Neural sources of visual working memory maintenance in human parietal and ventral extrastriate visual cortex

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ABSTRACT

Maintaining information in visual working memory is reliably indexed by the contralateral delay activity (CDA) — a sustained modulation of the event-related potential (ERP) with a topographical maximum over posterior scalp regions contralateral to the memorized input. Based on scalp topography, it is hypothesized that the CDA reflects neural activity in the parietal cortex, but the precise cortical origin of underlying electric activity was never determined. Here we combine ERP recordings with magnetoencephalography based source localization to characterize the cortical current sources generating the CDA. Observers performed a cued delayed match to sample task where either the color or the relative position of colored dots had to be maintained in memory. A detailed source-localization analysis of the magnetic activity in the retention interval revealed that the magnetic analog of the CDA (mCDA) is generated by current sources in the parietal cortex. Importantly, we find that the mCDA also receives contribution from current sources in the ventral extrastriate cortex that display a time-course similar to the parietal sources. On the basis of the magnetic responses, forward modeling of ERP data reveals that the ventral sources have non-optimal projections and that these sources are therefore concealed in the ERP by overlapping fields with parietal projections. The present observations indicate that visual working memory maintenance, as indexed by the CDA, involves the parietal cortical regions as well as the ventral extrastriate regions, which code the sensory representation of the memorized content.

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Introduction

A number of cortical and subcortical structures have been identified to subserve the operation of visual working memory (VWM) in humans and monkeys. Among those structures, regions within the prefrontal and parietal cortex feature the most prominent roles (Awh and Jonides, 2001; Baker et al., 1996; Cohen et al., 1997; Friedman and Goldman-Rakic, 1994; Funahashi et al., 1989; Jonides et al., 1993; Klingberg et al., 1997; McCarthy et al., 1994; Miller et al., 1996; Muller et al., 2002; Pessoa et al., 2002; Reinhart et al., 2012; Rypma and D'Esposito, 1999; Sakai et al., 2002; Smith and Jonides, 1998; Ungerleider et al., 1998; Voytek and Knight, 2010). Although the brain regions important for VWM are well documented, comparably little is known about how VWM performance depends on the spatio-temporal dynamic of activity changes in and across these regions. Insights in this respect were substantially advanced recently by the discovery of the Contralateral Delay Activity (CDA). The CDA is an ERP

modulation that was found to index the maintenance of item information in VWM (Carlisle et al., 2011; Drew et al., 2011; Ikkai et al., 2010; Klaver et al., 1999; Luria and Vogel, 2011a, 2011b; McCollough et al., 2007; Perez and Vogel, 2012; Reinhart et al., 2012; Vogel and Machizawa, 2004; Vogel et al., 2005; Woodman and Arita, 2011; Woodman and Vogel, 2008). It appears as a lasting negative voltage deflection at posterior scalp electrodes contralateral to the position of memorized items (Vogel and Machizawa, 2004). The CDA was recently identified in the monkey as well, where it appears as contralateral positivity (Reinhart et al., 2012). An important characteristic of the CDA is that its amplitude increases gradually with the increase of the number of items to be held in working memory. This increase is typically seen for up to 4 items, after which the CDA shows an asymptotic limit (McCollough et al., 2007; Vogel and Machizawa, 2004). Moreover, the CDA has been proven to be a measure of individual working memory capacity as well as of individual differences in the selectivity of what gains access to memory (Luck and Vogel, 2013; Vogel et al., 2005). Whether the CDA also reflects the type of information stored in memory is currently debated (McCollough et al., 2007; Perez and Vogel, 2012; Woodman and Vogel, 2008).

Given that the CDA is an extensively used tool in the analysis of VWM processes, it is notable that there has been little effort and

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progress thus far to define its cortical origin (Robitaille et al., 2009). The ERP scalp topography of the CDA seems to point to a current origin in parietal cortex (McCollough et al., 2007). However, as shown previously for other ERP components (Hopf et al., 2000), the scalp topography of ERPs may not always be a sufficient basis for garnering reliable information about underlying current sources. For example, field effects from current sources with a certain orientation may go unnoticed due to insufficient coverage from the electrode-cap. As a consequence, the number of contributing brain structures may be underestimated. It is currently unclear whether the CDA arises from a single current source in the posterior (parietal) cortex, or whether it is generated by multiple current sources in different areas. Cell recordings in the monkey ventral extrastriate cortex have documented firing effects indexing working memory (Fuster and Jervey, 1981; Miller and Desimone, 1994, 1994; Chelazzi et al., 1998, 2001; Miller et al., 1993). Current source activity in these regions may give rise to field-distributions that are hard to register with ERP recordings. Finally, given that functional brain imaging studies typically document a network of structures, including visual cortex areas, to subserve the maintenance of VWM (Awh et al., 1999; Courtney et al., 1996; Druzgal and D'Esposito, 2001, 2003; Greenlee et al., 2000; Jonides et al., 1993; Lepsien and Nobre, 2007; Pessoa et al., 2002; Postle et al., 2004; Postle and D'Esposito, 1999; Sneve et al., 2012; Ungerleider et al., 1998; Xing et al., 2013; Xu and Chun, 2006), it is not unreasonable to expect that more than one current source contributes to the CDA.

Here, we combine electroencephalographic (EEG) and magneto-encephalographic (MEG) brain recordings in human observers to characterize the current origin of the CDA response. To this end, we first verify the presence of the CDA in the ERP and then characterize its magnetic analog in the simultaneously recorded MEG data. We then localize underlying current sources based on the magnetic data. For source localization, MEG provides important information as it complements the electric field response and reduces the risk to overlook field components critical for proper source localization. Furthermore, MEG has inherent advantages due to negligible influences of volume conductivity changes, and this allows for higher spatial resolution and more reliable source localization (Hämäläinen et al., 1993; Hämäläinen, 1995). Our results show that the CDA is indeed generated by current sources in the parietal cortex areas, but that there are additional sources in the ventral extrastriate cortex contributing to the CDA. Using MEG-based forward modeling and simulation of the ERP responses, we will outline the reasons why ventral current sources can be hard to identify based on the EEG signal alone.

Material and methods

Subjects

Nineteen subjects (12 female, mean age: 23.6) with no neurological disease participated in the experiment for financial compensation. All subjects were right handed with normal or corrected-to-normal visual acuity and normal color vision. All subjects gave informed consent. The experiment was approved by the ethics committee of the Otto-von-Guericke University of Magdeburg.

Stimuli and procedure

Subjects performed a variant of the delayed match to sample task as illustrated in Fig. 1a. Subjects were cued (location cue) on each trial to memorize items in one visual hemifield (memory array) and report whether information provided on a subsequent test array matches the memory array. The memory array consisted of two sets of 3 or 5 colored dots in the left and right visual field (VF) with the number of dots always matching between VFs (Fig. 1a shows example arrays with 3 dots). The dots were randomly placed within a 6° × 4° (visual angle) imaginary rectangle that was centered on the horizontal meridian and
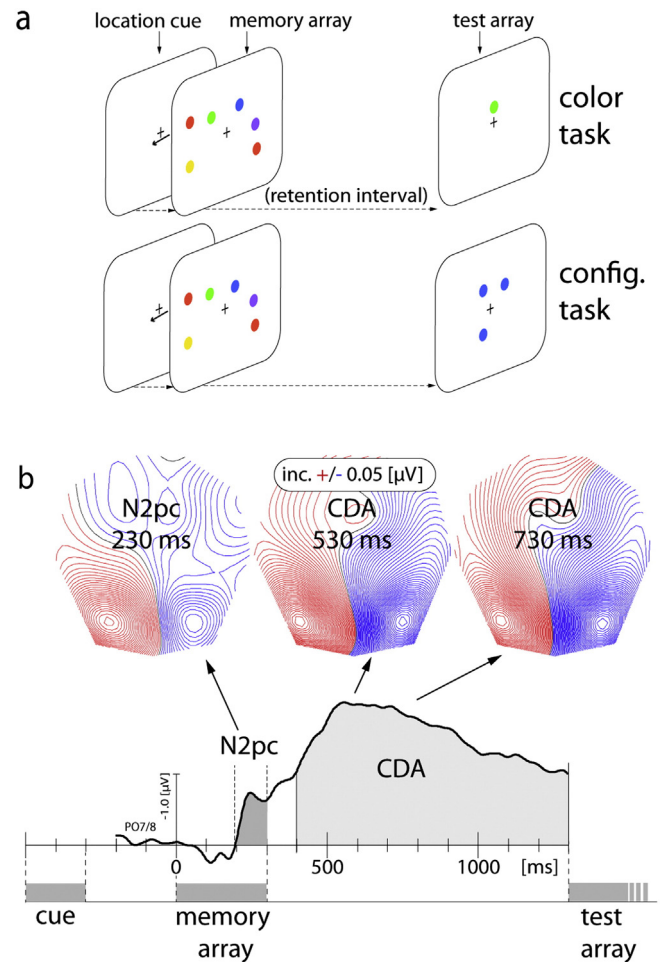

Fig. 1. Stimuli and trial structure as well as CDA waveforms and field distributions (ERPs). (a) Illustration of stimuli and trial structure of the delayed match-to-sample task. Shown are examples of the color (upper row) and configuration task (lower row) requiring the memorization of three dots in the cued visual field. (b) Waveforms and topographical field maps of the ERP response in the retention interval. Shown are hemisphere-collapsed CDA-difference waveforms at a lateral posterior electrode site PO7/8, together with topographical maps of the overall CDA-difference at three selected time points after memory-array onset. The waveforms represent data collapsed over the task (shape, color) and load conditions (load-3, load-5). The first map at 230 ms shows the N2pc response (dark gray area in the waveforms), the following maps show the field distribution of the CDA (bright gray area in the waveforms) at 530 and at 730 ms.

with its inner border being displaced 1° lateral from fixation. Color was randomly assigned to the dots (subtending 0.9°) from a set of nine colors (red, cyan, blue, yellow, purple, green, brown, black, white). The colors within one VF always differed, while color assignment was independent in the left and right VF. The test array was either a single color-dot shown immediately above fixation (color task) or an array of 3 or 5 blue dots placed in an imaginary rectangle (6° × 4°) centered at fixation (configuration task). Note, while the test arrays differed between experimental tasks, the corresponding memory arrays were identical. Stimuli were programmed and presented using Presentation® (Version 0.70, www.neurobs.com).

While fixating a small cross in the center of the screen, subjects were symbolically cued (a small leftward or rightward pointing arrow above fixation) to attend the left or right VF and to memorize the items presented in this VF. The cue was shown for 200 ms and then followed by the presentation of the memory array (SOA = 500 ms) for 300 ms. The test array appeared with an SOA of 1300 ms after the memory array, and remained on screen for 2000 ms. The ISI between experimental trials was randomized between 2500–3000 ms (rectangular distribution). At the beginning of each trial block subjects were informed