



Transcranial direct current stimulation over the parietal cortex alters bias in item and source memory tasks



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ABSTRACT

Neuroimaging data have shown that activity in the lateral posterior parietal cortex (PPC) correlates with item recognition and source recollection, but there is considerable debate about its specific contributions. Performance on both item and source memory tasks were compared between participants who were given bilateral transcranial direct current stimulation (tDCS) over the parietal cortex to those given prefrontal or sham tDCS. The parietal tDCS group, but not the prefrontal group, showed decreased false recognition, and less bias in item and source discrimination tasks compared to sham stimulation. These results are consistent with a causal role of the PPC in item and source memory retrieval, likely based on attentional and decision-making biases.

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1. Introduction

Neuroimaging studies have consistently shown activity in the lateral posterior parietal cortex (PPC) during episodic memory retrieval (Kahn, Davachi, & Wagner, 2004; Shannon & Buckner, 2004; Wagner, Shannon, Kahn, & Buckner, 2005). Specifically, the PPC was more active during retrieval of studied than unstudied items (Cansino, Maquet, Dolan, & Rugg, 2002; Henson, Hornberger, & Rugg, 2005; Wagner et al., 2005), and source memory judgments compared to item memory judgments (Dobbins, Rice, Wagner, & Schacter, 2003; Hayes, Buchler, Stokes, Kragel, & Cabeza, 2011; Hutchinson et al., 2012). Lesions to the PPC, however, did not produce amnesia (e.g. Haramati, Soroker, Dudai, & Levy, 2008; for review see, Corbetta & Shulman, 2002); PPC damage primarily resulted in deficits in attention (Bays, Singh-Curry, Gorgoraptis, Driver, & Husain, 2010; Steinmetz & Constantinidis, 1995). Thus, the contributions of the PPC to memory accuracy is likely to reflect attentional processes (Cabeza, 2008; Ciaramelli, Grady, & Moscovitch, 2008; Wagner et al., 2005). Because lesion

studies are limited in that behavior can also reflect encoding deficits or functional recovery (Corbetta, Kincade, Lewis, Snyder, & Sapir, 2005; Kolb, Brown, Witt-Lajeunesse, & Gibb, 2001) and neuroimaging studies are correlational, the goal of this experiment was to test the role of the PPC in memory retrieval by directly manipulating cortical activity in intact neurological populations using transcranial direct current stimulation (tDCS). We compared performance on item and source memory tasks with active tDCS over the PPC to both sham tDCS and tDCS over the prefrontal cortex (PFC), another brain region that has been implicated in memory (Cansino et al., 2002; Rugg, Fletcher, Chua, & Dolan, 1999; Shimamura, Jurica, Mangels, Gershberg, & Knight, 1995).

TDCS is a technique by which weak electrical currents are applied at the scalp by means of two electrodes, one stimulating electrode, often referred to as the “anode”, and one return electrode, typically referred to as the “cathode” (DaSilva, Volz, Bikson, & Fregni, 2011; Reato, Rahman, Bikson, & Parra, 2010). Application of tDCS has been shown to alter the likelihood of neuronal excitation in the cortex of non-human animals (Bikson et al., 2004; Reato et al., 2010) and humans (Antal, Kincses, Nitsche, Bartfai, & Paulus, 2004; Nitsche & Paulus, 2000). Notably, the effects of tDCS can be modulated by the charge of the overlying electrode, such that excitability under the anode increases while the excitability under the cathode decreases, at least in the case of primary visual and motor cortices (Antal et al., 2004; Nitsche & Paulus, 2000). Interestingly, bilateral montages, which place

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the anode over the region of interest of one hemisphere and the cathode over the region of interest in the contralateral hemisphere, have been shown to have enhanced effects on behavior compared to unilateral montages, likely by attenuating interhemispheric inhibition (Vines, Cerruti, & Schlaug, 2008). An additional benefit of a bilateral montage is that the current flow of tDCS is more restricted to the cortical regions of interest compared to unilateral montages (Vines et al., 2008), which is important because tDCS brings about network changes even in regions that are not stimulated (Keeser et al., 2011; Lang et al., 2005), suggesting that unilateral stimulation can modulate the contralateral hemisphere and lead to behavioral effects. Bilateral tDCS can therefore oppose such modulation and, in the case of the PPC, may be a better model for mnemonic contributions because changes to memory have been primarily noted in patients with bilateral lesions (Berryhill & Olson, 2008; Berryhill, Phuong, Picasso, Cabeza, & Olson, 2007; Drowos, Berryhill, André, & Olson, 2010; Simons, Peers, Mazuz, Berryhill, & Olson, 2010). Thus, in our study we used bilateral montages, placing the anode over the left hemisphere and cathode over the right hemisphere, to determine the nature of the causal role of the PPC in item and source memory retrieval.

Previous research has shown that bilateral tDCS effectively alters attentional processes when applied over the PPC (Benwell, Learmonth, Miniussi, Harvey, & Thut, 2015; Giglia et al., 2011; Sparing et al., 2009), executive control processes when applied over the PFC (Leite, Carvalho, Fregni, Boggio, & Gonçalves, 2013; Nelson, McKinley, Golob, Warm, & Parasuraman, 2014; Nozari & Thompson-Schill, 2013), which we used as a control site, and bilateral tDCS has been used to dissociate the PPC and the PFC (Iuculano & Cohen Kadosh, 2013), suggesting that tDCS could manipulate these underlying processes during memory retrieval. It is worth noting, however, that the efficacy of tDCS has been questioned in recent meta-analyses (Horvath, Carter, & Forte, 2014; Horvath, Forte, & Carter, 2015), but these meta-analyses were limited by available published data, and did not have enough data to account for parameters known to effect tDCS such as stimulation duration (Antal, Keeser, Priori, Padberg, & Nitsche, 2015) or task difficulty (Berryhill, Peterson, Jones, & Stephens, 2014). Thus, behavioral changes may be selective to the combination of tDCS and task parameters used, and should be interpreted as such.

The PPC has been argued to support memory retrieval by way of attentional mechanisms that influence what mnemonic information is sought after (Cabeza, Ciaramelli, Olson, & Moscovitch, 2008; Ciaramelli et al., 2008; Wagner et al., 2005), or decision-related mechanisms that influence criterion setting (Aminoff et al., 2015; Dobbins, Jaeger, Studer, & Simons, 2012; Donaldson, Wheeler, & Petersen, 2010; Pisoni et al., 2015; Sestieri, Capotosto, Tosoni, Luca Romani, & Corbetta, 2013; Wagner et al., 2005). Patients with PPC damage have shown deficits in orienting attention to external stimuli (Corbetta & Shulman, 2002), leading to the hypothesis that the contents of retrieval, as relevant internal stimuli, reorient attention in a manner that enhances the processing of task-relevant information, and this is mediated by the parietal cortex (Cabeza et al., 2008; Ciaramelli et al., 2008; Wagner et al., 2005). Consistent with this hypothesis, patients with parietal lesions had less confidence in their memories (Davidson et al., 2008; Simons et al., 2010), were less likely to report detailed memories either through spontaneous recall (Berryhill, Picasso, Arnold, Drowos, & Olson, 2010; Berryhill et al., 2007) or subjective “remember” responses (Davidson et al., 2008; Drowos et al., 2010), had less false memories for associated words (Drowos et al., 2010), and were less likely to use memory cues to support retrieval (Ciaramelli, Grady, Levine, Ween, & Moscovitch, 2010). Thus, attention may support the ability to select what information will be retrieved, and the experience associated with recovering such selected information. Correspondingly, evidence from fMRI and

event-related potentials (ERPs) studies converged to implicate the PPC in memory processes that were supported by attentional functions. For example, because “new” items are unstudied, they should not elicit retrieval-related activity but may elicit attentional processing, and studies have shown greater activation in the PPC for falsely recognized new (unstudied) items compared to correctly rejected new items (Kahn et al., 2004; Wheeler & Buckner, 2004), high confidence compared to low confidence false recognition of strongly related lures (Kim & Cabeza, 2007), high confidence correct compared to low confidence correct old and new judgments (Kuchinke, Fritzmeier, Hofmann, & Jacobs, 2013), and invalidly cued compared to validly cued correct old and new judgments (Jaeger, Konkel, & Dobbins, 2013; O'Connor, Han, & Dobbins, 2010). Also consistent with the idea that the parietal cortex is involved in attentional selection of mnemonic information, ERPs over parietal areas were increased for specific recollections such as when a probe was self-generated compared to imagined (Leynes, 2012), was endorsed as accompanied with greater details (Vilberg & Rugg, 2009), and was identical to what was studied compared to when changed (Ally, Simons, McKeever, Peers, & Budson, 2008).

In a related hypothesis, the PPC may subserve decision-making aspects of memory tasks. Evidence for a role of the PPC in decision-making can be seen from work showing that, during a sensory task, neurons in the primate parietal cortex responded based on the accumulation of attentional sensory information that formed the basis for a response decision (Platt & Glimcher, 1999; Shadlen & Newsome, 1996). Memory researchers have hypothesized that the human parietal cortex may play a similar role in memory; parietal neurons may modulate based on the accumulation of mnemonic (old and new) information as a basis for a goal directed response (Donaldson et al., 2010) or that attention serves to establish a decision bias (Dobbins et al., 2012). From this perspective, the reduced confidence, recollected detail, and associative false recognition in patients with PPC damage (Berryhill et al., 2007; Davidson et al., 2008; Drowos et al., 2010; Simons et al., 2010) reflects an inability to incorporate attended information as a basis for a decision. In line with a decision-making role for the parietal cortex in retrieval, one study used a paradigm that yields high rates of false alarms and showed tDCS over the parietal cortex increased false recognition (Pergolizzi & Chua, 2015), whereas another study used a standard item recognition paradigm and showed decreased false recognition (Pisoni et al., 2015). These opposing effects on false recognition when different paradigms were used are consistent with decisional aspects of retrieval and the idea that task demands can differentially influence or bias item recognition judgments. Thus, if the role of the parietal cortex in memory is via attention and/or decision processes, then, in a combined item and source memory task, the parietal cortex may play a role in prioritizing attention to source recollection (because source information is the most task-relevant), which could lead to improved source recollection or biased responding based on criterion setting toward features that are weighted more or less importantly according to task demands.

We compared the effects of tDCS over the PPC to effects of sham tDCS and tDCS over the PFC because the PFC has also been implicated in memory tasks (for review see; Mitchell & Johnson, 2009; Preston & Eichenbaum, 2013; Rugg, Otten, & Henson, 2002; Simons & Spiers, 2003), and potentially dissociating the roles of the PPC vs. PFC is of interest. The PFC has been argued to support memory retrieval under conditions when retrieval is difficult and demands executive control, such as establishing strategies to search for specific information (Nolde, Johnson, & Raye, 1998), monitoring and evaluating memories (Rugg et al., 1999), or inhibiting irrelevant or competing memories (Shimamura et al., 1995). In general, source memory retrieval is considered to be more difficult,

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