Journal Club

Editor's Note: These short, critical reviews of recent papers in the *Journal*, written exclusively by graduate students or postdoctoral fellows, are intended to summarize the important findings of the paper and provide additional insight and commentary. For more information on the format and purpose of the Journal Club, please see http://www.jneurosci.org/misc/ifa_features.shtml.

How Attention Affects Border Ownership in Early Visual Areas

Shruti Baijal
Centre of Behavioural and Cognitive Sciences, University of Allahabad, Allahabad, Uttar Pradesh 211002, India

Review of Fang et al. (http://www.jneurosci.org/cgi/content/full/29/2/460)

The classic problem of figure-ground segregation draws from a more general problem of determining the side to which the border belongs. The one-sided assignment of the border to regions is termed as "border ownership" and the region to which the border is assigned is perceived as the figure (Nakayama et al., 1989). There is considerable evidence to show that figure-ground assignment is not completed before the influence of spatial attention, thereby resulting in mutual interactions possibly through inputs from higher visual areas (Vecera et al., 2004). Fang et al. (2009) elegantly demonstrated that attention modulates border ownership in early visual areas.

Fang et al. (2009) used functional magnetic resonance imaging (fMRI) adaptation to investigate whether the neural population in V1 and V2 are selective for border ownership and whether its processing is influenced by inputs from higher visual areas. Attention was manipulated by two separate tasks that used stimuli whose contextual information determined the border ownership [Fang et al. (2009), their Fig. 1]. The stimuli used for the experimental condition were square-wave radial-grating annulus with bright and dark alternating stripes. Either the bright or the dark stripes were longer in the radial direction, both inwards and outwards, causing the borders to be assigned to the bright or the dark regions, respectively. The control condition used stimuli in which figure-ground distinction was not possible. A trial began with an adaptation period followed by the test stimulus interleaved by blank interval. In one-third of the trials, the test stimulus differed from the adapting stimulus resulting in change in border ownership (different trial). In the rest of the trials, the adapting stimulus was either the same as the test stimulus (same trials) or followed by only blank intervals without any test stimulus (blank trials). In the attention-demanding task, the observers were asked to detect a transient change in luminance of the fixation point that occurred randomly throughout the trial. During the less demanding task, the observers had to identify the test stimulus (bright border or dark border) at the end of the trial.

Event-related averages of blood oxygenation level-dependent responses were obtained for each condition. To isolate the activity underlying test stimulus, blank trial response was subtracted from responses of both same and different trials. The adaptation effect (measure of response toward border ownership) was calculated as the difference between neural response for the same and the different trials. In addition to this, the adaptation index was computed to quantify the proportion of neurons selective for border ownership.

The performance in the attention-demanding task was lower than in the task involving less attention, indicating that attention was successfully manipulated in the two tasks. With analysis of fMRI data, a difference in signal for same and different trials was observed. This difference was not caused by change in stimulus per se (as confirmed by the control experiment). The attention-demanding task resulted in no adaptation effect in V1 and V2. However, a strong adaptation effect was observed in the less attention-demanding task, especially for V2 compared with V1. Therefore, more attention during adaptation abolished border ownership as indicated by the weak adaptation effect.

Whereas higher visual areas have been shown to be sensitive to border-ownership (Murray and Wojciulik, 2004), the present study provides evidence for border ownership in early visual areas, especially V2. The authors suggest that the resolution of border ownership occurs in early visual areas. This is consistent with the idea that figure-ground information is a necessary precursor to visual perception. Moreover, an attention effect on border ownership indicates that recurrent inputs arrive in V2 from higher visual areas. Together, the findings are consistent with a top-down model in which lower visual areas provide an integrated representation of figure-ground information. These early representations incorporate information from higher visual areas through feedback connections.

Yet it is important to understand how attention modulates neural responses that eventually lead to perception of objects. One possibility is that attention narrows the selectivity of neural responses in the visual cortex. The indication comes from other studies that have measured the re-

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Correspondence should be addressed to Shruti Baijal, Centre of Behavioural and Cognitive Sciences, University of Allahabad, Allahabad, U.P. 211002, India. E-mail: shrutz.b@gmail.com.
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sponses of selective population of neurons in the visual cortex when attention is directed to an object (Murray and Wojciulik, 2004). Murray and Wojciulik (2004) showed that attention increased the overall signal gain in the visual cortex for attended compared with unattended objects. Most importantly, even within the visual cortex, separate populations of neurons were excited depending on the attended orientation of the same object (Murray and Wojciulik, 2004). This suggests that attention increases selectivity by reducing the overlap of neural populations representing different object properties. Similarly, it is likely that the effects of attention on border ownership in V2 as shown by Fang et al. (2009) may be selective for subsets of neurons in V2.

Whereas attention during adaptation as used in the study by Fang et al. (2009) determined the ability to segregate figure and ground, other methods of adaptation have been used to study color, motion, etc. Adaptation of color produces negative afterimages, and studies of these afterimages show that attention during adaptation produces weaker afterimages (Suzuki and Grabowecky, 2003). This fits with the findings of Fang et al. (2009) who showed weaker adaptation with greater attention during the task. Although this link was not made explicit by Fang et al. (2009), it has important implications for the complex mechanisms serving attention and adaptation. However, in studies of tilt (Spivey and Spirn, 2000) and motion (Alais and Blake, 1999) aftereffects, attention during adaptation produced stronger aftereffects.

Based on their findings, Suzuki and Grabowecky (2003) postulated that attention produces weaker afterimages by facilitating polarity-independent rather than polarity-selective processes. The polarity-selective cortical cells contribute to formation of color afterimages. They selectively respond to object properties (e.g., the contrast polarity-selective cells discriminate between light and dark stimuli). However, the contrast polarity-independent cells respond to appropriate stimuli regardless of whether it is light or dark. The polarity-independent processes are mediated by the complex cells in V1 and V2 with some proportion of cells in V4 and inferior-temporal, whose responses are invariant to luminance and color polarity. Contrary to the color afterimages, the effects of attention on tilt and motion aftereffects could potentially act by facilitating polarity-selective mechanisms mediated by simple cells and color-opponent cells in early visual areas, V1 and V2 (Suzuki and Grabowecky, 2003).

Indeed, this points to the shared attentional mechanisms involved in adaptation that gives rise to negative afterimages and border ownership. Given the findings from studies of negative afterimages, it is likely that the effect of attention on figure-ground segregation is triggered by polarity-independent mechanisms. Therefore, assessing the selective activity of polarity-independent and polarity-selective cells could potentially unravel their relationship with border-ownership. The prediction would be that greater adaptation effect may be observed for polarity-independent complex cells in early visual areas. Perhaps, it is possible that the weak adaptation effect observed in V1 (Fang et al., 2009) was attributable to responses of polarity-independent cells being suppressed by those of the polarity-selective cells. Therefore, the separate evaluation of the responses of the polarity-independent and polarity-selective cells will provide greater insight into the precise mechanisms involved in border ownership and its relationship with attention. Future work directed toward investigating the adaptation responses of selective neural populations in the early visual cortex will be of great importance in understanding the effect of attention on neural representation of objects.

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