

Paying Attention to the Details of Attention

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Attention selects behaviorally relevant stimuli for greater neural representation. In this issue of *Neuron*, Luo and Maunsell (2015) show that attention acts, in part, by boosting the signal-to-noise ratio (SNR) of sensory neurons.

We live in a complex and dynamic world where every moment is a flood of sensory stimuli and internal thoughts. To avoid drowning in this deluge, we must selectively prioritize those inputs or thoughts relevant to our current task. Attention acts as this filter: It is our ability to selectively prioritize specific stimuli or thoughts for greater neural representation. Now in *Neuron*, Luo and Maunsell (2015) provide evidence that this filter is enacted by modulating the signal-to-noise ratio (SNR) of sensory neurons.

This control is at the center of cognition, and so it is no surprise that attention has been well-studied. Many studies of attention use a variant of the “Posner cueing task” (Posner et al., 1980). In this task, subjects are cued to attend to a specific location in order to detect a change in a stimulus. As expected, subjects are able to allocate attention, enhancing detection at the cued location. The Posner task has been particularly powerful for studying attention because, by comparing neural responses of stimuli inside and outside of attentional focus, one can study how attention modulates neural response to stimuli. Using this method, we have gained insight into how attention changes neural representations (for review, see Carrasco, 2011). For example, attention has been found to improve the response of single neurons, either by increasing their sensitivity (Reynolds et al., 2000) or by boosting the gain of their response (Lee and Maunsell, 2010). Attention also increases the information content of populations of neurons by reducing noisy, uninformative, correlations between neurons (Cohen and Maunsell, 2009). At the same time, attention synchronizes the activity of selected neural populations, increasing their impact on downstream regions (Fries et al., 2001). Notably, all of

these results, and many more in the field, have relied on the Posner attention task. Because attentional cueing in the Posner task is assumed to selectively enhance an attended stimulus, these changes in neural responses are often interpreted as increasing the SNR ratio of attended stimuli. However, this assumption is not always correct.

Subjects performing Posner-like tasks actually use two different strategies to increase the likelihood of detecting a target: (1) decrease the threshold for deciding a stimulus is a target and/or (2) selectively increase a stimulus' neural representation, making it easier to detect a change. This effect has been known for several decades and is best understood from a signal detection theory perspective (for review, see Kinchla, 1992). As an example, Figure 1A outlines a typical Posner-like attention task where subjects must monitor the orientation of an attended stimulus. Their task is to determine if it changes from the sample orientation to a target orientation. Signal detection theory predicts the estimate of a stimulus will be noisy, leading to variability in its perceived orientation. This is true when the stimulus is at the sample orientation (Figure 1B, black distribution) and at the target orientation (Figure 1B, orange distribution). Deciding whether a given stimulus has changed from its original sample orientation therefore requires one to use a discriminating threshold: below the threshold a stimulus will be perceived as a non-target, having the sample orientation; above the threshold it will be perceived as a target (Figure 1B, green line). Given the noise in perception, there will also be noise in detecting a change in orientation. For example, occasionally a non-target stimulus at the sample orien-

tation will be misperceived as having the target orientation. Subjects will then incorrectly report a change (a “false alarm,” shown as blue area in Figure 1B). Similarly, a stimulus at the target orientation may be misperceived as having the sample orientation (a “miss,” shown as red area in Figure 1B). Attentional cues clearly enhance the probability of detecting a change in target orientation but, as noted above, this can be done in two ways.

First, one could improve their SNR. In effect, this would reduce the uncertainty of the orientation of the sample and the target (Figure 1C, left). Reducing the uncertainty would lead to a reduction in both misses and false alarms. Second, one could simply change the threshold for detecting a target change (Figure 1C, right). For example, decreasing the change threshold would greatly reduce misses (while necessarily increasing false alarms). In this issue, Luo and Maunsell (2015) find that when monkeys perform a typical Posner cueing task, they use both strategies: they increase their SNR and lower their threshold for detecting a target stimulus.

This then presents a conundrum: If animals adopt a mixed strategy to solving this attention task, then how should one interpret neural correlates of attention? Are they reflecting the increased SNR, or are they reflecting a reduced change threshold? To address this question, Luo and Maunsell trained animals to perform two variants of a Posner-like cueing task that independently manipulated the SNR and threshold. First, they biased the monkeys to selectively increase/decrease the SNR of the attended stimuli by rewarding them more/less for correctly responding to changes at a single location. Importantly, this can be behaviorally

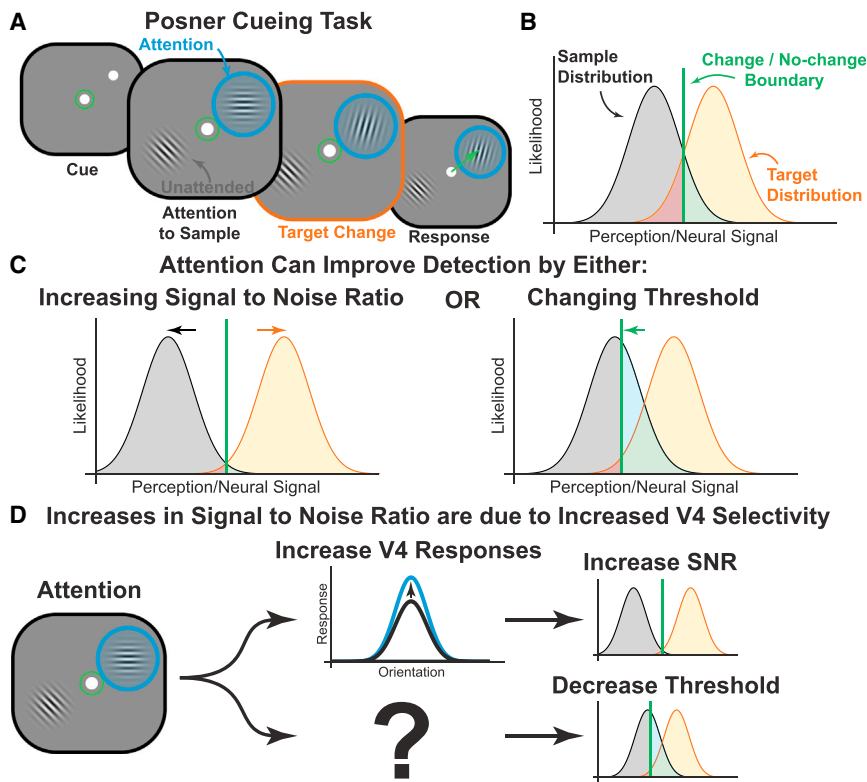


Figure 1. Attention Improves Target Detection by Increasing Signal to Noise and Changing Detection Threshold

(A) A typical Posner attention task. Subjects are asked to attend to a stimulus in order to detect (and respond to) a change in its properties (in this case, orientation).

(B) Neural responses to stimuli are noisy, leading to noise in perception (black and orange lines for two different orientations). Signal detection theory predicts stimuli are discriminated into different orientations using a decision threshold (green line). If distributions are overlapping, stimuli will occasionally be misperceived (red and blue areas). This would lead to errors in a Posner-like task to detect changes.

(C) Detection rate of targets can be improved by either (left) boosting neural responses such that the two distributions do not overlap or (right) changing the decision threshold in order ensure more target stimuli are accurately discriminated.

(D) Attention in a Posner attention task seems to do both: increasing SNR by improving V4 responses (top) and decreasing thresholds through a currently unknown mechanism (bottom).

measured as a shared change in false alarms and misses (e.g., both decrease, as shown in Figure 1C, left). Second, they biased the monkeys to either increase or reduce their discrimination threshold by differentially rewarding the animals for correctly identifying change trials (“hits”) and no-change trials (“correct rejections”). This is measured as opposite changes in false alarms and misses (as shown in Figure 1C, right).

To determine whether the neural correlates of attention follow changes in SNR or threshold, Luo and Maunsell use a chronically implanted electrode array to simultaneously record from dozens of V4 neurons during both task variants. Interestingly, Luo and Maunsell find changes in V4 neural responses only

occurred on those trials when the monkeys were improving their SNR (Luo and Maunsell, 2015; summarized in Figure 1D). Individual V4 neurons increased their firing rate to an attended stimulus during the high SNR condition. In effect, this acts to increase the SNR of individual neurons: an increase in firing rate to a target stimulus will separate it from the response to a sample stimulus, improving their discriminability. Similarly, correlated noise in the population was reduced only in the high SNR condition. Such “noise correlations” reflect a shared signal across a population of neurons, which reduces the information-carrying capacity of the population as a whole. Therefore, by reducing these noise correlations, the population has a higher SNR.

Together, these results provide early evidence that attention acts on sensory representations in V4 solely to improve the SNR. In many ways, this makes sense: The best way to increase the information one has about a stimulus is to improve the quality of your detectors. Furthermore, Luo and Maunsell’s results are consistent with prominent models of attention that suggest it increases SNR by resolving competition between stimuli (Reynolds and Heeger, 2009). However, it remains to be seen whether other neural correlates of attention are also associated with increasing SNR or if instead they act to reduce the threshold for detecting a target. For example, there is a large body of evidence showing attention synchronizes selected neurons at high-frequency ‘gamma-band’ oscillations (e.g., Fries et al., 2001). Such increases in synchrony ensure the activity of selected neurons are coincident on downstream regions, increasing their efficacy and boosting the propagation of information. It seems natural that these increases in synchrony would increase the SNR of a population by selectively boosting the “signal” while removing competing “noise” representations. However, they could also act to reduce the threshold if, by becoming coincident, fewer neurons are required to trigger downstream “decision” neurons. Future work is needed to determine which model is correct (or if both are).

Future work is also needed to determine which brain regions reflect and control changes in threshold. A distributed network, including frontal cortex, parietal cortex, and subcortical regions are involved in decision making and so they seem like a natural place to begin looking for “threshold” neurons. In addition, as these same regions are thought to control where we attend (for review, see Miller and Buschman, 2013), future work should determine their relative roles in controlling increases in SNR and/or changes in threshold.

An intriguing alternative model comes from Lo and Wang (2006). They hypothesize that the brain adjusts decision thresholds by modulating cortico-striatal connections. In their model, the integration threshold of accumulator neurons can be changed by modulating the strength of afferent synapses: greater

synaptic strength lowers the number of spikes needed to reach a given level, effectively lowering the threshold. This model has growing experimental support. First, it is clear that cortico-striatal projections are involved in decision making (Znamenskiy and Zador, 2013). Second, human neuroimaging experiments have shown that the effective connectivity between cortex and striatum is correlated with decision-making thresholds (Green et al., 2012). This model is particularly intriguing given the known role of dopamine in modulating cortico-striatal connections and the growing understanding of dopamine's role in attention (Noudoost and Moore, 2011).

Finally, Luo and Maunsell's results highlight the advantage of building more complete models of behavior in order to understand the many facets of a task (Luo and Maunsell, 2015). In this case,

signal detection theory led to a more complete understanding of the behavior and, thus, a more complete understanding of the neural correlates of attention. Similarly, exhaustive behavioral models have recently provided novel insights into the underlying neural mechanisms of decision making (Brunton et al., 2013). The brain exists to produce behavior and, therefore, understanding the brain should begin with complete descriptions of behavior.

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Cortical Cliques: A Few Plastic Neurons Get All the Action

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Adjustments in neural activity can drive cortical plasticity, but the underlying circuit components remain unclear. In this issue of *Neuron*, Barnes et al. (2015) show that visual deprivation-induced homeostatic plasticity invokes specific changes among select categories of V1 neurons.

The brain has evolved extensive mechanisms to maintain stable activity levels in the face of fluctuating synaptic drive. Indeed, when these mechanisms fail, devastating consequences can occur such as runaway excitation and epilepsy. At the same time, there are a number of instances in which neural circuits need to greatly increase their levels of activation, such as during sensory plasticity.

How does the brain reconcile these seemingly contradictory needs? One way is through homeostatic plasticity or the ability to fine tune the excitability of specific neuronal networks (Turrigiano, 2012). In this issue of *Neuron*, Barnes et al. (2015) addressed whether homeostatic recovery of cortical activity in response to visual deprivation reflects the involvement of specific subsets of

neurons and how those cells contribute to the plasticity of the larger circuits in which they are embedded.

Classic paradigms for manipulating sensory drive and cortical plasticity, such as eye-lid suture, dark rearing, or retinal lesions, have been shown to trigger homeostatic regulation of firing rate in the developing (Desai et al., 2002; Hengen et al., 2013) and in the mature (Keck et al.,