Neural Activity in the Anterior Striatum during Comparison of Reward Values
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Abstract—To elucidate the contribution of basal ganglia to decision-making, we recorded the neural activity of the anterior striatum in macaques while they performed a choice task and an instructed task. We found that the striatum, particularly the anterior striatum, exhibited higher activity when reward values were compared to choose one of two stimuli than that when the stimulus was forced without a choice.

Keywords—Basal ganglia, decision-making, anterior striatum, macaque, reward value

1. Introduction
Comparing the reward values of multiple options and choice the most suitable option is a fundamental decision-making strategy. Recent neurophysiological studies have suggested that basal ganglia are involved in value-based decision making [1][2]. However, how and where the brain implements value comparison and action choice remains unclear. To elucidate the contribution of basal ganglia to decision making based on the comparison of reward values, we recorded single unit activities of anterior striatum neurons of macaques, performing a decision-making task in which reward values were compared and option choice was dissociated from motor choice and preparation.

2. Task and behavior
We trained two macaques to perform a choice task and an instructed task (Fig.1). In the choice task (Fig.1A), macaques had to choose one of two visual stimuli presented on the screen during the choice cue period. The choice cue forms 2 × 2 presentation in order to attenuate the effect of the neural activity that is associated with spatially specific decisions. After a delay period (0.8–1.2 s), two stimuli were individually presented again in random order (target stimulus). The macaques had to choose a stimulus by releasing or holding the button when the first stimulus was presented. Each macaque received differing quantity of apple juice as reward, which was associated with the stimulus presented when the monkey released the button. The selected cue stimuli were associated with four quantities of juice reward in a block of 144 trials and differed in each block. Each block consisted of four sub-blocks with 12 instructed trials and 24 choice trials (Fig.1C).

Association between color (or shape) of the stimuli and reward amounts were fixed in a block of 144 trials and differed in each block. Each block consisted of four sub-blocks with 12 instructed trials and 24 choice trials (Fig.1C).

Fig.1 Task and choice behavior. Time course of choice task (A) and instructed task (B) in a trial. (C) Reward schedule. (D) Optimal choice performance.
Macaques learned optimal policy through sequence of choosing stimuli and receiving reward feedback. Fig.1D shows the average of the optimal choice ratio in the choice trials. Choice ratio for the stimulus with a greater reward gradually increased from the chance level (50%) in early trials to 90% in the last trial of block (Fig. 1D, blue and green lines). The choice ratio for the target with a greater reward in the previous block decreased from 80% to the chance level (Fig 1D, cyan and red lines).

3. Neural activity in the anterior striatum

We recorded activity in 360 task-related neurons in the striatum of the two macaques performing choice and instructed tasks.

We found two types of cue-response neurons: One is the choice-preferred (CP) neurons, which were defined by the mean firing rates for each of four temporal different period (early cue, 0–0.4 s from cue onset), late cue (LC, 0.4–0.8 s from cue onset), early delay (ED, 0.8–1.2 s from cue offset) and late delay (LD, 1.2–1.6 s from cue offset)) were significantly higher at least one period in the choice task than in the instructed task (Fig.2A, p < 0.01). The other is the Instructed-preferred (IP) neurons, which had the reverse characteristics of the CP neurons (the mean firing rate in the instructed task > in the choice task) (Fig.2B, p < 0.01).

To elucidate when and which parts of the striatum contributed to comparing the reward values, we performed population analysis in two separate recorded areas (anterior part, A26–30; posterior part, A21–25) for each of four different periods (EC, LC, ED and LD period). In this analysis we included neurons for the mean firing rates were significantly higher in each of the four periods (EC, DC, ED, and LD) compared with that in the pre-fixation period (−1.2 to −0.8 s from cue onset) (p < 0.01).

Although the number of non-significant neurons that were no significant difference in the mean firing rates during each four period between choice and instructed task were greatest among the cue-response neurons for all four period, we focused on the difference between the number of CP and IP neurons. The number of CP neurons was significantly greater than the number of IP neurons for all four periods in the anterior part of the recorded area, whereas no significant difference was observed between the number of IP and CP neurons in the posterior part (Fig.2C). The ratio of CP/IP neurons increased in the anterior striatum from EC period until the ED period and slightly decreased in the LD period, whereas the ratio of CP/IP neurons did not increase (Fig.2C).

4. Discussion and conclusion

We observed that the number of CP neurons was a greater than that of IP neurons in the anterior part of the rostral striatum. The ratio of the CP/IP neurons peaked during the temporal period when the macaques compared reward values and choose one stimulus. These results are consistent with anatomical evidence indicating the presence of multiple cortico-basal ganglia loops [3]. The anterior striatum receives massive projections from the anterior cingulate, orbitofrontal, and dorsolateral prefrontal cortices [4]. These cortices have been implicated not only in economic choice behavior but also in higher-order cognitive processes, such as executive function, rule-based inference, and cognitive control. Human imaging study have suggested that the value comparison process in economic choice behavior activates medial prefrontal regions, even in subjects who could not initiate a motor selection [5]. Our findings of choice-specific activity in the anterior striatum without motor selection suggest that the anterior striatum is involved in cognitive decision-making through reward value comparison along with multiple regions of the prefrontal cortices through a “cognitive loop” of the cortico-basal ganglia circuit.

5. References