

# Experience-Dependent Representation of Visual Categories in Parietal Cortex

David J. Freedman and John A. Assad

## Supplementary Methods

**Computation of BCD, WCD and category-tuning index values.** The strength of neuronal category-tuning was estimated by a category-tuning index that was computed from two values: (1) the average within-category difference (WCD) in firing rates between pairs of directions in the same category, and (2) the average between-category difference (BCD) in firing rates between pairs of directions in different categories. Our goal was to have equal numbers of paired comparisons for the BCD and WCD calculations, and to only include comparisons that were represented in both BCD and WCD calculations. For these reasons, both BCD and WCD values were determined by computing the average absolute firing-rate differences for 18 pairs of directions, including comparisons across 30°, 60°, 90°, 120°, and 150° intervals. 180° was excluded from the BCD calculation because there were no corresponding pairs of directions for the WCD calculation that were 180° apart and in the same category (although, including the 180° BCD interval gave qualitatively similar results). The 18 pairs used for the WCD calculations were identical in structure to the 18 pairs used for the BCD, except that they were all rotated 90° with respect to the category boundary. In other words, we used the 18 within-category pairs of directions (nine in each category) for the WCD calculation that, when rotated 90°, crossed the category boundary. For example, the 30° BCD value was computed across the two pairs of directions that were 30° apart and crossed the category boundary (i.e. 120° - 150° and 300° - 330°; Suppl. Fig. 7a). The 30° WCD value was computed across the two pairs of directions that crossed the line perpendicular to the category boundary (e.g., 210° - 240° and 30° - 60°; Suppl. Fig. 7b). This process was repeated for the other four direction intervals (60°, 90°, 120°, and 150°) giving average BCD and WCD values for each of the five intervals. These five average values were in turn averaged, giving one BCD and one WCD value for each neuron.

A standard index was constructed from the BCD and WCD values by the following formula:  $(\text{BCD} - \text{WCD}) / (\text{BCD} + \text{WCD})$ . Values of the index can vary from -1.0 to 1.0. Positive values of the index indicate larger differences in firing across the category boundary and more similar firing within each category. Very large index values (near 1.0) indicate “binary-like” responses to the 12 directions according to their category membership (i.e. uniform responses to directions in the same category and sharp distinctions between categories). A value of -1.0 would indicate a neuron that would be perfectly category selective if the category boundary was perpendicular to the actual category boundary. We verified that the category tuning index was not inherently biased (i.e. shifted towards positive or negative values) by computing the index for sets of 12 randomly generated values (simulating the firing rates to the 12 directions) that could vary from 0 to 100. We repeated this process one million times to generate a distribution of category indices, and found that the mean index value (0.00011) was not significantly different from zero (t-test,  $p = 0.33$ ).

It is important to note that, in principle, any neuron that is direction selective could have a positive index if its preferred direction is sufficiently far from the category boundary. For example, Suppl. Fig. 1c shows a single direction-tuned MT neuron with a preferred direction of ~240° and a category index value of 0.438. We found many such neurons in MT (Suppl. Fig. 2c),

as expected. However, if there is a uniform distribution of preferred directions among neurons, we should find just as many neurons with preferred directions *near* the category boundary—and thus just as many neurons with *negative* category indices. For example, the MT neuron in Suppl. Fig. 1a has a preferred direction of  $\sim 0^\circ$  and category index of -0.413. Thus, overall, the *average* category index across a population of such neurons should be zero. This was exactly what we found for MT (Suppl. Figs. 2c,d). The fact that we found that the distributions of category indices were shifted positively for LIP (Fig. 3c,d in main text) indicates that there were more LIP neurons with preferred directions away from the category boundary than near the category boundary. This was confirmed in Fig. 4 of the main text.

Note that in calculating the BCD and WCD we did not include all of the possible pairs of comparisons ( $(6:2) \times 2 = 30$ ). For example, we could also have included the  $30^\circ$  interval between  $60^\circ$  and  $90^\circ$  in the WCD calculation (Suppl. Fig. 7). Including these intervals is problematic, because it results in an interdependence between the BCD and WCD values that distorts the symmetry of the distribution of possible index values. For example, if BCD and WCD are interdependent, it would be impossible to have a non-zero value of the WCD and a value of zero for the BCD. Thus if we had included all comparisons in the index, the value of the category tuning index could be +1.0 but could never approach values near -1.0. Therefore, we did not include these comparisons in calculating the actual BCD, WCD and category-tuning index. Although, including these direction pairs in the calculation of BCD and WCD values gives nearly identical results.

The general results of the BCD, WCD and category-index analyses did not critically depend on the details of how BCD and WCD were computed. Similar results (i.e., larger firing rate differences between categories) were obtained for LIP neurons using the BCD and WCD values computed separately at each of the five direction intervals ( $30^\circ$ ,  $60^\circ$ ,  $90^\circ$ ,  $120^\circ$ , and  $150^\circ$ ). For example, if the BCD and WCD were computed using only the pairs of directions that were  $30^\circ$  apart, BCD values were significantly greater than WCD values during both the sample (BCD: 6.26 Hz, WCD: 4.73 Hz, t-test,  $p \approx 10^{-5}$ ) and late-delay epochs (BCD: 5.66 Hz, WCD: 2.61, t-test,  $p \approx 10^{-7}$ ) across the populations of LIP direction-selective neurons ( $N = 102$  sample,  $N = 48$  late-delay). These results are qualitatively similar to the results obtained (and shown in Fig. 3) by computing the average BCD and WCD values across the 18 between-category and 18 within-category intervals described above. Similar results were obtained by evaluating the significance of neuronal effects by using non-parametric tests (e.g. Wilcoxon rank-sum and sign tests) in addition to the parametric statistics described here.

## Supplementary Results

**LIP Selectivity During Test-Epoch.** During the test epoch, we also observed category-selectivity for the *currently visible* test stimulus (Supplemental Fig. 5a). A majority of direction-selective neurons (sample epoch,  $N = 115$ ) showed the same category preference for both the sample stimulus (during the sample epoch) and the test stimulus (during the test epoch) ( $N = 98/115$  or 85%, Supplemental Fig. 5b). In contrast with previous studies of secondary somatosensory cortex<sup>1</sup>, premotor cortex<sup>2</sup>, inferior temporal cortex<sup>3</sup>, and prefrontal cortex<sup>4,5</sup>, relatively few ( $N = 12/156$  or 8%) LIP neurons showed activity that differentiated between match and non-match (hold vs. release) trials during the test epoch (t-test,  $P < 0.01$ ), with equal numbers (6/12 or 50%) showing a preference for matches as non-matches.

**Error-Trial Analyses.** To compare neuronal category selectivity on correct and error trials, we conducted a choice probability analysis of neuronal firing rates with respect to the two categories (breaks of fixation and lever releases during the sample or delay epochs were not included as error trials). We focused this analysis on sample directions closest to ( $15^\circ$ ) the category boundary (where the monkeys made the largest number of errors). Each neuron's category preference was determined by averaging the firing rates to directions in each category on correct trials, excluding those closest to ( $15^\circ$ ) the category boundary. For each neuron, we computed the area under the ROC curve generated by comparing average firing rates between preferred and non-preferred stimuli on both correct and error trials. This analysis returned values between 0.0 and 1.0, where values greater than 0.5 indicate stronger responses for the preferred category. Values less than 0.5 indicate stronger responses to the non-preferred category. As shown in Supp. Fig. 4, this analysis revealed that category selectivity (area under the ROC curve) among direction selective neurons was significantly stronger on correct trials (sample: mean ROC area = 0.64; delay: mean ROC area = 0.70) vs. error trials (sample: mean ROC area = 0.44; delay: mean ROC area = 0.46) according to a paired t-test (sample:  $p \approx 10^{-12}$ ; delay:  $p \approx 10^{-9}$ ). Across the population of direction-selective neurons, neuronal category selectivity during the sample epoch was "reversed" (average ROC values were significantly less than 0.5) on error trials (mean error-trial ROC = 0.44, t-test,  $P = 0.013$ ). During the late-delay, we observed a similar trend that did not reach statistical significance (mean error-trial ROC = 0.46, t-test,  $p = 0.16$ ).

**Relationship between category task and memory-saccade task selectivity.** We evaluated the relationship between spatial selectivity during the memory saccade task and category selectivity during the DMC task. To do so, we first determined the best memory saccade target location (of 8 total locations) and constructed a selectivity index by taking the difference between best and opposite (the target located  $180^\circ$  away) locations divided by their sum. This produced index values that could vary from 0 (no selectivity) to 1 (strong selectivity). For each neuron, memory-saccade index values were computed during both the saccade-target presentation and subsequent delay epochs. We then compared the values of the memory-saccade index to those of the category-selectivity index across the entire population of neurons, using a correlation analysis. Interestingly, there was no obvious relationship between the strength of memory-saccade spatial selectivity and category selectivity during either the sample (correlation coefficient = -0.015,  $p = 0.86$ ) or delay (correlation coefficient = 0.051,  $p = 0.53$ ) epochs.

**Relationship between LIP receptive field location and category-boundary selectivity.** To determine whether the pattern of LIP category selectivity varied according to the location of neurons' receptive fields, we recomputed the best boundary analysis (as in figure 4) separately for the populations of LIP neurons with receptive field locations in the upper and lower quadrants of the visual field (relative to fixation). For each neuron, we determined which of the six possible category boundaries (i.e., the "new" and "old" boundaries, plus the four other boundaries that we did not use) gave the largest difference in average firing rate across directions on either side of the boundary. This revealed that category selectivity did not vary systematically with receptive field location. Supplementary figs. 6a and 6b show polar distributions of the best boundary during the late delay epoch with monkeys trained on the original category boundary, separated according to the location of LIP receptive fields (a: upper quadrant; b: lower quadrant). Supplementary figs. 6c and 6d show polar distributions of the best boundary during the late delay

epoch with monkeys trained on the new category boundary, separated according to the location of LIP receptive fields (c: upper quadrant; d: lower quadrant).

**Relationship between LIP activity and reward probability.** Previous studies suggest that LIP neurons are sensitive to the expected-reward or value associated with stimuli and/or actions<sup>6,7</sup>. In our study, monkeys were more likely to make categorization errors for stimuli near the category boundary, resulting in a lower probability of reward on those trials (Fig. 1c). Because of this, it is plausible that the monkeys' might have a lower expectation of reward on trials with sample stimuli that were close to the category boundary. This might be reflected in LIP activity, for example, by weaker average responses for stimuli closest to the category boundary. In principle, a reward-probability signal such as this combined with a population of direction selective neurons with uniformly distributed preferred directions could result in a non-uniform distribution of preferred directions that is biased along an axis perpendicular to the category boundary.

To determine whether there was a tendency for lower average LIP activity for stimuli close to the category boundary that might reflect a reward probability signal, we computed average firing rates across the entire population of 156 LIP neurons at the three distances from the category boundary (15°, 45°, and 75°) during the late-delay epoch (where category effects were strongest). The results showed that average LIP firing rates were not significantly different between the easiest (75°) and most-difficult (15°) stimuli (15°: 23.82 Hz, 45°: 23.96 Hz, 75°: 24.07; 15° vs. 75° paired t-test,  $p = 0.12$ ; Wilcoxon Ranksum Test,  $p = 0.91$ ). This suggests that there was not an obvious relationship between reward-probability and LIP activity during the DMC task. Similar results were observed when the analysis was applied separately to the populations of direction-selective and non-selective neurons.

## References

1. Romo, R., Hernandez, A., Zainos, A., Lemus, L., & Brody, C.D. Neuronal correlates of decision-making in secondary somatosensory cortex. *Nat Neurosci* **5**, 1217-25 (2002).
2. Romo, R., Hernandez, A., & Zainos, A. Neuronal correlates of a perceptual decision in ventral premotor cortex. *Neuron* **41**, 165-173 (2004).
3. Miller, E.K., Li L., & Desimone, R. Activity of neurons in anterior inferior temporal cortex during a short term memory task. *J Neurosci* **13**, 1460-1478 (1993).
4. Miller, E.K., Erickson, C.A., & Desimone, R. Neural mechanisms of visual working memory in prefrontal cortex of the macaque. *J Neurosci* **16**, 5154-5167 (1996).
5. Freedman, D.J., Riesenhuber, M., Poggio, T., & Miller, E.K. Visual categorization and the primate prefrontal cortex: neurophysiology and behavior. *J Neurophysiol* **88**, 914-928 (2002).
6. Platt, M.L. & Glimcher, P.W. Neural correlates of decision variables in parietal cortex. *Nature* **400**, 233-238 (1999).
7. Sugrue, L.P., Corrado, G.S. & Newsome, W.T. Matching behavior and the representation of value in the parietal cortex. *Science* **304**, 1782-1787 (2004).