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Lumping and Splitting the Neural Circuitry of Visual Attention

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DOI 10.1016/j.neuron.2012.01.011

Shifts of gaze and of covert attention rely on tightly linked yet divergent neural mechanisms. In this issue of *Neuron*, Gregoriou et al. (2012) provide interesting evidence that different functional classes of neurons within the frontal eye field contribute uniquely to these two functions.

The gaze shifts we make four or five times per second are crucial to our exploration of a visual scene. They somehow succeed in repeatedly and accurately repositioning the eyes so that the most acute region of each retina (the fovea) acquires the target of greatest interest. For foveate animals like us, this is where visually guided behavior begins; that is, with the selection of a peripheral visual stimulus for further visual processing. One refers to this behavior as the *overt* orienting of visual attention because the selection of the target culminates in an observable movement of the eyes (or the eyes and the head) to acquire a specific target. Thus, for example, before crossing the street we might shift our gaze to a car moving toward us while ignoring another car moving away from us, the gaze shift being exclusively driven by velocity of the target car. This example depicts the more mundane, or one might say pedestrian, form

of visual attention. However, this is not the type of attention most often studied by those who seek to identify its neural basis. The type of attention typically studied by neurophysiologists is the kind devoid of changes in gaze, namely *covert* attention, in which the only measurable effects on behavior are perceptual.

As several 19th-century scientists (e.g., Helmholtz, 1867) noted, detection, discrimination, and memory of peripheral visual information can change considerably, depending on the locus of attention, and those changes occur even when our gaze remains (atypically) fixed in space. Much of the current work on visual attention is focused on identifying the neural circuits driving the perceptual benefits that accompany attention when it is covertly directed. How does a behaviorally relevant stimulus get selected and an irrelevant stimulus get ignored when neither is actually foveated? In the past

ten years or so, much evidence has established that the neural circuits underlying this phenomenon are nonetheless related to mechanisms of gaze control (Awh et al., 2006). Yet, how closely those circuits are related remains unclear, and this question has been the subject of considerable controversy. Should the mechanisms of covert attention and overt attention be “lumped” together as one in the same, as the so-called “premotor” theory of attention argues (Rizzolatti et al., 1994), or can they be “split” into distinct mechanisms, as others argue (e.g., Thompson et al., 1997)? Below, we suggest that the solution to the lumping versus splitting debate seems to depend largely on whether the term “mechanism” refers to brain structures or individual neurons within them. In the current issue of *Neuron*, Gregoriou and colleagues describe exciting new evidence nicely illustrating this point and suggest how

particular classes of neurons might contribute uniquely to covert and overt visual attention.

Motivated in large part by earlier psychophysical studies revealing an interdependence of saccades and covert attention, more recent neurophysiological work has identified a set of key brain structures that appear to contribute causally to both functions. These structures include the superior colliculus (SC) in the midbrain, the lateral intraparietal area of parietal cortex (LIP), and the frontal eye field (FEF) of prefrontal cortex. Each of these structures contains neurons that contribute in some way to gaze control and to the deployment of covert visual attention (Awh et al., 2006). Gregoriou et al. build on this evidence, as well as their previous work on the functional interactions between the FEF and extrastriate area V4 (Gregoriou et al., 2009). In the latter work, they found that when monkeys covertly attended to stimuli in the overlapping response fields (RFs) of simultaneously recorded FEF and V4 neurons, not only was there an enhancement of visual activity in both areas, but there was also a robust enhancement in the synchrony of neuronal spiking activity with the gamma band component (40–60 Hz) of the local field potentials (LFPs) between areas. The authors interpreted this observation as indicative of an attention-driven increase in the effective coupling of the two areas and as a possible mechanism by which the transfer of selected visual information is facilitated during attentional deployment. In the present paper, the authors sought to discover whether different functional types of FEF neurons contribute differently to attention-related changes in spike-field coherence between the FEF and V4. FEF neurons are typically classified by whether they respond to the onset of a visual stimulus (“visual” neurons), before the onset of a saccade (“movement” neurons), or both (“visuomovement” neurons). As is typically done, Gregoriou et al. employed a memory-guided saccade (MGS) task to classify FEF neurons along those lines and asked whether these different functional classes exhibit different changes in coherence with the gamma-band LFP within V4 when attention was directed inside versus outside of a neuron’s RF.

Among several noteworthy results reported by Gregoriou et al. is the finding of a substantial difference in the attention-related increase in spike-field synchrony between the functionally defined classes of FEF neurons. Specifically, the authors found that increases in coherence were only present in FEF visual neurons. When attention was directed to the V4 RF, the spiking responses of FEF visual neurons with spatially corresponding RFs were significantly more synchronized with the gamma-band component of the V4 LFP than when attention was directed elsewhere. In contrast, for FEF visuomovement and movement neurons, there was not a significant increase. This observation is exciting because it suggests a clear division of labor among the functional subclasses of FEF neurons with respect to covertly and overtly directed attention, a division in which neurons with only visual, and no movement-related, properties synchronize their activity with visual cortical signals corresponding to the target of attention. If one assumes, as many do (but see Ray and Maunsell, 2010), that gamma-band spike-field coherence is not only a correlate of attention, but also an important mechanism, then this observation identifies a functional split within the FEF between neurons associated with the perceptual effects of attention (visual) and those associated with the motor effects (visuomovement and movement).

More importantly, the above result suggests that FEF visual neurons may be the ones projecting to visual cortex (e.g., area V4) and driving the modulation in visual responses that have been so widely reported. Other studies employing either electrically (e.g., Moore and Armstrong, 2003) or pharmacologically (Noudoost and Moore, 2011) driven changes in FEF activity have provided key causal evidence of an influence of FEF neurons on visual cortical signals. Anatomical studies further suggest that it is the superficial-layer FEF neurons that directly modulate neurons within visual cortex via long-range projections (Anderson et al., 2011), whereas it is the deep-layer FEF neurons that principally project motor commands to the SC and brainstem (Pouget et al., 2009). The present findings of a cell-type-specific spike-field coherency effect of attention between the FEF and

V4 suggest that FEF visual neurons are among the class, and perhaps are the primary class, of FEF neurons projecting to visual cortex and exerting modulatory influences. Because one tends to assume that modulation of visual cortical activity is the basis of the perceptual benefits of attention (though it may not be), the possibility of identifying a single functional class of neurons as driving that modulation is certainly an exciting one. Determining which classes of FEF neurons project to visual cortex will require further experiments, ones employing either newly developed cell-type-specific perturbation techniques (e.g., optogenetics) or more traditional electrophysiological approaches (e.g., Sommer and Wurtz, 2001). But, given the present results, coupled with other recent studies, one can begin to see how the components of this particular neural circuit might fit together and how we might determine the role spike-field synchrony actually plays. If, for example, only visuomovement neurons project to V4, it would seem less likely that synchrony, as opposed to firing rate, plays an important role, particularly because firing rate increases are observed in both visual and visuomovement neurons during covert attention (Thompson et al., 2005; Gregoriou et al., 2012).

Returning to the question of whether the neural circuitry of covert attention should be lumped with or split from the neural circuits controlling gaze, it is apparent from the results of Gregoriou et al. that although FEF neurons collectively contribute to both functions, there is an apparent division of labor at the single-neuron level. Thus, although it might be appropriate to lump the two functions together at the level of whole brain structures as “networks” (e.g., FEF, SC, and LIP), it is also reasonable to split those functions at the level of underlying neuronal contributions. For the latter, one might argue that we should expect the two functions to be split at the level of single neurons, given that we already know that at some level in gaze control circuitry (e.g., oculomotor nucleus) neurons can only be involved in the gaze command (Awh et al., 2006). The major question then may not be whether overt and covert attention share the same underlying neural circuitry—they do, though not completely—but rather at

what stage the circuitry diverges. At which point, is neuronal activity independent of one or the other function? Although the Gregoriou et al. results demonstrate differences in the profile of modulation between FEF neurons, it is nonetheless important to note that all types were modulated by covert attention in some way. For example, movement neurons were suppressed by covert attention, similar to a previous study (Thompson et al., 2005); thus, their activity is not independent of the behavior, just anticorrelated with it. Perhaps it might be wise to consider that, at least within the FEF, all neurons participate in the control of covert and overt attention, but in separable ways. Given that the only clear difference between the two behavioral functions is that in one case a shift in gaze is generated, this might seem a reasonable possibility. As in covert attention, overt attention also involves the visual selection of a target, and all of its component visual features, to the exclusion of other stimuli, as in our opening example. To achieve accurate visual guidance of saccades, saccades that incorporate the target's component visual features, this must be true (e.g., Schafer and Moore, 2007).

Correspondingly, as in covert attention, overt attention is accompanied by a selective enhancement of visual cortical signals (e.g., Moore and Chang, 2009), an effect that is consistent with the perceptual enhancement known to occur at the target of gaze shifts (Deubel and Schneider, 1996). In other words, there are perceptual effects that accompany both types of attention, as well as neural correlates of those effects, in spite of the clear differences in motor outcome. Therefore, future studies might include a comparison of FEF activity, including its synchrony with other brain structures, between tasks in which attention is directed to (identical) visual stimuli with or without the execution of a gaze shift.

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