Cortical Dynamics Underlying Waves of Perceptual Dominance: Gestalt Psychology Vindicated

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During the first part of the last century the Gestalt psychologists proposed that the dynamics evident in visual perception were attributable to ever-changing electrical potentials within topograpically organized brain fields (Kohler, 1920). Dynamic field theory, as it was called, was subsequently discredited on grounds that the brain does not comprise a field but, instead, a richly interconnected network of discrete computing elements. But even within this modern conceptualization of brain function, we still face the challenge of explaining the phenomena that inspired the Gestalt psychologists: the nature of the medium does not change the fact that perception is dynamic in space and in time. To tackle the challenge of relating perceptual and cortical dynamics, my colleagues, Sang-Hun Lee and David Heeger, and I have been studying the phenomenon of binocular rivalry together with brain imaging using functional magnetic resonance imaging (fMR). Our findings to date reveal the existence of waves of cortical activity that travel across the retinotopic map in V1, in correspondence with the subjective perception of spreading waves of dominance during binocular rivalry. This brief paper summarizes some of our initial findings.

Introduction

By way of background, binocular rivalry is the alternation in perception that occurs when the two eyes view dissimilar monocular patterns (Blake and Logothetis, 2002). When viewing rivalry, people readily notice the smooth transitions in dominance as one stimulus sweeps the other out of conscious awareness. These dominance waves are particularly prominent with larger rival patterns subtending many degrees of visual angle -- they appear as a wave of dominance that is ignited locally and then seen to spread rapidly over the remainder of the previously suppressed target. These waves thus provide a paradigmatic phenomenon for studying cortical dynamics. In collaboration with Hugh Wilson and Sang-Hun Lee, I developed a novel procedure for measuring the speed of rivalry dominance waves propagating around a large, essentially one-dimensional annulus. To measure wave speed, we introduced an abrupt, brief contrast increment at one location of a suppressed annular stimulus (see Figure 1), an event that triggered a spreading wave of dominance that emerged at this trigger location. Observers indicated when the wave of dominance reached another, reference point around the annular rival target, thereby providing us with an estimate of the speed of the travelling wave of dominance. By varying the size and eccentricity of the rival targets, we discovered that the propogation speed of these travelling waves is independent of eccentricity. Moreover, we found that propagation speed doubles when waves travel along circular contours rather than radial contours, which may reflect the operation of collinear facilitation. When mapped onto the magnified retinotopic map of V1, we estimated that travelling waves spread through the cortical tissue at approximately 2.24 cm/sec. But is it actually the case that waves of cortical activation underlying rivalry transitions occur in V1?

Several fMRI experiments indicate that the blood-oxygen-level-dependent (BOLD) response of V1 is indeed modulated depending on whether the evoking stimulus is dominant or suppressed during rivalry (Polonsky et al, 2000; Tong and Engel, 2001; Lee and Blake, 2002). But this does not necessarily mean that travelling waves are also evident in V1. To learn whether this also is true, Lee, Blake and Heeger (2004) devised a novel technique to find out. Specifically, we had observers view a pair of annular rival targets (see Figure 1a), one a low contrast radial grating and the other a high contrast spiral grating; the two gratings were presented separately to the two eyes (using the anaglyphic technique) and observers fixated a small cross located in the enter of the annular region. Using a flash suppression procedure (Wolfe, 1984) we could insure that the high contrast spiral pattern was initially dominant, and we produced shifts in perceptual dominance by introducing a brief and abrupt increase in the contrast in a small region at the top of the low-contrast radial grating. As expected, this contrast pulse generated a perceptual travelling wave: observers perceived the local dominance of the low-contrast image to spread around the annular region, starting at the top of the annulus and progressing to the bottom of this region. Observers indicated when the wave reached the bottom of the annulus by pressing a key.

The logic of our procedure is based on established properties of the BOLD signal. We know that the BOLD signal in V1 is proportional to the contrast of the pattern evoking neural responses, and so if the contrast of the effective, evoking stimulus changes over time the magnitude of the BOLD response should change too, taking into account the BOLD signal's hemodynamic lag.

Consequently, if waves of dominance during rivalry are accompanied by waves of cortical activity within V1, we should see corresponding modulations in the BOLD signal, as the high contrast stimulus gives way in dominance to the low contrast stimulus. Specifically, cortical areas further from the trigger point will receive high contrast stimulation for longer durations, and this should produce a larger BOLD signal whose peak occurs later in time relative to the initiation of the perceptual transition from high contrast to low contrast. Thus by measuring BOLD responses along the retinotopically defined regions of stimulation, we could test for the existence of travelling waves of cortical activity. Note that it is the *perceptual* state of the evoking stimuli that is changing over space and time, not the conditions of physical stimulation, which stay constant throughout the observation interval.

We did indeed observe travelling waves of V1 activity coincident with observers' reports of perceptual waves of dominance (Figure 1). Details of our fMRI mapping procedures and analysis techniques are given elsewhere (Lee, Blake and Heeger, 2004). In brief, we defined the retinotopic region corresponding to the annular rival stimuli and determined the time elapsing between the onset of the dominance trigger and the peak in the BOLD response within individual voxels around the retinotopic representation of the annuli. These temporal delays became systematically longer as the locations of the voxels were situated farther away from the V1 representation of the top of the annulus where the wave originated; the correlation between BOLD delay and distance was statistically significant in all three observers. As expected based on earlier work, the perceptual wave speed estimates varied from trial to trial, thus giving us the opportunity to determine whether the dynamics of these cortical waves of V1 activity correlated with the latency of the perceptual waves. To test for such a correlation, we divided all trials into three categories – slow, medium and fast -- based on perceptual wave speed. We then computed the average BOLD delay for each of the three perceptual data sets and found that BOLD latency was positively correlated with wave speed, as one would predict if the cortical waves were causally related to the perceptual waves.

So we did indeed find strong correspondence between V1 activity and the spatiotemporal dynamics of perception during rivalry. We are currently seeking to learn whether these cortical waves actually arise within V1, perhaps spreading via long-range intracortical connections, or if they might be carried by feedback connections from higher-order visual cortical areas. We are also trying to determine whether waves of cortical activity in V1 and other retinotopic visual areas occur when attention is diverted from the perceptual waves. An answer to this question could have important bearing on the neural bases of binocular rivalry (Blake and Logothetis, 2002) as well as on the role of V1 in conscious visual awareness, a question that has generated lively debate in recent years (Crick and Koch, 2003; Tong, 2003).

Whatever the answers to those questions, our results confirm that variations in the BOLD signal can reveal timing differences on the order of 115 msec over distances covering about 3.5 mm of cortex. This means that fMRI provides sufficient spatial and temporal resolution to study cortical dynamics. We would like to believe that the Gestalt psychologists would be gratified by these discoveries and the vindication of their ideas.
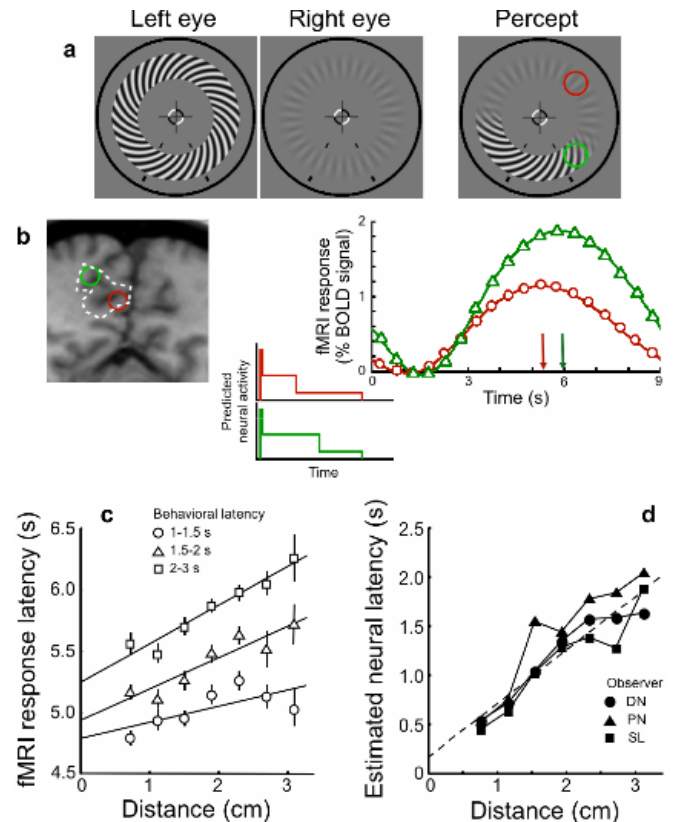

Figure 1. Travelling waves of cortical activity in human V1. (a) Stimuli, rival gratings viewed dichoptically. Percept, snap shot of traveling wave in which the low contrast pattern was seen to spread around the annulus, starting at the top. . (b) Gray scale, anatomical image passing through the posterior occipital lobe, roughly perpendicular to the Calcarine sulcus. Red outline, subregion of V1 corresponding retinotopically to the upper-right quadrant of the stimulus annulus. Green outline, subregion of V1 corresponding to the lower-right quadrant. Inset, time series of the predicted neural activity according to a simplified model described in Lee, Blake and Heeger (2004). Red and green curves, time series of the measured fMRI responses corresponding to the two outlined subregions, averaged across ~1000 trials for one observer. Red and green arrows, locations in time where these curves peak. (c) Temporal delay in the fMRI responses as a function of cortical distance from the V1 representation of the top of the annulus, categorized by behavioral latency, and averaged across observers. Steeper slope corresponds to slower speed. Larger y-intercept corresponds to longer initial delay. Error bars, SEM. (d) Estimated propagation speed of the underlying neural activity, averaged across behavioral latencies. Dashed line, best-fit to the mean across observers. (Figure reproduced, with permission, from Lee, Blake and Heeger, 2004).

Acknowledgements

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