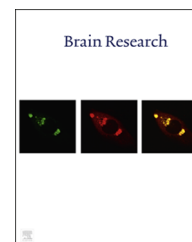


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Research article

Neuronal activity in primate prefrontal cortex related to goal-directed behavior during auditory working memory tasks

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ABSTRACT

Prefrontal cortex (PFC) has been documented to play critical roles in goal-directed behaviors, like representing goal-relevant events and working memory (WM). However, neurophysiological evidence for such roles of PFC has been obtained mainly with visual tasks but rarely with auditory tasks. In the present study, we tested roles of PFC in auditory goal-directed behaviors by recording local field potentials in the auditory region of left ventrolateral PFC while a monkey performed auditory WM tasks. The tasks consisted of multiple events and required the monkey to change its mental states to achieve the reward. The events were auditory and visual stimuli, as well as specific actions. Mental states were engaging in the tasks and holding task-relevant information in auditory WM. We found that, although based on recordings from one hemisphere in one monkey only, PFC represented multiple events that were important for achieving reward, including auditory and visual stimuli like turning on and off an LED, as well as bar touch. The responses to auditory events depended on the tasks and on the context of the tasks. This provides support for the idea that neuronal representations in PFC are flexible and can be related to the behavioral meaning of stimuli. We also found that engaging in the tasks and holding information in auditory WM were associated with persistent changes of slow potentials, both of which are essential for auditory goal-directed behaviors. Our study, on a single hemisphere in a single monkey, reveals roles of PFC in auditory goal-directed behaviors similar to those in visual goal-directed behaviors, suggesting that functions of PFC in goal-directed behaviors are probably common across the auditory and visual modality.

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1. Introduction

A large part of human behaviors are oriented towards achieving a particular goal. For implementing these goal-directed behaviors, we need to be able to identify events in the environment that are relevant to achieving the goals and temporarily keep ourselves in certain mental states to guide our behaviors. These mental states include, e.g., sustainedly engaging in a specific behavior or maintaining the information about goal-relevant events in working memory (WM). Prefrontal cortex (PFC) has been documented to play critical roles in goal-directed behaviors. Lesions in PFC are associated with impairments in goal-directed behaviors (Balleine and Dickinson, 1998; Miller and Cohen, 2001). PFC neurons respond to multiple goal-relevant events (Asaad et al., 1998, 2000; Wallis and Miller, 2003; Warden and Miller, 2010). Persistent activity has been found in PFC during maintenance of information in WM (Funahashi et al., 1989; Fuster, 2001; Fuster et al., 1985; Goldman-Rakic, 1995; Miller et al., 1996).

Neurophysiological evidence for these PFC roles has been obtained mainly in visual studies, whereas there are very few studies about the auditory modality. The ventrolateral part of PFC (vLPFC) receives projections from auditory cortical areas and preferentially processes non-spatial auditory information (Cohen et al., 2009; Plakke and Romanski, 2014). vLPFC has been shown to be involved in non-spatial auditory goal-directed behaviors in the way that neurons in this area respond to multiple goal-relevant events including auditory stimuli, behavioral choices, decision making, motor responses and delivery of reward (Hwang and Romanski, 2015; Plakke et al., 2013; Russ et al., 2008). However, electrophysiological evidence is limited and inconsistent for roles of vLPFC in representing mental states like engaging in behaviors and holding information in auditory WM. For example, one study has shown persistent activity in vLPFC during the delay in a WM task using audiovisual stimuli (Hwang and Romanski, 2015). In contrast, such persistent activity was almost missing in another study using purely auditory stimuli (Plakke et al., 2013). Thus, more studies are needed to reveal roles of vLPFC in non-spatial auditory goal-directed behaviors, especially in representing mental states like engaging in behaviors and holding goal-relevant information in WM.

In the present study, we recorded from the left vLPFC in one monkey when he performed two non-spatial auditory WM tasks. Each of the two tasks consisted of a sequence of visual and auditory stimuli, in response to which the monkey had to execute a specific and timely series of actions, which was followed by a drop of water as reward to the monkey. To accomplish the tasks, the monkey needed to detect task-relevant sensory stimuli and recognize their behavioral meaning, temporarily store information in WM and adjust subsequent information processing accordingly, as well as appropriately control his actions. We hypothesized that processing of task-relevant stimuli and initiation of appropriate actions were reflected in phasic event-related neuronal responses in PFC, and that mental states like engaging in the task and holding information in WM were reflected in persistent neuronal activity in PFC. Here, we report results of analyzing local field potentials instead of spike activity for the following

reasons. First, local field potentials could be recorded more easily and stably over longer period of time than spike activity. Second, local field potentials reflect both neuronal inputs and local processing (Buzsáki et al., 2012; Pesaran, 2009) while spike activity reflects neuronal outputs. We expected that in local field potentials it would be more likely to observe activity related to different aspects of the tasks.

2. Results

2.1. Rationale

One monkey was trained to be able to perform two WM tasks consisting of visual stimuli as well as tone sequences which differed in WM load (Fig. 1A and B). In task 1, a trial started with the illumination of a green LED ('LED-on') located on the monkey's right side. After LED-on, the monkey had to grasp a touch bar ('bar touch'), after which two pure tones, S1 and S2, separated by a delay, were presented sequentially. Depending on the frequency of S1 and S2, the monkey then had to make either a go response to the target sequence (bar release) or a no-go response to the other sequences (holding the bar at least until the LED was turned off). The frequency of S1 and S2 could be either 3 kHz or 1 kHz, which resulted in four two-tone sequences: 3-3 kHz, 3-1 kHz, 1-3 kHz, and 1-1 kHz, of which the 3-3 kHz sequence was the target (Fig. 1B). A drop of water (~0.2 ml) was then given to the monkey as reward for correct go and no-go responses. The four sequences were randomly presented during the task.

To obtain reward, the monkey had to perform several cognitive operations and actions. These included detecting LED-on which signaled the monkey to engage in the task, grasping and holding the touch bar to start and continue the trial, and identifying S1. If S1 was 3 kHz, the monkey had to utilize auditory WM to memorize either the frequency of S1 for comparison with S2, or the two stimulus-response associations for S2 (a go response if it was 3 kHz; a no-go response if it was 1 kHz). If S1 was 1 kHz, the monkey only needed to memorize to make a no-go response in this trial and nothing else. Therefore, the WM load was higher in trials where S1 was 3 kHz ('high-WM-load trials') than in trials where S1 was 1 kHz ('low-WM-load trials'). S2 needed to be identified only in high-WM-load trials. Using this task, we could therefore test whether neuronal activity in vLPFC represents multiple task-relevant sensory events as well as actions and reflects mental states like engaging in the task as well as holding information in WM.

We were aware that high- and low-WM-load trials in this task differed not only in WM load but also in the frequency of S1 and in the decision and preparation of the behavioral response after S2 ('motor response'). To control for these two confounding factors, we trained our monkey to perform another WM task on the same two-tone sequences (task 2; Fig. 1B; details and results of task 1 are depicted in green and those of task 2 in red in this as well as all other figures unless stated otherwise). Task 2 was similar to task 1, except that a red LED, located at the monkey's left side, was used, that the sequence 1-1 kHz was the target and required a go response, and that the other three sequences 1-3 kHz, 3-3 kHz, and 3-

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