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Neuronal Bases of Color Categorization in Monkey Inferior Temporal Cortex

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Categorization and fine discrimination are two distinct aspects of our visual perception, both of which are clearly apparent in color vision. We can switch between these two modes of perception depending on the situation or task demands. To explore how visual cortical neurons behave in such situations, we recorded the activities of color-selective neurons in the inferior temporal (IT) cortex of two monkeys trained to perform a color categorization task, a color discrimination task and a simple fixation task. Many IT neurons changed their activity depending upon the task. A majority of neurons showed stronger responses during the categorization task. Moreover, for the population of IT neurons as a whole, signals contributing to performing the categorization task were enhanced. The task difference could be explained by the change in the response gain, indeed, the color selectivity was well conserved. These results imply that judgment of color category by color-selective IT neurons is facilitated during the categorization task and suppressed during the discrimination task as a consequence of task-dependent modulation of their activities.

1. Introduction

We are able to discriminate subtle differences in color, on the other hand, we often categorize similar colors into a single group, such as ‘red’ or ‘green.’ It is not known whether neuronal activity in the sensory cortices changes when these two cognitive functions are switched. In the present study[1)], we determined whether the responses of color-selective neurons in the inferior temporal (IT) cortex, which is an important area in color vision[2–4)], change depending upon whether the task requires the monkeys to make a categorical judgment or a fine discrimination in response to the same color stimulus.

We trained monkeys to perform a categorization task, a discrimination task and a simple fixation task. For the categorization task, monkeys were required to classify sample colors into two color categories (reddish or greenish; **Fig. 1**a). For the discrimination task, monkeys were required to make a fine color discrimination (Fig. 1b). In the simple fixation task, the monkey needed only to passively view the stimulus.

2. Methods

Behavioral tasks were alternated in blocks. There was no explicit cue to indicate the ongoing task. There were eleven sample colors that ranged from red (color 1, x=0.631, y=0.343) to green (color 11, x=0.286, y=0.603), had the same luminance (30 cd/m^2) and were equally spaced on the CIE-xy chromaticity diagram. The stimulus was usually a 2.0-deg-wide circle. The background was 10 cd/m^2 gray (x=0.3127, y=0.3290).

Single neuronal activities were recorded from the anterior part of the IT cortex, which is a

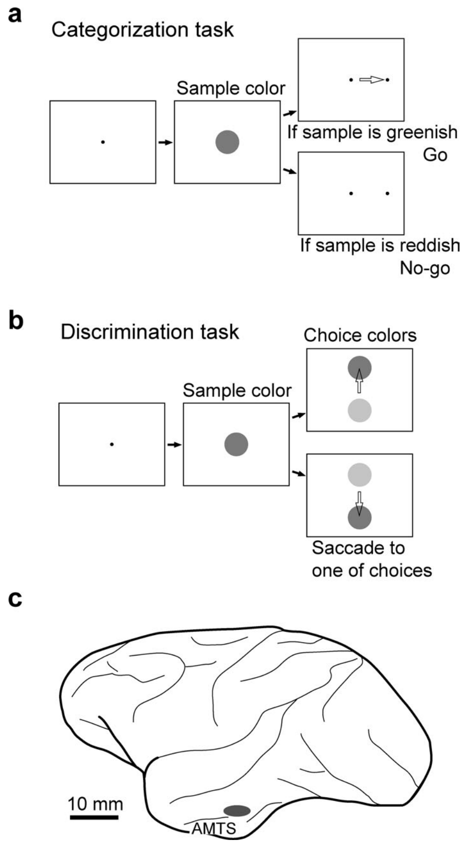

Fig. 1. Experimental paradigm and cortical area explored in this study. (a) Sequence of the categorization task. (b) Sequence of the discrimination task. Open arrows in a and b indicate required saccades. (c) Schematic illustration of the recording site within a lateral view of the monkey cerebral cortex (shown in gray).

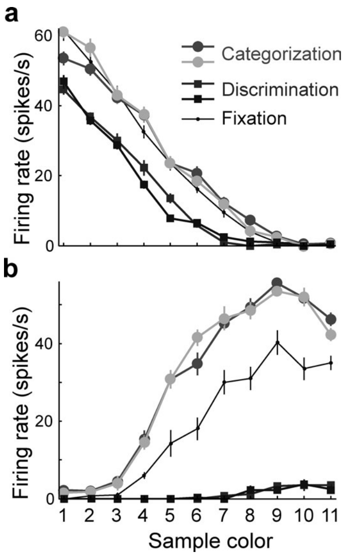

Fig. 2. Responses of two representative color-selective neurons that exhibited task dependency. The graphs show color tuning curves. Shown are mean firing rates (with s.e.m.), during the sample presentation period. The categorization and the discrimination tasks were run in two blocks, and the graphs have two sets of circles and squares for each sample color.

region where color-selective neurons are concentrated (Fig. 1c). The visual response to a sample stimulus was computed as the firing rates between 50 and 550 ms after the sample onset.

3. Results

Task dependency of neuronal responses

We found that many TE neurons showed task-dependent activities, and two such neurons are shown in **Fig. 2**. One neuron (Fig. 2a) responded strongly to red colors in all three tasks. However, the response magnitude differed across the three tasks: the response magnitudes during the categorization and fixation tasks were about the same and were consistently larger than those during the discrimination task. The color tuning curves obtained for each task block indicate that the task effect was reproducible across separate blocks. The other neuron (Fig. 2b) recorded from a different monkey showed a particularly large task effect. In the categorization task, this neuron responded strongly to green colors. The color selectivity was similar in the fixation task, although the response magnitude was considerably reduced. In the discrimination task, only tiny responses to the green stimuli were observed, and again the task dependence was reproduced in repeated task blocks.

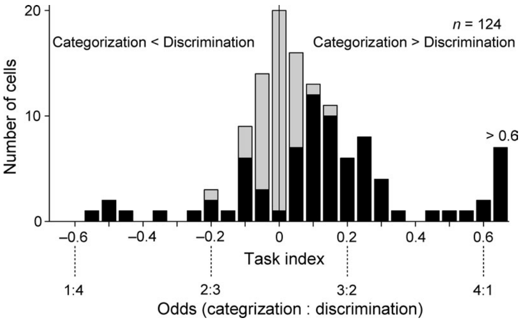

Fig. 3. Distribution of the task indices across the entire population of 124 cells. Filled bars represent 79 cells showing a significant and reproducible task effect.

To evaluate the strength of the task dependency, a task index was calculated based on the response differences during the categorization and discrimination tasks: (AC−D)/(AC+AD), where AC (AD) is the mean firing rate elicited by all sample colors in the categorization task (discrimination task). The distribution of task indices shows that index values were scattered across a wide range although there was a peak at zero (**Fig. 3**). The mean of the task index for all 124 neurons was 0.094, which was significantly different from zero (t-test, $P<0.01$). Seventty-nine neurons showed statistically significant and consistent effects of the task ($P<0.01$, 2-way ANOVA with sample colors and tasks as main factors). Dominant neurons showed stronger activity in the categorization task ($n=61$), while some neurons showed stronger activity in the discrimination task ($n=18$). The activity during the simple fixation task was generally comparable to that during the categorization task. Taken together, these results indicate that the activities of color-selective neurons in area TE are modulated by the ongoing task demands.

Difference in preferred color

The distribution of the preferred color for each group of cells showed that categorization-preferring cells tended to prefer either end of the spectrum of sample colors (1 or 11), whereas discrimination-preferring cells showed no such tendency. This confirms that categorization-preferring cells have selectivity more suited to distinguish red vs. green categories than discrimination-preferring cells.

Stability of color selectivity

As can be seen from examples of neurons (Fig. 2), the color selectivity was very similar during the two tasks, even though there are clear differences in the response magnitudes. A large majority of the 79 task-dependent neurons (61/79; 77%) showed similar color selectivity (correlation coefficient, $r>0.8$). Furthermore, the colors generating the largest responses were nearly identical in the two tasks. For most neurons (69/79; 87%), the peak distance fell within a 1-step shift. These results indicate that there was generally no task-dependent change in color selectivity.

4. Discussion

We found that neurons preferring the categorization task (categorization-preferring cells) are more common than those preferring the discrimination task, which is consistent with the idea that color processing in the IT cortex is primarily involved in the categorical perception of color[5]. Categorization-preferring cells tended to prefer either end of the spectrum of sample colors, and had selectivity that was well suited to distinguish the red vs. green categories. Because these cells carry important information needed to perform the categorization task, we can expect that up-regulation of these neurons will result in a greater selectivity for red vs. green.

The activities during the fixation task were generally more similar to those in the categorization task than in the discrimination task. This suggests that neuronal processing within the IT cortex during passive viewing of a color stimulus is similar to that during the categorization task. Assuming that the activity during the fixation task represents default processing, this observation is consistent with the idea that there is a strong tendency for color to be perceived categorically[6,7].

The present results provide new insight into the neural mechanisms underlying the cognitive control required for object recognition tasks in which mapping between sensory stimuli and motor responses must be switched. There are dense interconnections between the prefrontal cortex (PFC) and the anterior IT cortex[8], we can assume that the task-coding neurons in the PFC[9] selectively control the activities of specific populations of color-coding neurons in the anterior IT cortex.

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