Current Biology

Article

Attentional Modulation of Neuronal Activity Depends on Neuronal Feature Selectivity

Highlights

- Recordings were made from a large sample of monkey V1 neurons spanning cortical layers
- Attention differentially modulates simple and complex V1 neurons
- Attention facilitates neurons with feature selectivity matching task features
- Results support integration of spatial and feature attention models

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In Brief

Short et al. record from V1 neurons spanning the cortical layers in monkeys performing an attention task and reveal that attentional modulation of neuronal firing rate varies systematically across neuronal types. Attention facilitates the activity of V1 neurons with feature selectivity matching the features required for successful task completion.

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Attentional Modulation of Neuronal Activity Depends on Neuronal Feature Selectivity

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SUMMARY

Attention exerts a powerful influence on visual perception. The impact of attention on neuronal activity manifests at early visual information processing stages and progressively increases throughout the visual cortical hierarchy. However, the neuronal mechanisms of attention are unresolved. In particular, the rules governing attentional modulation of individual neurons, whether they are facilitated by or suppressed by attention, are not known. To obtain a more granular or neuron- and circuit-level understanding of the mechanisms of attention and to directly test the feature similarity gain model in V1, we compared attentional modulation with neuronal feature selectivity across a large population of V1 neurons in alert and behaving macaque monkeys trained on an attention-demanding contrast-change detection task. We utilized emerging multi-electrode array technology to record simultaneously from V1 neurons spanning all six cortical layers so that we could characterize the laminar position and physiological response properties of diverse V1 neuronal populations. We found significant relationships between attentional modulation and neuronal position within the cortical hierarchy, neuronal physiology, and neuronal feature selectivity. Our results support the feature similarity gain model and further suggest that attentional modulation depends critically upon the match between neuronal feature selectivity and the features required for the task.

INTRODUCTION

Attention could augment sensory perception by enhancing the activity of select neuronal populations that encode attributes of attended objects. In the visual cortex, attention directed to a particular location in visual space modulates the activity of neurons responsive to stimuli at that location [1–3]. Attention to specific stimulus features, such as direction of motion, also facilitates the activity of similarly feature-selective neurons in the visual cortex [4, 5]. However, the mechanism by which attention modulates neuronal activity is not known. Furthermore, whether the same mechanism underlies neuronal modulation by spatial versus feature-based attention is also unresolved. Part of the difficulty in elucidating the neuronal mechanisms of attention may be due to the fact that most studies of visual attention involve examining average attentional modulation across large numbers of neurons irrespective of neuronal variation, such as position in the cortical circuit hierarchy or feature selectivity. Indeed, when some neuronal variation is taken into account, such as narrow- versus broad-spike shape as a proxy for putative inhibitory/excitatory neurons, differences in attentional modulation across neuronal classes are observed [6, 7]. Our goal was to obtain a mechanistic understanding of attentional modulation by utilizing a more granular or neuron- and circuit-specific approach to directly test whether attentional modulation depends on neuronal feature selectivity.

Visual attention modulates the firing rate of neurons as early in the visual processing hierarchy as the visual thalamus, the lateral geniculate nucleus or LGN [8–10]. Attentional modulation of firing rate, averaged across neurons within each visual cortical area, scales up at progressive stages of the visual cortical hierarchy. In primary visual cortex (V1), attention has negligible or modest effects on average neuronal firing rate; in intermediate visual cortical areas such as MT (middle temporal) and V4, attention significantly modulates average neuronal firing rate; and, in the frontal eye fields, attention robustly modulates average neuronal firing rate [2, 3, 11–15]. The most common metric for attentional modulation of firing rate is the attention index, which is the difference divided by the sum of neuronal firing rates measured in each attention condition, i.e., when the subject is attending toward versus away from the visual stimulus in the receptive field of recorded neurons. Interestingly, the distributions of attention index values for recorded visual cortical neurons are broad, including neurons that are not modulated or even suppressed by attention [2, 3, 15]. This variation in attentional modulation of neuronal firing rate within each visual cortical area suggests that intuitive "attention spotlight" or simple gain enhancement models of attention cannot explain the full diversity of attention effects. Furthermore, it is possible that we may learn more about the neuronal mechanisms of attention by examining the variation in attentional modulation across neurons within a visual cortical area than by simply focusing on the average attentional modulation in a given visual cortical area.

We sought to understand the rules governing attentional modulation of neuronal firing rate. In other words, we wanted to discover why some neurons are facilitated, some suppressed, and others not modulated by attention. In parallel, we also

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