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Research Report

Saturation of auditory short-term memory causes a plateau in the sustained anterior negativity event-related potential

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ABSTRACT

The maintenance of information in auditory short-term memory (ASTM) is accompanied by a sustained anterior negativity (SAN) in the event-related potential measured during the retention interval of simple auditory memory tasks. Previous work on ASTM showed that the amplitude of the SAN increased in negativity as the number of maintained items increases. The aim of the current study was to measure the SAN and observe its behavior beyond the point of saturation of auditory short-term memory. We used atonal pure tones in sequences of 2, 4, 6, or 8 t. Our results showed that the amplitude of SAN increased in negativity from 2 to 4 items and then levelled off from 4 to 8 items. Behavioral results suggested that the average span in the task was slightly below 3, which was consistent with the observed plateau in the electrophysiological results. Furthermore, the amplitude of the SAN predicted individual differences in auditory memory capacity. The results support the hypothesis that the SAN is an electrophysiological index of brain activity specifically related to the maintenance of auditory information in ASTM.

1. Introduction

One of the major goals of neuroscience is to understand the neuronal mechanisms underlying the processing of sensory events in the central nervous system. A limited number of representations of these sensory events from all modalities (e.g., brief visual, auditory, or tactile stimuli) are temporarily stored in short-term memory (STM). Such sensory memory systems have innumerable applications in daily cognition. For instance, we would be unable to understand any form of spoken language without auditory short term memory (ASTM), given that we need to retain each word as a phrase unfolds over time. Limitations of STM capacity are directly related to individual aptitude in high-level cognitive functions such as the maintenance of temporary representations that allows planning steps required to achieve or to modify a goal (Engle and Kane, 2003; Vogel and Machizawa, 2004). A better understanding of the capacity limits of STM is thus

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relevant to our understanding of many dependent aspects of cognition.

Our present goal was to determine if an electrophysiological index (the sustained anterior negativity (SAN); Guimond et al., 2011; Lefebvre et al., 2013), previously shown to be sensitive to the number of items held in ASTM, would level off (i.e., reach a plateau) as the behavioral maximal number of stored representations is reached. Such an observation would further confirm the SAN as a neural correlate of the maintenance of auditory information in ASTM.

In this study, we focus on STM that lasts a few seconds and is presumed to require sustained neural firing for its maintenance. This maintenance is also limited in the number of items it can hold, which is typically on the order of 4 (Luck and Vogel, 1997; Cowan, 2000). In the auditory domain, the span found in tasks using atonal tones was around 2 (Prosser, 1995; Li et al., 2013). A common measure of STM span is the K value obtained with a formula: $K=(S\times(H-F))$, where K is the memory capacity, S is the number of items presented during the encoding, H is the hit rate,[1] and F is the false alarms rate[2] (Pashler, 1988; Cowan, 2000). The correct detection of difference is considered a hit whereas signaling a difference when the sequences are identical is considered a false alarm. Given the assumption that memory mechanisms work harder when more representations need to be maintained, it is equally reasonable to assume that an index reflecting this mnemonic activity should be modulated by the number of items to be maintained in STM. The increase in activity should occur to the point of saturation, beyond which additional items should not be held in STM.

Studies of visual short-term memory (VSTM) have verified memory saturation and its neural correlate with electroencephalography (EEG), magnetoencephalography (MEG), and functional magnetic resonance imaging (fMRI) (Robitaille et al., 2010; Todd and Marois, 2004; Vogel and Machizawa, 2004). Klaver et al., 1999 first reported a contralateral negative slow wave (CNSW), an event-related potential (ERP) component related to VSTM that was strongest at posterior electrodes over the hemisphere contralateral to the visual field in which visual shapes were presented. In another ERP study, Vogel and Machizawa (2004) focused on brain activity observed during the retention interval and referred to it as contralateral delay activity (CDA). The CDA amplitude increased in negativity as the number of items maintained in VSTM increased. Importantly, they showed that its amplitude reached a plateau corresponding to the group average span. They suggested that variation in CDA across memory loads reflects the maintenance of different numbers of visual representations and, for this reason, was a good index of the span of VSTM.

The sustained posterior contralateral negativity (SPCN), a lateralized EEG component, was also observed during the maintenance of visual items in memory tasks (Jolicoeur et al., 2008). Likely to be the same component as the CNSW and CDA, its amplitude increased in negativity with the number of items to maintain, until where a plateau was formed corresponding to the memory span (Robitaille et al., 2010). The SPCN has been studied in a variety of cognitive tasks going beyond simple short-term memory tasks (e.g., the attentional blink, Dell'Acqua et al., 2006; Jolicoeur et al., 2008; Jolicœur et al., 2006a, 2006b; or mental rotation, Prime and Jolicoeur, 2010). Due to its involvement in tasks that are not memory tasks *per se*, and/or in tasks in which the stimulus remains visible throughout, it seems prematurely restricting to refer to this component as delay activity (e.g., Drew et al., 2009; Lefebvre et al., 2010). Therefore, we will use the SPCN nomenclature for the remainder of the paper. To date, it seems the SPCN for visual memory bears some similarity to the SAN for auditory memory.

Robitaille et al. (2010) extended the work in EEG with MEG recordings of neuronal activity during VSTM maintenance and found a similar pattern to that in EEG. Source localization analyses suggested generators in the superior parietal lobes, consistent with fMRI studies (e.g., Harrison et al., 2010; Robitaille et al., 2010; Todd and Marois, 2004). The authors also found that SPCN amplitude during the retention period was significantly predicted by the behavioral estimate of retention capacity, K, such that as K increased toward the group average span, SPCN amplitude levelled off. This correlation was the first demonstration using MEG linking individual differences in capacity to changes in neuronal activity in superior parietal cortex during the retention of visual representations. These results dovetailed nicely with the earlier work of Vogel and Machizawa (2004) and Todd and Marois (2004).

Since several studies show the existence of modality-specific processing streams, we extend the approach used to study VSTM to the study ASTM. Although previous work has shown interesting relationships between ERPs and memory, none has found a clear plateau as a function of number of items or linked the results to individual differences in span (e.g., Lang et al., 1992; Ruchkin et al., 1992; Schumacher et al., 1996).

In early ASTM studies using verbal information, ERP differences were observed between aurally and visually presented stimuli during the presentation and retention periods (Lang et al., 1992; Ruchkin et al., 1997). Lang et al. (1992) observed a negativity that was more predominant at the frontal scalp electrodes for 3 digits presented aurally than for 3 digits presented visually. Ruchkin et al. (1997) also observed a frontal negativity present in both modalities, but they divided this negativity into a left-lateralized component that was common to both modalities and a bilateral component that was more pronounced in the auditory modality. It is not clear if the authors used "bilateral" in their description of a central distribution to suggest bilateral generators in the auditory cortices. Unlike Lang et al. (1992), the study of Ruchkin et al. (1997) manipulated the number of syllables presented in non-words and, therefore, memory load. Their results revealed that the amplitude of the frontal negativity varied with memory load.

As valuable as these collected results are, a major question remains: is the use of verbal information the best way to study ASTM? Several additional mnemonic codes support the retention of such information (e.g., semantic, phonological,

[1] Hits rate: hits/(total number of trials where the sequences were different).

[2] False alarm rate: false alarms/(total number of trials where the sequences were identical).