Paying Attention to the Cortical Layers

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In this issue of *Neuron*, Nandy et al. (2017) reveal a number of important new insights into the neural mechanisms that are responsible for attentional selection.

We live in a cluttered world. It is hard to overestimate the sheer number of visual items that surround us, while typically only a few of them are relevant for guiding our actions. This is why we need attention, the key process by which the brain selects one or a few objects for processing in depth. The mental representations of the attended items become enhanced and elaborate in the cortex, while distracting stimuli are filtered out.

In this issue of *Neuron*, Nandy et al. (2017) reveal a number of important new insights into the neural mechanisms that are responsible for attentional selection. Many of the insights about the neuronal processing underlying attention shifts have come from studies in the visual cortex of monkeys that were trained to direct their attention to some visual items while ignoring others. These studies revealed that neurons in the visual cortex are not only influenced by the stimulus in their receptive field but that there are also strong top-down influences associated with attention shifts. Researchers have proposed several candidate neuronal mechanisms for these attention shifts. First, studies have consistently shown that attention increases the spike rates of neurons encoding attended stimuli compared to non-attended stimuli (Desimone and Duncan, 1995). The effect on firing rates has been observed in many, if not all, areas of the cerebral cortex, ranging from primary visual cortex to areas of the frontal cortex (Pooresmaeili et al., 2014). Second, attention makes neural responses more reliable. The exact number of spikes fired to different repetitions of a visual stimulus is quite variable. This variability can be quantified using the Fano factor, the variance of the spike rate across trials divided by the mean. Attention reduces the Fano factor (Mitchell et al., 2007). Third, attention reduces low-frequency correlations between neurons. The activity of groups of neurons tends to be positively correlated across trials. These slow correlations, termed ‘‘noise correlations,’’ impair visual discrimination performance under some circumstances, because shared noise cannot be removed by pooling information across neurons. Some studies suggested that a reduction of noise correlations is the primary source of improvements in attentional performance (Cohen and Maunsell, 2009). Lastly, researchers have suggested a critical role for attention-based increases in correlations at higher gamma frequencies (Fries et al., 2001), because they might enhance the impact of visual cortical neurons on downstream target areas. These proposed mechanisms are not mutually exclusive and the question of how much each of them contributes to attentional selection has not been fully resolved.

Nandy et al. (2017) addressed these questions by investigating neuronal activity in the different cortical layers, which have distinct roles in visual analysis and attentional processing (Figure 1A). The bottom-up driving visual input from lower brain regions arrives in layer 4, whereas the top-down inputs associated with attention shifts tend to avoid layer 4. The superficial layers project to downstream cortical areas, whereas the deep layers project backward to upstream cortical areas as well as subcortically. The authors took advantage of this division of labor between the layers in area V4, a mid-tier visual area where activity is strongly modulated by attention. Nandy et al. (2017) also examined the contribution of two functionally defined subclasses of cells: broad-spiking (putative excitatory) and narrow-spiking (putative inhibitory) cells as previous studies suggested that inhibitory neurons contribute strongly to attention shifts (Mitchell et al., 2007). Nandy et al. (2017) had to overcome a number of technical challenges to identify the different layers in V4. They used laminar electrodes with multiple contacts along a single shaft that needed to be positioned perpendicular to the cortical layers, which is challenging in area V4 because it has a complex shape. They implanted a transparent artificial dura so that they could see the cortical surface and they obtained high quality laminar recordings of a part of V4 that sits on a narrow gyrus.

Nandy et al. (2017) trained the monkeys to perform a task in which the animals monitored a stream of oriented visual stimuli (Gabor patches) presented at one location to detect a stimulus with a deviant orientation appearing with a high likelihood (Figure 1B). They tended to ignore another, distractor stream presented elsewhere because the deviant stimulus was much more unlikely to appear at that position.

Nandy et al. (2017) observed a number of surprising findings that are of crucial importance for our understanding of the mechanisms of visual attention (Figure 1C). First, attention increased spike rates in all layers. Interestingly, the effect of attention was stronger on the firing rate of neurons in the input layers (layer 4) than in the superficial and deep layers. This contrasts with the laminar profile of top-down influences in lower-level area V1, which tend to be strongest outside layer 4 (Self et al., 2013). Nevertheless, the study confirmed that the dominant effect of attention is an increase of firing rates of neurons that represent the attended location. Second, Nandy et al. (2017) found that the effects of attention on firing rates are largest in broad-spiking, putative excitatory cells, and weaker in narrow-spiking cells, which are putative inhibitory neurons. This finding represents another surprise, because some previous studies revealed strongest effects of attention in narrow-spiking neurons. Third, the influence of attention on the variability of neuronal responses, as measured with the Fano factor, were relatively modest and confined to broad-spiking cells in the superficial layers. Fourthly, Nandy et al. (2017) replicated previous findings that attention reduces noise correlations (Cohen and Maunsell, 2009; Mitchell et al., 2009), but in the present study this reduction was largely confined to the input layers of cortex and did not occur in the deep layers. This finding is problematic for theories that emphasize that attention works by reducing noise correlations, because a reduction in the output layers of cortex would be essential if downstream areas are to benefit from this effect. Finally, Nandy et al. (2017) observed no evidence for previously reported increases in high-frequency spike synchrony in the superficial layers of V4 if a stimulus is attended (Buffalo et al., 2011). Instead, attention caused a modest enhancement of beta- and gamma-band spike synchrony in the deeper layers.

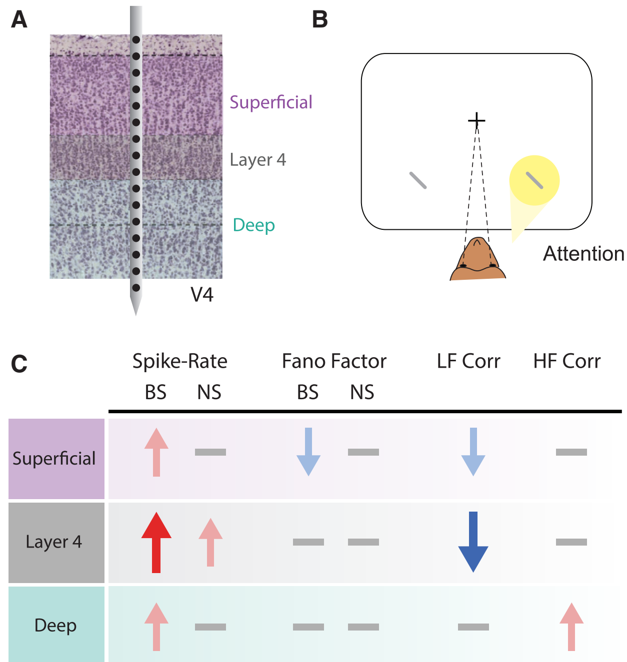

Figure 1. Summary of the Results
(A) Nandy et al. (2017) recorded spiking activity simultaneously from each layer of V4 with a laminar electrode.
(B) The monkey covertly attended to one stream of oriented visual stimuli while ignoring the other stream.
(C) The arrows indicate attention-induced changes in neuronal activity in the different layers of V4. Red colors indicate attention-induced increases, blue indicates decreases, gray lines indicate no (significant) change. BS, broad-spiking cells; NS, narrow spiking cells; LF, low-frequency; HF, high-frequency.

If the present results are combined with previous studies, it appears that the main effect of attention is an increase in firing rates across the different layers of area V4, which nicely dovetails with the generality of firing rate increases that occur across the entire cerebral cortex. The influence of attention on the correlations between neurons appears to depend on the exact task that the animal performs, which casts some doubt on the general importance of these effects for the ability to preferentially process important stimuli over less important ones.

It is also of interest to compare the laminar profile of noise correlations in V4, with the strongest correlations in the input layers, to the laminar profile previously found in V1, where correlations in the input layers are close to zero (Hansen et al., 2012). Apparently, spike-count correlations do not form canonical laminar patterns throughout the visual system but vary from area to area instead. Nandy et al. (2017) construct a simulation suggesting that neurons in the input layers are strongly correlated because of strong recurrent interactions between excitatory and inhibitory cells in these layers. They hypothesize that excitatory and inhibitory neurons in the superficial and deep layers have weaker interactions and, hence, weaker correlations. Although this model would explain the observed laminar profile of spike-count correlations, it remains to be tested whether the laminar correlation profile might also arise through differences in the correlation structure of bottom-up and top-down inputs into the different layers.

The results of this study emphasize the benefits of simultaneously examining neuronal activity in the different layers of a visual area. Studies using implanted electrodes or single-electrodes may sample in a biased way from the layers and produce an incomplete view of the processing carried out by a particular area. Information about how attention modulates activity in different layers is also critical for the development of biologically plausible computational models of attentional processing. The laminar approach highlights the consistency of attention related spike rate increases and brings into question whether attention-related changes in spiking reliability or spike-count decorrelations are robust enough to mediate the enhanced visual processing that attended stimuli enjoy.

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