A Causal Effect of Macaque V2 in a Coarse Disparity Discrimination Task

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Abstract:
Many V2 neurons are selective for binocular disparity. V2 is also the earliest site in the visual processing hierarchy for which systematic correlations across the population between neural responses and an animal’s behavioral choice in disparity based tasks have been observed. However, while these choice correlations suggest a link between the neural activity and perceptual choice, it has long been recognized that they do not establish a causal relationship. Here, we sought to test whether macaque V2 plays a causal role on coarse disparity judgements. We used microstimulation on disparity selective sites in V2 whilst animals performed a coarse disparity discrimination task. We found that microstimulation led to a systematic shift of the psychometric function towards the preferred disparity of the stimulated site, supporting a causal role for V2 neurons in disparity discrimination.

Keywords: decision-making; binocular disparity; microstimulation;

Introduction
In a 3D environment, we can use various cues to judge the depth of objects of interest, including binocular disparity. Neurons in several visual areas are selective for binocular disparities, including V1, but V2 is the earliest to show evidence of a topographical map for binocular disparities (Chen et al, 2008). Moreover, V2 is the earliest area for which across the population, disparity selective neurons correlate significantly with an animal’s choice during disparity-discrimination tasks (Nienborg & Cumming, 2006, Prince et al. 2002, Clery et al. 2017). These choice correlations suggest a link between the activity of V2 neurons and perception in disparity discrimination tasks.

Here we sought to test whether V2 neurons exert a causal effect on behaviour in a coarse disparity discrimination task.

Methods
All procedures were in agreement with the Public Health Service policy on humane care and use of laboratory animals and approved by the Institute Care and Use Committee. Two macaque monkeys performed a coarse disparity discrimination task (Fig 1, left). The stimulus was a dynamic random-dot stereogram, whose central portion was either ‘near’ or ‘far’ with respect to the fixation plane and surrounding annulus. Difficulty was manipulated either by varying the number of binocularly correlated dots (Nienborg and Cumming, 2006) or the proportion of signal frames (Nienborg and Cumming, 2009) in each stimulus. Animals responded by making a saccade to the corresponding near or far target.

Prior to the task, sites for electrical microstimulation (cf. Salzmann et al. 1990) were selected by measuring the disparity selectivity of V2 neurons in 100µm steps over 300µm, and selecting a site roughly in the middle of a cluster with similar tuning preferences, similar to DeAngelis et al. (1998). The disparities that elicited the highest and lowest responses (Fig 2, left) were used as the preferred and null signal disparities in the task.

Figure 1 – Coarse disparity discrimination task.  
Left: Spatial arrangement of fixation, stimulus and targets. Right: Sequence of trial events.
Microstimulation was applied at 20µA (biphasic 200 µs cathodal followed by 200µs anodal pulses at 200Hz) in randomly interleaved trials for the entire duration of the stimulus presentation (Fig 1, right).

We measured the psychophysical performance of the animals, and divided trials into two conditions dependent on whether microstimulation was applied or not. Cumulative Gaussians were fit to the behaviour for each condition in each session. Sessions in which the fits did not explain >80% of the variance were excluded from further analysis. We quantified the effect of microstimulation on behaviour as the shift in the point of subjective equality (PSE: defined as the mean of the cumulative Gaussian; Fig 2).

Results
Microstimulation led to a significant shift in the PSE, towards the preferred disparity of the V2 stimulated sites (Fig 3; both monkeys: µ=5.7, p=.001; monkey D: µ =7.1, p=.02; monkey R: µ=4.4, p=.02, n=37).

![Figure 2: Disparity tuning (left) and psychophysical performance (right) for two example sessions from monkey D (top) and monkey R (bottom). Left: gray arrows indicate disparities used as signal values in the task. Right: microstimulation behavioral data and fits shown in red, control in blue.](image)

![Figure 3: Behavioural effect of microstimulation on V2 neurons. Rightward shifts in the PSE indicate a bias towards the preferred choice of the stimulated neurons.](image)

Conclusion
We found that electrical microstimulation during a coarse disparity discrimination task significantly biased the animals’ perceptual choices towards the preferred disparity of stimulated sites in V2. This supports a causal role of activity in V2 on perception in this task.

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References
Chen, (2008). A map for horizontal disparity in monkey V2. Neuron, 58(3), 442-450.

Clery, S., Cumming, B.G., Nienborg, H. (2017). Decision-related activity in macaque V2 for fine disparity discrimination is not compatible with optimal linear readout. Journal of Neuroscience, 37(3), 715-725

DeAngelis, G.C., Cumming, B.G., Newsome, W.T. (1998). Nature, 394(6694), 677-80

Nienborg, H., Cumming, B.G. (2006). Macaque V2 neurons, but not V1 neurons, show choice-related activity. Journal of Neuroscience, 26(37), 9567-78

Nienborg, H., Cumming, B.G. (2009). Decision-related activity in sensory neurons reflects more than a neuron’s causal effect. Nature, 459(7243), 89-92

Prince, S.J.D., Pointon, A.D., Cumming, B.G., Parker, A.J. (2002). Quantitative Analysis of the Responses of V1 Neurons to Horizontal Disparity in Dynamic Random-Dot Stereograms. Journal of Neurophysiology, 87(1), 191-208

Salzman, C.D., Britten, K.H., Newsome, W.T. (1992). Cortical microstimulation influences perceptual judgements of motion direction. Nature, 346, 174-177