established that manipulating attention during the adaptation phase can influence V5/MT activity and subsequent perception of the MAE (Chaudhuri, 1991; Rees et al., 1997). However, Huk's new findings add the important observation that these strong effects of attention extend to the test phase. The authors note that their use of the term "attention" in this context is deliberately broad, encompassing both nonspecific effects of arousal and task-dependent attentional changes. Indeed, Huk and colleagues show that the elimination of V5/MT activation in the test phase is independent of the exact nature of the behavioral task, as either speed or contrast discrimination tasks produce equivalent effects on V5/MT activation. Thus,



Experimental Design

Solid arrows represent the grating motion, dashed arrows show direction of MAE. Small arrows indicate added motion.

the effect of task performance on activation in the MAE test phase is not specifically associated with selective attention to the motion of the stimulus, and may instead reflect nonspecific arousal effects. Nevertheless, these findings provide a powerful argument for controlling performance (or some other proxy for attention/arousal) during such experiments.

If V5/MT shows no significant fMRI activation during MAE perception, what then is the neural substrate of the MAE? One possibility is that MAE perception is reflected in activity in other visual (or nonvisual) cortical areas. Some studies have suggested that the MAE is associated with activity in a more broadly distributed network of areas (Hautzel et al., 2001; Taylor et al., 2000). A second possibility is that the MAE reflects an imbalance in the baseline activity of directionally selective populations of neurons. There is increasing evidence that motion perception reflects the overall balance of activity in populations of neurons with different directional selectivities, and unbalanced adaptation of selective populations of neurons could be the basis of the MAE. Such an account would predict no difference (or perhaps a very slight decrease) in V5/MT activity comparing perception of the MAE and a static control, as Huk et al. observed. Huk and colleagues sought to provide additional evidence for adaptation with two further fMRI experiments that tapped signals from directionally selective neural populations.

They reasoned that if exposure to a stimulus moving in a single direction adapts a population of directionally selective neurons, then subsequent exposure to a test stimulus moving in the same direction should elicit a smaller response than to a stimulus moving in the opposite direction. Consistent with this notion, both V5/MT responses and psychophysical speed-discrimination thresholds were significantly lower for the same direction test stimuli (following a short period of adaptation) than for opposite direction test stimuli. In a complementary experiment, they compared fMRI responses during blocks of trials in which a stimulus repeatedly moved in a single direction with blocks in which the stimulus varied from trial to trial. This type of paradigm has previously been used to probe the effects of adaptation on object perception (Grill-Spector et al., 1999). However, Huk and colleagues made an important modification by asking subjects to perform a speed discrimination task in both same direction and mixed direction blocks, thus attempting to equate attentional demands. Nevertheless, strong direction-selective adaptation was evident in V5/MT, with lower signal in the same direction blocks compared to the mixed direction blocks. Direction-selective adaptation was strongest in V5/MT, but also evident to varying degrees in earlier visual areas, including V1. This is consistent with earlier findings of weaker motion selectivity of these areas (Tootell et al., 1996) and the idea that the MAE is supported by adaptation of distributed neuronal populations.

Taken together, these results are exciting because they present strong evidence for directionally selective adaptation in human V5/MT (and other visual cortical areas) following prolonged exposure to a moving stimulus. The results support models of the MAE suggesting that the illusion reflects an anisotropy in the response of large populations of directionally selective cells, resulting from a decrease in the responses of neurons with a preferred direction similar to the adapting direction. Many fascinating questions arise for further study. For example, Huk and colleagues used the "storage" phenomenon to separate in time the hemodynamic responses to adaptation and test phases. "Storage" refers to the preserved strength of the MAE if the period between adaptation and test is spent in darkness, or even if a wide range of patterns other than the stationary adaptation pattern are present. Surprisingly, this period can be very extended; the MAE has been reported to still be visible 26 hr after adaptation (Masland, 1969). The long-term and stimulus-specific nature of this adaptation places interesting constraints on possible detailed mechanisms. In addition, the findings of Huk et al. strongly emphasize the need to accurately control performance during measurements of brain activity, and further illustrate how psychophysical measurements can be fruitfully combined with functional neuroimaging to gain a deeper understanding of visual perception.

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