Title: Hierarchical shape processing and position tolerance in rat lateral visual cortex.

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Summary: Recent studies have revealed a surprising degree of functional specialization in rodent visual cortex. However, these studies fall short of establishing a functional hierarchy. We designed a study in rats that targets two hallmarks of the hierarchical object vision pathway in primates: higher tolerance for image transformations and selectivity for behaviorally relevant dimensions. We targeted five visual areas from primary visual cortex (V1) over areas LM, LI, LL, up to lateral occipito-temporal cortex (TO).We examined the responses of single neurons in these regions to six simple shapes used previously to probe monkey anterior infero-temporal cortex. These shapes were slowly jittering around a particular position of the stimulus display during 4s per presentation. After delineating the receptive field (RF) of each neuron, we presented the six shapes around one (Exp. A; N=299 cells) or two (Exp. B; N=258 cells) positions within the RF. First, we quantified the selectivity of populations of neurons in each visual area using all data from Exp. A plus the most responsive position of Exp. B. Overall discrimination performance was highly significant in all visual areas, although it decreased from V1 to higher visual areas. Neighboring areas were correlated with respect to which shape pairs were easiest to discriminate. This correlation suggests that the representation of shape transforms gradually across areas. In addition, we found evidence for an increase in position tolerance along the five areas. In TO, the preference for different shapes at one position was most closely related to the shape preference at another position. Finally, we found strong correlations between TO selectivity and behavioral performance of rats in a discrimination task. These findings demonstrate that the functional specialization in lateral rodent visual cortex reflects a processing hierarchy resulting in the emergence of tolerance and complex selectivity.

Additional Detail: Exp. A: Neural responses to 6 translating geometric shapes were recorded and used in population analysis (N cells per area: 105; 96; 161; 91; 104). We trained and cross-validated pattern classifiers (linear SVM) in pairwise shape discriminations. The average SVM performance over 15 shape pairs for 5 areas is shown in Fig. 1A. The correlation between areas in terms of the variation in performance across shape pairs is shown in Fig. 1B and indicates that the representation of shapes changes gradually over areas (Fig. 1C). The representation in V1 corresponded best with benchmark physical similarity measures (pixel-wise difference, Pix, and simulated V1 responses, V1s). The representation in TO was not correlated with V1 or the physical similarity benchmarks.



Figure 1: Summary of neural discriminability results. A) Average SVM performance per area; red bars indicate significance thresholds. B) Correlation matrix comparing 5 neural areas and 2 benchmark measures of physical similarity. C) The correlation between two areas is inversely related to the physical distance between the two areas.

Exp. B: Shapes were presented at two non-overlapping positions within the RF and responses at one position were used to train an SVM model, which was then asked to generalize to the other position. Compared to the selectivity in each area, generalization performance (position tolerance) increased over areas (Fig. 2). Also, correlations between selectivity and tolerance increased from V1 to TO, with the highest area showing near perfect correlation between both measures for individual pairs. These properties might underlie earlier behavioral work (e.g. Vermaercke & Op de Beeck, 2012, Current Biology) showing position-tolerant object recognition capabilities in rats.



Figure 2: Comparison of shape selectivity and position tolerance over areas. A) The response to the same stimulus at two different positions was compared, revealing higher tolerance (train Position 1, test generalization at Position 2; hatched bars) relative to selectivity (train/test at same position; open bars) in higher areas. B) This panel shows the increasing ratio between selectivity and tolerance for higher areas. C) For sub-populations with matching selectivity, tolerance was significantly higher in area TO.

Neural shape discriminability (Exp. A) was compared to learning speed of a different batch of animals trained to discriminate 6 out of 15 shape pairs (2 animals per shape pair). We found that the V1 representation was uncorrelated to behavior, while representations in higher areas showed significant correlations to behavior. Again, the representation in V1 and not in TO were correlated to physical similarity measures.