

Journal Club

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In-Depth Investigation: How Low Can You Go?

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Review of Nienborg and Cumming (<http://www.jneurosci.org/cgi/content/full/26/37/9567>)

Since Hubel and Wiesel's pioneering work on orientation selectivity in primary visual cortex (V1), the response properties of more than thirty visual areas within the primate brain have been studied. Some of these reports emphasize the hierarchical structure of the visual pathways. Within these streams, it is commonly found that visual neurons at successive stages of processing display more complex receptive fields than their afferents. However, it is not uncommon for different areas to respond to similar stimulus properties. Most prominently, cells selective for small position differences on corresponding retinas (binocular disparity), have been found at numerous cortical sites in both the dorsal and ventral processing streams (Cumming and DeAngelis, 2001). The close correspondence between spatial and temporal resolution of binocular disparity signals in V1 and stereoscopic vision raises the question of why additional representations in extrastriate cortex are needed (Nienborg et al. 2004; 2005). Recently, an intriguing study in the *Journal of Neuroscience* provides a possible answer, suggesting that despite the exquisite sensitivity of V1 neurons to binocular disparity; perceptual decision-making might be based on downstream areas, starting in V2 (Nienborg and Cumming, 2006).

To examine the relationship between perception and neural activity in disparity selective cells in V1 and V2 of macaque

monkeys, Nienborg and Cumming (2006) recorded extracellularly from single neurons while the animals performed a coarse disparity discrimination task. The monkeys were trained to report whether a central patch of random dots appeared closer or farther than a surrounding annulus which was fixed at zero disparity. Task difficulty was manipulated by adjusting the number of binocularly correlated dots in the central patch-uncorrelated dots are akin to noise in the stimulus. Previously, it had been shown that single neuron firing rates in the cortical middle temporal area (MT) could be used to discriminate between such stimuli with a precision equivalent to that of the observer (Uka and DeAngelis, 2003). Importantly, there is also a significant trial-by-trial correlation between variations of neural activity in area MT and perceptual judgments of a constant [choice probability (CP)] (Uka and DeAngelis, 2004).

In the study by Nienborg and Cumming (2006), the authors specifically examined whether (other things being equal) there were differences in choice probability between neurons in V1 and V2. To do so, they first determined whether signals from cells in these areas were equally informative for this task and whether neuronal and psychophysical sensitivity was well matched. For a direct comparison of neuronal and behavioral performance, the authors used standard signal detection methods (Parker and Newsome, 1998) to generate neurometric thresholds that they then compared with equivalent psychometric measures [Nienborg and Cumming (2006), their Fig. 1 ([\[full/26/37/9567/F1\]\(http://www.jneurosci.org/cgi/content/full/26/37/9567/F1\)\]\]. The authors report that, on average, the sensitivity of V2 neurons matches psychophysical sensitivity, whereas in V1 neural sensitivity was ~1.5 times lower than psychophysical sensitivity \[Nienborg and Cumming \(2006\), their Fig. 2 \(<http://www.jneurosci.org/cgi/content/full/26/37/9567/F2>\)\]. To be sure that any observed differences in the strength of neuroperceptual correlation in V1 and V2 could not be attributed to a difference in sensitivity, subsequent choice probability analyses were only performed on neurons with neuronal/psychophysical threshold ratios near unity. This relies on the assumption that these cells are the basis for the perceptual performance of the monkey.](http://www.jneurosci.org/cgi/content/</p>
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Interestingly, the authors found a significant choice probability only in their sample of V2 neurons [Nienborg and Cumming (2006), their Figs. 5 (<http://www.jneurosci.org/cgi/content/full/26/37/9567/F5>) and 6 (<http://www.jneurosci.org/cgi/content/full/26/37/9567/F6>)]. In addition, these "choice effects" were slightly smaller than those reported previously for area MT (Fig. 1) (Uka and DeAngelis, 2004). The authors went to great lengths to rule out potential confounds that could account for the observed differences in choice probabilities between visual areas. Specifically, they controlled for the effects of eye position, stimulus size, and symmetry of disparity tuning curves. These measures reflect the level of technical rigor permeating this study, lending credence to the reported results. Our sole concern rests on the fact that because of the requirement that neuronal sensitivity be matched between the

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V1 and V2 samples, many neurons in V1 had to be excluded from the choice probability analysis.

Finally, Nienborg and Cumming (2006) measured the interneuronal correlation (or “noise” correlation) between single unit (SU) and multiunit (MU) activity on a single electrode. When this noise correlation was weighted by the similarity in tuning (“signal correlation”) between the SU and MU samples, a significant correlation between weighted noise correlation and choice probability was found in V2 but not V1, potentially because of corresponding anatomical clustering of similar response properties in these areas [Nienborg and Cumming (2006), their Fig. 10 (<http://www.jneurosci.org/cgi/content/full/26/37/9567/F10>)]. This is particularly exciting, as it provides empirical evidence in support of previous models suggesting that the choice probability signal arises because of greater interneuronal correlation between neurons with similar tuning preferences (Shadlen et al., 1996). Hence, this effect could perhaps provide a mechanistic explanation for the observed differences in neuroperceptual correlations in the present study.

The authors propose several possible interpretations for their results. Most straightforwardly, it is possible that V1 neurons play no role in the perceptual decision. Significant CPs, that is, a greater trial-by-trial relationship between neuronal activity and perceptual reports than we would expect by chance alone, have by now been reported for many extrastriate visual areas and tasks; establishing a boundary between areas that do and do not exhibit significant CPs for a given task is crucial as it sheds light on the specific computations and pathways underlying perceptual decisions.

However, it is also possible that although V1 signals are integral in the formation of the percept, choice related modulations are the result of a feedback process that terminates in extrastriate cortex. Finally, it also could be the case that V1 neurons contribute to the decision in a feedforward manner, but given current methods, this contribution is undetectably small. The authors admit that there is presently no empirical basis for a differentiation among these theoretical alternatives.

To reach a more definite conclusion regarding the relation between V1 activity and perception, it would be interesting to replicate this study with an orientation

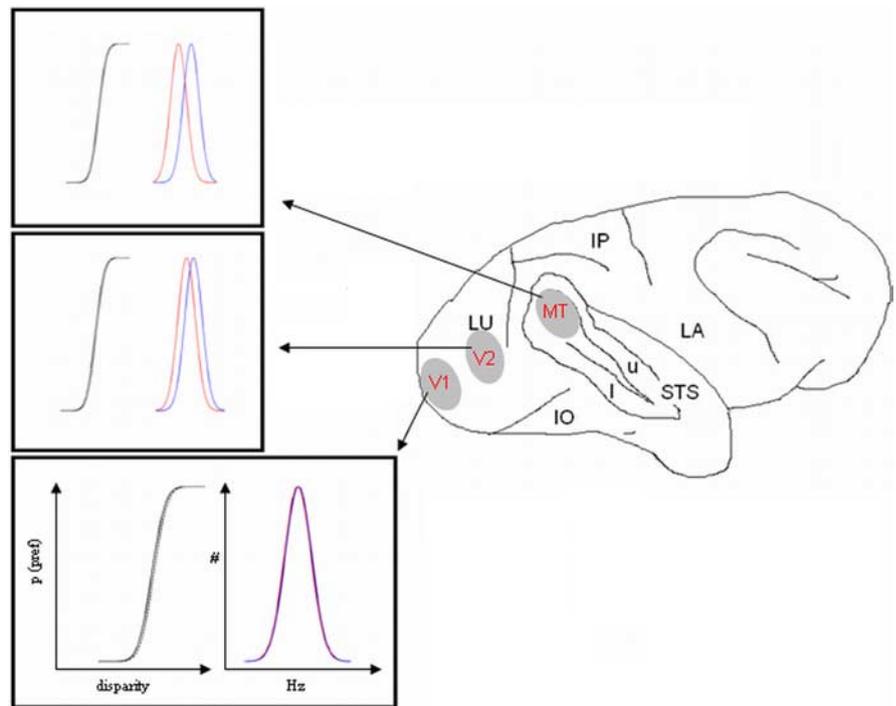


Figure 1. A schematic lateral view of the macaque brain. The superior temporal sulcus (STS) is opened to show the upper bank (u), floor (f), and lower bank (l). Visual areas relevant to this study are emphasized in gray. The panels to the left represent the idealized psychometric (—) and neurometric (---) functions as well as firing rate histograms for preferred (blue) and antipreferred (red) choices for a given stimulus in area V1 (bottom), V2 (middle), and MT (top). Insets (from left), panel 1: ordinate, proportion of preferred disparity choices; abscissa, binocular disparity; panel 2: ordinate, number of trials; abscissa, firing rate in hertz.

discrimination task. Because orientation tuning preferences are clustered in V1, the model accounting for the effects observed in this study (Shadlen et al., 1996) would predict high CPs in both V1 and V2.

The issue of whether the choice-related modulations observed in studies of neuroperceptual correlation is caused by feedforward or feedback effects is relevant far beyond the field of depth perception. For example, it is striking that the choice effects seen in extrastriate areas are typically similar to the effects observed in studies of attentional modulation of sensory activity. Determining the mechanistic cause underlying these effects will be of chief importance for future investigations of the neural substrates of subjective perception.

Finally, we can also ponder the functional cause for the lack of neuroperceptual correlates in primary visual cortex. We suggest that the need for global and reliable representations of the visual environment is a very plausible explanation. High-resolution estimates of visual features are often noisy, this means that multiple local samples must be integrated to obtain veridical estimates of global object properties. As such, signals from primary visual cortex might accurately reflect the

local structure, but not the global properties of objects and surfaces.

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