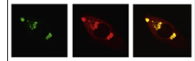


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## Research Report

# Local field potential correlates of auditory working memory in primate dorsal temporal pole

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## ABSTRACT

Dorsal temporal pole (dTP) is a cortical region at the rostral end of the superior temporal gyrus that forms part of the ventral auditory object processing pathway. Anatomical connections with frontal and medial temporal areas, as well as a recent single-unit recording study, suggest this area may be an important part of the network underlying auditory working memory (WM). To further elucidate the role of dTP in auditory WM, local field potentials (LFPs) were recorded from the left dTP region of two rhesus macaques during an auditory delayed matching-to-sample (DMS) task. Sample and test sounds were separated by a 5-s retention interval, and a behavioral response was required only if the sounds were identical (match trials). Sensitivity of auditory evoked responses in dTP to behavioral significance and context was further tested by passively presenting the sounds used as auditory WM memoranda both before and after the DMS task. Average evoked potentials (AEPs) for all cue types and phases of the experiment comprised two small-amplitude early onset components (N20, P40), followed by two broad, large-amplitude components occupying the remainder of the stimulus period (N120, P300), after which a final set of components were observed following stimulus offset (N80<sub>OFF</sub>, P170<sub>OFF</sub>). During the DMS task, the peak amplitude and/or latency of several of these components depended on whether the sound was presented as the sample or test, and whether the test matched the sample. Significant differences were also observed among the DMS task and passive exposure conditions. Comparing memory-related effects in the LFP signal with those obtained in the spiking data raises the possibility some memory-related activity in dTP may be locally produced and actively generated. The results highlight the involvement of dTP in auditory stimulus identification and recognition and its sensitivity to the behavioral significance of sounds in different contexts.

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## 1. Introduction

Dorsal temporal pole (dTP) is a cortical region of the primate brain at the rostral end of the superior temporal gyrus (STG). Anatomical studies indicate this area receives dense projections from auditory association areas including STG and parabelt (Munoz-Lopez et al., 2015), as well as auditory thalamic areas including medial geniculate nucleus (Markowitsch et al., 1985; Morán et al., 1987; Yeterian and Pandya, 1989). Consistent with these connections, single-unit and neuroimaging studies have revealed this area is activated by auditory stimuli (Poremba et al., 2003, 2004; Poremba and Mishkin, 2007; Ng et al., 2014). In particular, dTP may be important for processing communication sounds (Devlin et al., 2000; Nakamura et al., 2001; Poremba et al., 2004; McCrea, 2008), consistent with its anatomical position in the proposed ventral auditory object processing pathway (Kaas and Hackett, 1999; Lomber and Malhotra, 2008; Poremba et al., 2003; Rämä et al., 2004; Rauschecker and Tian, 2000; Romanski et al., 1999).

In addition to projections from auditory-related areas, dTP is interconnected with amygdala, limbic thalamus, prefrontal cortex (PFC), and medial temporal lobe structures including entorhinal cortex, perirhinal area 35, and parahippocampal cortex (Munoz-Lopez et al., 2015). These anatomical connections raise the possibility that dTP may be important for auditory working memory (WM), i.e., retaining neural representations of auditory events after they have passed from the sensory environment (Pasternak and Greenlee, 2005). Consistent with this view, lesions of higher-order auditory areas in monkeys including STG and dTP lead to significantly impaired performance in auditory WM tasks (Fritz et al., 2005), and lesions of human dTP lead to impaired retrieval of famous musical melodies and proper names (Grabowski et al., 2001; Belfi and Tranel, 2014). In this regard, dTP may be analogous to areas in the ventral visual object processing pathway that are important for visual WM, such as ventral temporal pole (Nakamura and Kubota, 1995, 1996) and inferior temporal cortex (Fuster and Jervey, 1982; Fuster et al., 1985; Baylis and Rolls, 1987; Horel et al., 1987; Gaffan and Murray, 1992; Miller et al., 1993; Miyashita, 1993; Miyashita and Chang, 1988).

The putative involvement of dTP in auditory WM is supported by a recent single-unit recording study by Ng et al. (2014). In this experiment, monkeys performed an auditory delayed matching-to-sample task (DMS) wherein sample and test sounds were separated by a 5-s retention interval. A brief second delay period followed the test stimulus, after which subjects were trained to press a button if the sounds were identical (match trials), but to withhold button presses if the sounds were nonidentical (nonmatch trials). For many neurons, differential firing rates were evoked by matching versus nonmatching stimuli. This outcome held at the population level, such that population firing rates were significantly lower on match trials (match suppression) in the early stimulus period (30–60 ms post-stimulus onset). This trend reversed during the pre-response delay period, such that firing rates were significantly higher on match trials (match enhancement). In a similar study in PFC (Plakke et al.,

2013), similar elevated firing rates were observed on match trials several hundred milliseconds in advance of those in dTP, raising the possibility that match enhancement in dTP may reflect top-down feedback originating in frontal cortex and possibly elsewhere.

Although neurophysiological studies of WM have traditionally focused on spiking activity (single- and multi-unit recordings), increased attention has been given to the local field potential (LFP) over the past decade (e.g., Pesaran, 2009). This is because spiking data and field potentials are often functionally uncorrelated, and thus, information is available in combined analysis that cannot be derived from either signal alone (Anderson et al., 2008; Belitski et al., 2008; Berens et al., 2008; Fu et al., 2004; Ghazanfar et al., 2005; Kreiman et al., 2006; Logothetis, 2003; Mathiesen et al., 1998, 2000; Nielsen et al., 2006; Pesaran et al., 2002; Schroeder et al., 2001; Woloszyn and Sheinberg, 2009). For instance, it has been suggested that action potentials predominantly reflect efferent signals, whereas the LFP predominantly reflects synaptic potentials, i.e., afferent signals and local processing (Logothetis, 2002, 2003; Logothetis et al., 2007; Mitzdorf, 1985; Nielsen et al., 2006; Rasch et al., 2009). Based on these assumptions, considering information from both signals can potentially shed light on whether specific processes may be generated locally or as a product of feedback from other areas (Monosov et al., 2008; Nielsen et al., 2006; Woloszyn and Sheinberg, 2009). Thus, in the interest of providing a more detailed characterization of auditory WM-related activity in dTP, the present study investigated LFP activity recorded within dTP in two subjects performing an auditory DMS task. In addition, passive sound exposure phases were included both before and after the DMS task, using the same sounds that were presented as auditory WM memoranda, to provide an additional means of investigating whether sound evoked responses in dTP are modulated by behavioral significance and context.

## 2. Results

### 2.1. Behavior

Behavioral outcomes were comparable to previous studies of auditory WM in monkeys from our lab and others (Bigelow et al., 2013a, 2013b, 2014; Fritz et al., 2005; Ng et al., 2009, 2014; Plakke et al., 2008, 2013). Overall mean accuracy was 70.6% (SEM 0.7%) across 113 sessions. Repeated measures ANOVA evaluating match and nonmatch accuracy separately revealed a significant bias toward “go” responses: subjects correctly responded on 78.5% (SEM 1.2%) of the match trials and correctly withheld button responses on 62.8% (SEM 1.1%) of the nonmatch trials ( $F[1,112]=77.7, p<.05$ ). As in prior experiments, response latencies were significantly faster for correct match responses ( $350\pm 42$  ms) than incorrect button presses on nonmatch trials ( $430\pm 43$  ms;  $F[1,112]=429.0, p<.05$ ). Similar response biases and modest performance outcomes are common for monkeys performing auditory DMS tasks, even in extensively-trained subjects (Bigelow et al., 2013a, 2013b, 2014; Cohen et al., 2005; Colombo and D'Amato, 1986; Fritz et al., 2005; Hwang and Romanski, 2015;

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