

Decoding a Perceptual Decision Process across Cortex

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SUMMARY

Perceptual decisions arise from the activity of neurons distributed across brain circuits. But, decoding the mechanisms behind this cognitive operation across brain circuits has long posed a difficult problem. We recorded the neuronal activity of diverse cortical areas, while monkeys performed a vibrotactile discrimination task. We find that the encoding of the stimuli during the stimulus periods, working memory, and comparison periods is widely distributed across cortical areas. Notably, during the comparison and postponed decision report periods the activity of frontal brain circuits encode both the result of the sensory evaluation that corresponds to the monkey's possible choices and past information on which the decision is based. These results suggest that frontal lobe circuits are more engaged in the readout of sensory information from working memory, when it is required to be compared with other sensory inputs, than simply engaged in motor responses during this task.

INTRODUCTION

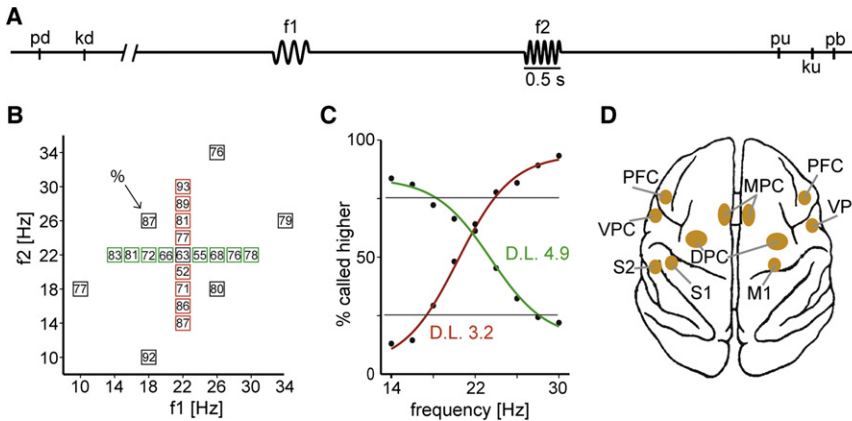
In its simplest formulation, a perceptual decision results from the interaction between past and current sensory information. A major problem in this formulation involves understanding how brain circuits represent past and current sensory events and how these representations are linked to perceptual reports (Romo and Salinas, 1999). Previously, we addressed this problem using a vibrotactile discrimination task (Hernández et al., 1997). In this task, trained monkeys compare information of the first stimulus frequency (f1) temporarily stored in working memory to the current sensory information of the second stimulus frequency (f2) to form a decision, i.e., whether $f2 > f1$ or $f2 < f1$, and to immediately report their perceptual evaluation by pressing one of two push buttons. Because this sequence depends on discrimination of highly simplified stimuli, the neuronal activity of diverse cortical areas can be examined during the same behavior (Brody et al., 2003; Chow et al., 2009; Hernández et al., 2000, 2002; Jun et al., 2010; Luna et al., 2005; Machens et al., 2005; Romo et al., 1999,

2002, 2003, 2004; Romo and Salinas, 2003; Salinas et al., 2000).

The task used in these studies simulates the behavioral condition in which the decision based on a sensory evaluation is immediately reported through a voluntary movement (Hernández et al., 1997). There are, however, behavioral conditions in which a perceptual decision can be postponed for later report. But, in theory, once the subject reaches a decision, this becomes categorical, no matter whether it must be reported immediately or reported later. If postponed, memory circuits may store the categorical decision for later report (de Lafuente and Romo, 2005; Shadlen and Newsome, 1996). However, an alternative could be that the memory circuits store not only the categorical decision, but also the information on which the decision is based (Lemus et al., 2007). This last possibility could be extremely advantageous since it gives flexibility for the decision-making process. In this case, it is possible that the decision is revised or updated as long as there is time for it to be reconsidered.

In a variant of the vibrotactile discrimination task, in which monkeys were asked to postpone their decision report, we found that the activity of medial premotor cortex (MPC, presupplementary motor area, and supplementary motor cortex) neurons during this period encodes both the result of the sensory evaluation (which corresponds to the monkey's two possible choices) and past information on which the decision is based (Lemus et al., 2007). These responses could switch back and forth with remarkable flexibility across the postponed decision report period. Moreover, these responses covaried with the animal's decision report. Thus, the MPC circuits appear critically suited to integrate and reorganize all of the elements associated with decision making in this task. Furthermore, they reflect the flexibility that is needed when a perceptual decision must be either immediately reported (Hernández et al., 2002) or postponed for later report (Lemus et al., 2007).

This result prompted us to further explore whether the neuronal responses recorded during the postponed decision period are a unique property of the MPC circuit (Lemus et al., 2007) or whether similar processes are also present in other cortical areas of the parietal and frontal lobes during this variant of the task. To further investigate this question, we recorded the neuronal activities of diverse cortical areas while trained monkeys reported a postponed decision based on previous sensory evaluation. In this task, monkeys must hold f1 in working memory and must compare it to the current sensory stimulus (f2) and must postpone the decision report until a cue triggers the

**Figure 1. Discrimination Task**

(A) Sequence of events during discrimination trials. The mechanical probe is lowered, indenting the glabrous skin of one digit of the restrained hand (pd); the monkey places its free hand on an immovable key (kd); the probe oscillates vertically, at the base stimulus frequency (f1); after a fixed delay (3 s), a second mechanical vibration is delivered at the comparison frequency (f2); after another fixed delay (3 s) between the end of f2 and probe up (pu), the monkey releases the key (ku) and presses either a lateral or a medial push-button (pb) to indicate whether the comparison frequency was higher or lower than the base, respectively.

(B) Stimulus set used during recordings. Each box indicates a base/comparison frequency stimulus pair. The number inside the box indicates overall pair.

(C) Percentage of correct trials for that (f1, f2) stimulus pair, except when the stimulus pair was identical (22 Hz; we plotted the number of times that animal pressed the lateral push button).

(D) Top view of the monkey brain and the cortical areas recorded during perceptual discrimination (orange spots). Recordings were made in primary somatosensory cortex (S1) and secondary somatosensory cortex (S2) contralateral to the stimulated hand (left hemisphere) and in primary motor cortex (M1) contralateral to the responding hand/arm (right hemisphere). Recordings were made contralateral and ipsilateral to the stimulated fingertip in prefrontal cortex (PFC), ventral pre-motor cortex (VPC), medial pre-motor cortex (MPC), and dorsal pre-motor cortex (DPC).

motor report, i.e., whether $f_2 > f_1$ or $f_2 < f_1$. Clearly, the neuronal processes associated with the postponed decision report and the task components that precede it can be analyzed across diverse cortical areas.

Here we report the extent to which the stimulus identity is encoded across diverse cortical areas in this task. We found that the encoding of f1 and f2 through all task periods is widely distributed across cortical areas. We also found that the activity of frontal lobe circuits encodes both the result of the sensory evaluation and past information on which those choices are based. Notably, the activity of primary motor cortex (M1) showed processes similar to those observed in the premotor areas (ventral premotor cortex, VPC; dorsal premotor cortex, DPC; and MPC) and prefrontal cortex (PFC), both during the comparison and postponed decision report periods. These results suggest that frontal lobe neurons have the capacity to encode during the comparison and postponed decision report periods both the final result of the sensory evaluation and past information about it.

Here we also document the nature of the neuronal responses during the stimuli and their interactions. In addition to the standard discrimination test, the neuronal activity of all cortical areas was studied when the stimuli were delivered but monkeys were not requested to perform the task. Under this condition, most neurons across the cortical areas no longer encode information about the stimuli and their interactions during these trials. The only areas that responded in this case were S1 and S2. This would suggest that those cortical areas central to S1 that encode information about the stimuli are more likely associated with the sensory evaluation, than engaged simply in encoding the sensory stimulus. We also tested each neuron in a simpler task, in which trials proceeded exactly as in the vibrotactile task, but the stimuli were not delivered to the skin and the movements were guided by visual cues. Neurons responded during

movement execution but not during the periods preceding it. These control tests show that the neuronal responses from all the cortical areas studied, except for S1, reflect both the active comparisons between f1 and f2 and the execution of the motor choice that is specific to the context of the vibrotactile discrimination task.

RESULTS

Optimal Conditions for Studying Perceptual Discrimination

Four monkeys (*Macaca mulatta*) were trained to discriminate the difference in frequency between two consecutive vibrotactile stimuli, f1 and f2 delivered to one fingertip (Figure 1A). Monkeys were asked to report discrimination after a fixed delay period of 3 s between the end of f2 and the cue that triggered the motor report (probe up, pu in Figure 1A). This delay period thus separates the comparison between the two stimuli from the motor response. In this task, monkeys must hold f1 in working memory, must compare the current sensory input f2 to the memory trace of f1, and must postpone the decision until the sensory cue triggers the motor report. Animals were trained to perform the task up to their psychophysical thresholds (Figures 1B and C). After training, we recorded the activity of single neurons from diverse cortical areas while the monkeys performed the task (Figure 1D). These recordings were made in primary somatosensory cortex (S1), secondary somatosensory cortex (S2), PFC, VPC, DPC, and MPC contralateral to the stimulated finger and in PFC, VPC, DPC, MPC, and M1 contralateral to the responding hand/arm. All neurons were recorded using the stimulus set of Figure 1B. In these trials, the comparison frequency (f2) can be judged higher or lower than f1. Thus, the neuronal responses across trials can be analyzed as functions of f1, f2, $f_2 - f_1$, or as functions of the monkey's two possible motor choices.

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