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.

Sources of Spatial and Feature-Based Attention in the Human Brain

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Review of Egner et al. (http://www.jneurosci.org/cgi/content/full/28/24/6141)

Attention is a critical component of visual perception because it involves the allocation of limited processing resources depending on current task demands. Most research has focused on our ability to covertly attend to specific regions within the visual field (spatial attention), often ignoring our perhaps equally important ability to attend to specific visual features across the visual field (feature-based attention).

The behavioral benefits of both spatial and feature-based attention are unmistakably clear during visual search, a task that we perform often in our daily lives. For example, when searching for an item in a room (e.g., a pencil), you may have prior knowledge of the item's spatial location (e.g., on top of the desk) and one or more of its visual features (e.g., yellow). Both types of information are typically used to guide the deployment of attention and speed the search process.

Converging evidence from neuropsychological, electrophysiological, neuroimaging, and neurostimulation studies points to a critical role of frontal and parietal regions in the top-down deployment of spatial attention (Kastner and Ungerleider, 2000). Much less is known about brain regions underlying feature-based attention, although several studies suggest that it may recruit a frontoparietal network similar to that involved in spatial attention (Liu et al., 2003). This raises the interesting possibility that spatial and feature-based attention involve common brain areas in frontoparietal cortex. To address this question, one would have to directly compare neural mechanisms of spatial and feature-based attention within the same subjects and using comparable tasks. With an appropriate design, such a study might also be able to address to what extent spatial and feature-based information are independently represented within these top-down source regions.

In a study published recently in *The Journal of Neuroscience*, Egner et al. (2008) took a novel and elegant approach to address these questions using functional magnetic resonance imaging (fMRI) in human subjects. Using a factorial design, spatial and feature-based information were independently manipulated in a parametric manner. On each trial, subjects were presented with a central cue followed by a search display consisting of a blue and red diamond presented on both the left and right sides of a central fixation point. One of these four diamonds was missing a corner; subjects were instructed to indicate whether the missing corner was on the top or bottom of this target diamond. The cue that preceded the search display could provide information about either the location of the target diamond (left or right of fixation; spatial information), the color of the target diamond (red or blue; feature-based information), or both. Furthermore, the reliability of the two types of cues was independently varied in a parametric manner (50, 70, or 90% reliable). For example, the cue could indicate that the target was 70% likely to be on the left side of the display and 90% likely to be red. Their design thus allowed for an investigation of the neural mechanisms of both spatial and feature-based attention, as well as their interaction.

Reaction time data indicated that subjects used both types of cues to locate the target, and more reliable cue information resulted in faster responses. Furthermore, the effects of spatial and feature-based information on reaction times were comparable in magnitude.

Whole-brain group analyses ($n = 14$) of fMRI data, testing for the parametric effects of both types of cue information separately, showed that an increase in either spatial or feature cue information (which were manipulated orthogonally) was associated with increased activity in a network of frontal and parietal regions typically observed in attention studies; both types of cues activated the intraparietal sulcus, frontal eye fields, inferior frontal cortex, and medial frontal cortex. A subsequent conjunction analysis, testing for regions significantly involved in processing both cue types, confirmed the overlap of the activations observed in the two separate analyses; significant activation was again evident in the frontoparietal network, including the four regions

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listed above. These results provide evidence that spatial and feature-based attention are represented, at least in part, in common brain regions. It should be noted, however, that these results came exclusively from group-averaged spatially smoothed data (9 mm kernel width). This leaves open the possibility that anatomically distinct regions for spatial and feature-based attention exist at the level of single subjects. The large intersubject variability in the location of attention-related frontal and parietal regions [Serences and Boynton (2007), their supplemental Fig. 7] highlights this point.

To further explore the relationship between spatial and feature-based attention, the authors focused on the regions activated in the conjunction analysis and compared responses across the nine cue conditions (3 spatial $\times$ 3 feature levels). Within these regions, there were significant linear effects of both spatial and feature-based information, confirming the previous analyses. Importantly, no interaction between the two types of cues was observed in any of the regions, suggesting that the effect of the spatial cues was independent from the information provided by the feature cues, and vice versa. Together, the authors argue, these findings suggest that spatial and feature-based information are independently represented in shared brain regions. Furthermore, and as conveyed by the title of their study, they argue that these findings provide evidence for an integrated representation of spatial and feature-based information in frontal and parietal regions.

What is meant by "integrated" and "independent" representations of these two types of attention? Each voxel contains several thousand neurons whose individual contributions to the blood-oxygen level-dependent (BOLD) signal cannot be directly assessed. Based on the results of the conjunction analysis, spatial and feature-based attention signals appear integrated at the gross anatomical level observable by the BOLD signal. At the same time, the additivity of spatial and feature-based attention in these regions suggests that the representation of spatial and feature-based information may be represented independently of each other at the neural level.

The current data are consistent with two alternative hypotheses regarding the representation of spatial and feature-based attention in the frontoparietal network. The first is that spatial and feature-based information are represented by a single neuronal population. On this account, neurons encode aspects of both spatial location (e.g., left) and the attended feature (e.g., red). Note that this model does not require "conjunction neurons," which would be active only when attending to, e.g., a red object in the left visual field. Rather, selectivity for spatial location and a given feature may be represented orthogonally, such that spatial tuning and feature tuning bear no systematic relationship to one another across the population of neurons. The alternative hypothesis is that spatial and feature-based information are represented by closely spaced, perhaps interspersed, but ultimately separate neuronal populations. This organization would appear integrated at the level of the BOLD signal, but not at the level of single neurons.

The authors note that single-unit recordings in monkeys will be useful in helping to differentiate between these two possibilities. Alternative imaging methods may also offer additional insights. In particular, fMRI-adaptation paradigms and multivoxel pattern analysis have been used successfully to indirectly dissociate closely spaced neuronal populations (Grill-Spector and Malach, 2001; Peelen and Downing, 2007). Additionally, using high-resolution fMRI and detailed individual-subject analyses may reveal a fine-grained organization not apparent at the group-average level (Schwarzlose et al., 2005). Each of these methods has its own associated disadvantages, but it is only through the convergence of evidence from multiple techniques that we will fully understand the neural mechanisms of spatial and feature-based attention.

The results of Egner et al. (2008) support the notion that the frontoparietal network might be a general-purpose attention control system, not specific to spatial tasks. Indeed, it seems unfeasible that each set of features that we can attend to would be represented in an anatomically distinct cortical region. However, spatial attention may be "special" in that visual space is a fundamental aspect of the visual world, whereas the specific features that are behaviorally relevant for guiding attention are often learned through experience. The study by Egner et al. (2008) provides an elegant approach to investigating the top-down contributions to spatial and feature-based attention signals. Variations on this paradigm, in conjunction with more advanced imaging and analysis methods, will further enhance our understanding of the basic mechanisms of spatial and feature-based attention in the human brain.

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