

REPLY TO DOI ET AL.:

# Functional architecture matters in the formation of perception

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We agree that elimination of false matches is a multistep process and show that V2 is an important step in the process. Below, we further show that by integrating disparity domain neuron responses (Fig. 1A, large red circle) with similar preferred disparity but across different preferences of other visual features [including spatial scale, receptive field size, and phase disparity (Fig. 1D), based on previously published data (1, 2)], our model preserves responses to correct matching (Fig. 1C, solid red line) and greatly attenuates responses to false matching (Fig. 1C, dashed red line). We extend the energy model to a population level as suggested by Doi et al. (3) to account for our findings in V2 (4). We start with neurons similar to previously described single-neuron responses: Each neuron (Fig. 1A, small blue circles) is responsive to both correct (defined by cRDS; Fig. 1B, solid blue line) and to false (defined by aRDS; Fig. 1B, dashed blue line) matches as predicted by the energy model. Based on an estimate of 110,000 neurons per cubic millimeter of cortical tissue (5) and the average size of a V2 disparity cluster of 3.5 mm<sup>3</sup> (4, 6, 7) for 10–15 different disparities within that cluster, each would integrate on the order of 30,000 neurons. We further estimated the number of neurons needed in the population to achieve a result that predicts the percept. To do this, we defined the “perceptual index” for different numbers of neurons in the population model. A perceptual index value of 100 indicates complete discarding of false matches and is close to the subject’s depth percept, while a value of 0 indicates no attenuation to false matches. As shown in Fig. 2, by examining a range of populations from 2 neurons to 100,000 neurons, the ability to discard false matching increases: the more

neurons included, the lower the response to false matching. With as few as 250 neurons, the amplitude of response to false matches is reduced by 91% (perceptual index of 91). A disparity domain with 30,000 neurons, according to our model, eliminates 97% of false matches. An additional layer of pooling inputs from multiple V2 neurons within one disparity domain could further reduce aRDS response among single neurons in V4 and inferior temporal cortex (8–10). These simulations illustrate that V2 can respond to correct matches and reject false ones by pooling over the population. The greater the numbers pooled, the better the performance. By pooling over a population of neurons with similar disparity preference, binocular correspondence for depth percept can be established.

Optical imaging demonstrates the importance of functional architecture: The selectivity of population response to cRDS and aRDS suggests the importance of neuronal clustering within a single cortical locus. The presence of a population of disparity preference neurons within single V2 disparity domains provides a key constraint to population pooling and provides a feasible number of neurons to help solve the binocular correspondence problem. Such a demonstration would be difficult with traditional single-unit approaches.

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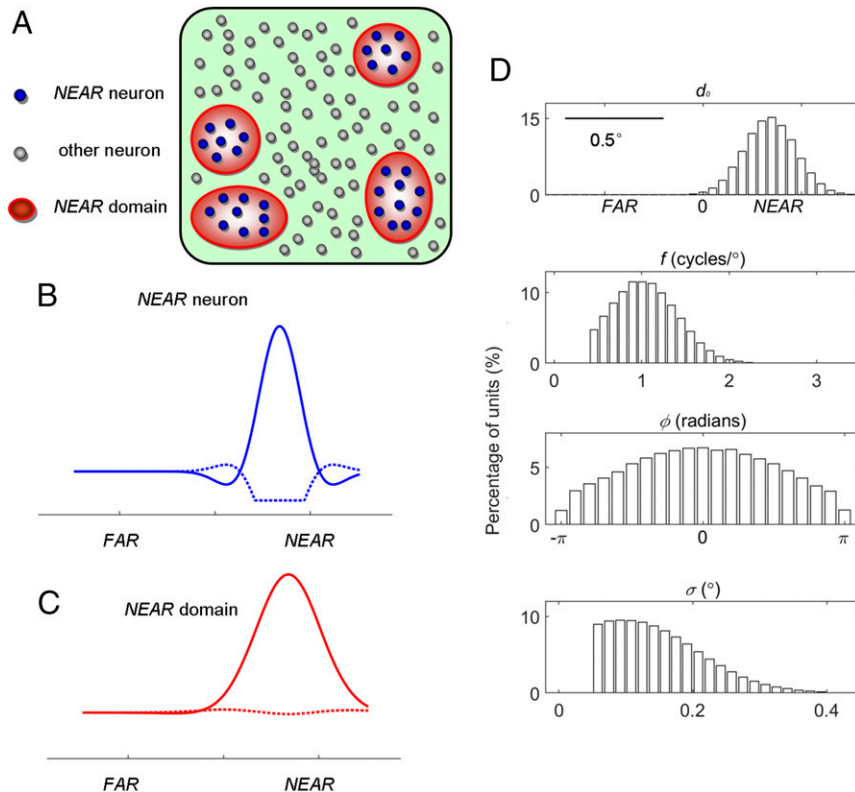
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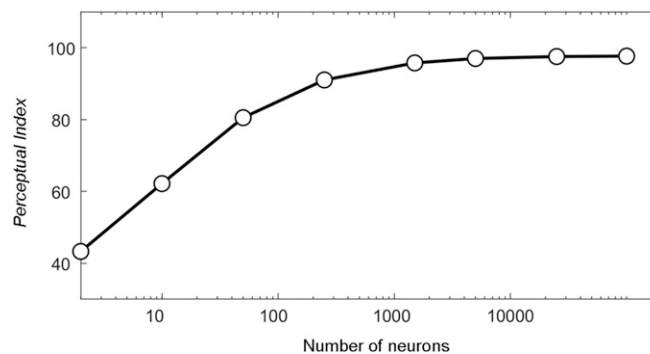
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**Fig. 1. Energy model with population extension. Tuning curve to binocular disparity  $d$ :  $R(d) \left[ A e^{-(d-d_0)^2/2\sigma^2} \times \cos(2\pi f(d-d_0) + \phi) + R_{\text{mean}} \right]$ .** The parameters ( $A$ , amplitude;  $d_0$ , preferred disparity;  $\sigma$ , width of receptive field size;  $f$ , spatial frequency;  $\phi$ , disparity phase; and  $R_{\text{mean}}$ , average response) of individual neurons were chosen independently and at random from distribution described in **D**. **(A)** Neurons with similar NEAR disparity preferences (blue circles) are shown clustered. **(B)** A single-neuron disparity tuning curve to cRDS (solid blue line) and to aRDS (dashed blue line). **(C)** Population disparity tuning curves show that tuning to cRDS (solid red line) is retained but that to aRDS (dashed red line) is lost.



**Fig. 2. Larger populations are better at discarding false matches.** For each population size, we simulated 500 unique neuron populations. The population responses were calculated by linearly summed the output of all simulated neurons. Neural noise was not modeled. Responses of single neurons to aRDS were obtained by using a decreased amplitude ( $0.52 \cdot A$ ) and  $\pi$  additional in phase.  $\text{Perceptual\_index} = 100 - 100(\text{SD}_{\text{aRDS}}/\text{SD}_{\text{cRDS}})$ .  $\text{SD}_{\text{aRDS}}$  and  $\text{SD}_{\text{cRDS}}$  are the SD of the simulated neuronal or population responses to aRDS and cRDS stimulus with binocular disparities between  $-1^\circ$  and  $+1^\circ$  at  $0.01^\circ$  step. The distribution of perceptual index among simulated populations of 2–100,000 neurons.

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