Event-Related Potential Measures of Visual Working Memory

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Key Words

Attention
Event-Related Potentials
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ABSTRACT

Visual working memory is a limited capacity system that temporarily maintains information about objects in the immediate visual environment. Psychophysical experiments have shown that most people are able to actively maintain 3 or 4 items in visual working memory at any point in time. To better understand how this process works and why our working memory capacity is so limited, a variety of neurophysiological approaches have been employed. In recent years, there has been a surge of interest in understanding how visual information is maintained in working memory at the neural level. Single-cell research with non-human primates has shown that neuronal firing during the retention period reflects the information that is currently held in working memory. In humans, event-related potentials (ERPs) have been used to examine the maintenance of information in working memory. An event-related potential component, known as the negative slow wave (NSW), has been used to measure the maintenance of information in working memory "online" during a given trial. More recently, another ERP component, the contralateral delay activity (CDA) has been shown to be a fairly specific correlate of the current contents of working memory. This component is sensitive to an individual's working memory capacity and may provide a window into the operations of this central cognitive construct.

INTRODUCTION

Working memory (WM) facilitates our ability to hold a limited amount of information in an active state so that it may be utilized in a broad range of cognitive tasks. Despite subjective experience to the contrary, only a small amount of information can be maintained in WM at once and thus this memory system reflects a central limitation within cognition.[1-4] The specific capacity of WM varies consistently across individuals, and an individual's specific memory capacity has been shown to be predictive of his or her performance on a broad range of cognitive measures.[5-7] Consequently, the operations of WM appear to reflect a core cognitive construct that is essential for a wide range of behaviors.

While WM can be divided into separate sub-systems for verbal and visual information, in this review we will concentrate primarily on the visual component. Visual WM is a system that maintains a small amount of information from the immediate visual environment so that it may be manipulated or acted upon. In the last 10 years there have been a number of studies that have begun to examine the characteristics of visual WM at the behavioral level.[8-12] For example, Vogel, Woodman and Luck[13] developed a simple procedure for measuring the storage capacity of visual WM using a change detection task. In this procedure, participants are presented with a brief array of simple objects (e.g., colored squares) followed by a blank one-second retention period in which they must remember the locations and identities of the objects. After this retention period, subjects are shown a test array of objects and they must decide whether the two arrays are identical or not. On half of the trials, the two arrays are the same; on the other half of trials they differ by the identity of one object. Subjects respond at the end of the trial by pressing one of two buttons (i.e., same or different). We measure memory capacity by charting performance on this task as a function of the number of objects in the memory array. Typically, performance is near perfect for 1, 2, or 3 items but it begins to decline for 4 items and approaches chance by around 8 or 10 items. Using a simple formula that takes into account the number of items in each array as well as false-alarm and correct rejection rate, visual WM capacity is typically estimated to be an average of roughly 3 items.[1,13,14] However, there are considerable individual differences and capacity estimates range from as low as 1.5 objects up to as many as 6 objects.[13,15]

Neurophysiological measures of working memory

Over the past 20 years, primate neurophysiology, functional neuroimaging and electrophysiological measures in humans have been used extensively to examine the brain processes that underlie the operations of WM.[16,17] These studies have made substantial progress in understanding the cortical networks that are responsible for the encoding,

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retention and retrieval of information held in WM. The current article reviews the recent developments using event-related potentials (ERPs) in humans that examine how visual information is maintained in an active state during the retention interval of WM experiments. The excellent temporal resolution provided by electrophysiological methods allows researchers to measure the timing and duration of the dynamic processes that underlie short-term memory and may begin to elucidate the operations of this core cognitive process.

Many of the recent findings in the neurophysiological literature in humans build upon the experimental methodology and theoretical approach stemming from single-unit studies in non-human primates. In a typical task, a monkey is taught to perform a delayed match-to-sample task in which the monkey is presented with an object that he must hold in WM during a blank intervening period before being asked whether the subsequently displayed object matches the identity of the target item.[18] The firing rate of many individual neurons has been shown to increase significantly above its baseline-firing rate and this activity is sustained throughout the retention period. This increased activity is generally referred to as delay activity and is thought to reflect some aspect of the information that the monkey is attempting to hold in WM during this period.[19] Critically, delay activity is often shown to be specific to neurons that code for either the specific object or location that is to be remembered.[20,21] That is, there is not simply a generalized increase of firing rate for all the neurons in a given cortical area during the retention interval. This suggests that delay activity contributes to the specific representation of active memory items rather than reflecting a generalized increase due to arousal or sustained attention.[22] Indeed, several studies have shown that delay activity directly contributes to memory performance on a given trial; when behavioral performance is slow or incorrect there tends to be significantly less delay activity on trials as compared to when the task is performed correctly.[21,23] While delay activity has been reported over a broad range of cortical areas, there appear to be three primary regions where there is a particularly high percentage of cells that show delay activity. These regions are the prefrontal cortex,[19,24,25] the posterior parietal cortex[26,27] and inferotemporal cortex,[20,28] and together these regions are thought to form a network which gives rise to the complex representations held in visual WM.

fMRI studies of working memory

There have been numerous studies that have used functional neuroimaging in humans to examine the operations of WM.[16,29-31] Typically, these studies find increased BOLD activation during the retention period of WM tasks. This sustained activation appears to be analogous to delay activity observed in monkey single-unit studies.[32] While this activity can be observed in many cortical areas it is also primarily observed in the prefrontal,[31,33-35] posterior parietal[16,36,37] and inferotemporal cortices.[38,39] Similar to the delay activity observed in single-unit studies, this fMRI activity has been shown to be specific to the particular demands of the memory task. For example, Sereno et al[36] found that an area of posterior parietal cortex showed location-specific mapping of the position of a remembered target. Moreover, WM-related fMRI activity has also been shown to be specific to the identity of the remembered stimuli.[38-40] Finally, this activity has been shown to be sensitive to both the correct performance on a given trial[40] as well as the current memory load imposed by the task,[34,37] which suggests that this activity reflects a process that is critical to the operation of WM.

Event-related potential measures of working memory

In the past 15 years, there has been increased interest in using ERP components to examine activity during the retention interval of WM paradigms. Much of this work has focused on an ERP component thought to be an electrophysiological correlate of WM, the NSW.[41-47] For example, Ruchkin et al[43] asked subjects to memorize either one or two schematic faces and probed memory for the faces after a 3600ms blank interval. ERPs were time locked to the offset of the memory array and continued throughout the retention interval. During this interval, a NSW was observed over the temporal-occipital electrode sites and was sustained throughout the retention period. The amplitude and scalp topography of the NSW has been found to vary as a function of the nature of the specific memory task, and several groups have used the NSW to measure spatio-temporal activation patterns during WM tasks.[43-45,48] For example, Mecklinger and Pfeifer[45] found that the scalp distribution of the NSW is different for spatial and object memory tasks which suggests that there are somewhat distinct neural substrates underlying these two types of WM. The NSW for spatial memory tended to be focused over the posterior parietal and occipital lobes while object memory resulted in a mid-frontally focused wave. In general, the component has been found to be more focused on the right parietal region during visual WM experiments[48] and left frontal areas during phonological tasks.[49] The NSW bears a number of similarities to individual neuron firing rates in the monkey single-unit literature. For example, the amplitude of the NSW was found to increase as WM load increased from one to two abstract faces.[43] In addition to these WM paradigms, Rösler and colleagues have used NSWs to gain insight into the activation of long-term memory representations during encoding and retrieval.[50-53] This group uses a variation on the fan-paradigm[54] to pair long-term memory associations with multiple cues. These studies have also demonstrated topographic specificity of the NSW to the type of information accessed during long-term memory retrieval as well as sensitivity to cognitive effort necessary to perform the task. While these studies have concentrated on the mechanisms of long-term memory, it is quite plausible that the NSW observed in these tasks

reflects active representations in WM that were retrieved from long-term memory.

A substantial difficulty in interpreting the functional significance of the NSW is that there are numerous processes that occur while a subject is performing a simple memory task that have little or nothing to do with WM per se. These non-specific, task-general processes (e.g., arousal, sustained attention, etc.) may directly contribute to the NSW and may obscure the mnemonic activity embedded within the waveform. One alternative explanation to the NSW modulation is that it reflects general preparatory processing for the response to the match stimulus. It's difficult to be sure how much of the NSW component is due to the anticipation or preparation for an impending event that requires an overt response. The anticipation of a response is associated with another ERP component known as the contingent negative variation (CNV). To address this alternative explanation, Ruchkin et al[42] monitored the NSW in an experiment where subjects always needed to prepare in a similar way for the next stimulus, but only one of the two conditions required active memory rehearsal during the retention interval. Their results suggest that preparation alone cannot explain the NSW. However, other task-general processes that could explain the modulation of this component are difficult to exclude. For instance, the amplitude of the NSW has been found to increase as WM load increases, which suggests that it is sensitive to the increasing number of item representations being held in WM. However, this finding could also be explained by an increase in generalized effort as task difficultly increases. Teasing apart the influence of WM load and generalized effort has proven very challenging because it is very difficult to increase memory load without also increasing the task difficulty. Although some portion of the NSW is likely related to WM processing, it is currently not clear which portions of the activity reflect WM and which reflect more task-general activity. In order for this activity to provide an unambiguous measure of WM, it is critical to control for task-general effects and ideally to show that the activity follows the known behavioral characteristics of visual WM.

Contralateral control method

The problem of separating out the activity that is specific to a particular cognitive process from more task-general activity is common within psychophysiology. One approach that several researchers have used to address this problem over the years is referred to as the contralateral control method.[55] This approach utilizes the contralateral organization of the visual system as a means to isolate a particular cognitive process and reduce the contribution of non-specific phenomena so that it is simpler to interpret the functional significance of the electrophysiological results. To do this, researchers typically present subjects with bilateral displays of stimuli and manipulate which side of the display the subject must engage in a particular task. The process of

interest can then be isolated by measuring the difference between the activity observed over the contralateral and ipsilateral hemispheres. The general logic is that the non-specific task-general processes should activate both hemispheres equivalently, and that the primary difference will be that the activity over the contralateral hemisphere will also contain the process of interest. Although this approach may not be appropriate for examining all cognitive processes, it is particularly well suited for cognitive systems that follow a strong lateral organization in the brain such as the visual and motor systems. For example, this approach has been used extensively in studies of visual selective attention as a means of isolating the attention-related activity from the perceptual activity evoked by the stimulus display.[56] In addition, this approach has been used to examine a broad range of cognitive phenomena such as visual search,[57,58] visual long-term memory,[59] and response preparation.[60,61] Indeed, there are a few ERP components that are specifically defined as a difference between the contralateral and ipsilateral activity under certain balanced task conditions (e.g., N2pc[57]; LRP[62]).Thus, this procedure has also been used to isolate single ERP components from other non-lateralized components that overlap in time.[55]

Recently, Klaver et al,[63] utilized this contralateral control approach to examine the operation of visual WM. In this study, they presented subjects with a bilateral array of abstract shapes, with one shape in each hemifield. At the beginning of each trial, subjects were instructed to remember the abstract shape in one hemifield (either the left or right side) across a 1500ms blank interval until a test object was presented. Shortly following the onset of the memory array, a sustained negative wave was observed at posterior electrode sites that were contralateral to the position of the remembered item and this activity persisted throughout the retention period. This sustained contralateral activity is potentially a useful candidate for a neural correlate of visual WM because it is sensitive to the position of the remembered item, which makes it less likely to be due to more task-general processes that would be expected to be equivalent across hemispheres. Nevertheless, it is still plausible that this activity is simply due to the subject sustaining attention to the position of the object during the delay rather than reflecting the maintained information in memory. Therefore, additional studies are necessary to further demonstrate the specificity of this activity to visual WM processing.

More recently, our laboratory has used a similar approach to examine processes involved in maintaining information in visual WM, and we have begun to test the specificity of this activity by examining whether it follows the known functional properties of this memory system.[64,65] Essentially, we have also used a bilaterally-presented memory array so that we can isolate the hemispheric-specific activity related to the position of the items that the subject is holding in memory so that we may exclude more
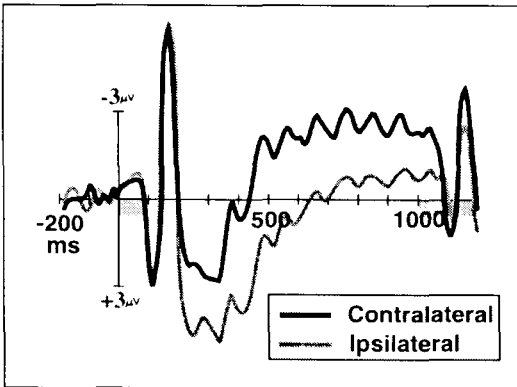
Figure 1.
Grand averaged ERP waveforms time-locked to the memory array averaged across the lateral occipital and posterior parietal electrode sites from Vogel and Machizawa.[64] The two grey rectangles reflect the time periods for the memory and test arrays, respectively. Note that, by convention, negative is plotted upwards.

task-general activity from the waveforms. To do this, we have used a variation on the visual WM task that we described at the beginning of this review. In our initial experiments, observers were presented with arrays of 8 simple objects (e.g., colored squares), with 4 on each side of the display. At the beginning of each trial an arrow cue signaled which side of the display the observer needed to remember over the one-second blank delay. Afterwards, a test array was presented and the observers reported whether the items on the cued side were the same or different. We time-locked the ERPs to the onset of the memory array, and recorded brain activity throughout the retention interval while the subject held the items in memory. Similar to Klaver et al,[63] approximately 200ms following the onset of the memory array we observed a large negative-going voltage over the brain hemisphere that was contralateral to the memorized hemifield, and this response persisted throughout the duration of the memory retention interval (Figure 1). This response was primarily focused over the posterior parietal and lateral occipital electrode sites and strongly resembles delay activity recorded from individual neurons in monkey visual cortex during WM tasks. Thus, we refer to this component as the Contralateral Delay Activity (CDA).

In subsequent experiments we have found that this activity closely mirrors several known properties of visual WM. For example, the amplitude of the CDA is significantly reduced on trials in which the observers report was incorrect, suggesting that this activity reflects a process that is necessary for correct performance on this task.[64,65] The amplitude and scalp distribution of this activity is similar for different types of simple memory items, which is comparable to known behavioral performance with different classes of stimuli.[65] In addition, we have shown that the amplitude of the CDA is not modulated by the size of the
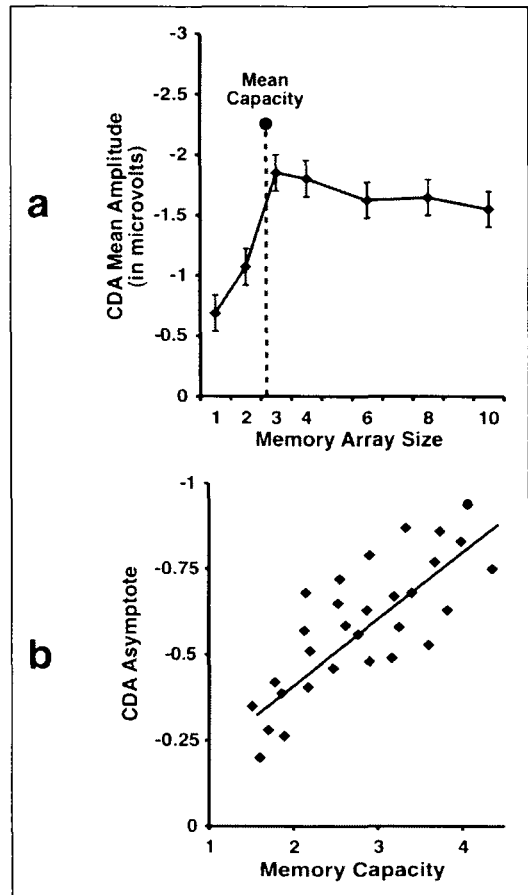

Figure 2.
(a). Mean amplitude (300-900 ms) of the CDA across several memory array sizes from Vogel and Machizawa.[64] Error bars reflect 95% confidence intervals. The vertical dashed line denotes the average memory capacity for the subjects in this sample. (b). The correlation between an individual subject's memory capacity and the increase in amplitude of delay activity between 2 and 4 item arrays.

"spotlight" of attention necessary to encompass the memory items in the display, which further indicates that this activity reflects the memory for the items rather than simply reflecting sustained attention to one side of the display during the retention period.[65]

The strongest evidence that this activity specifically reflects the operation of visual WM is that the amplitude of the CDA is strongly modulated by the number of items that the subject is holding in memory on a given trial, suggesting that it reflects the active representations that are being held in memory.[64,65] Although CDA activity gets larger in amplitude for arrays of one, two, or three items, it ceases to increase for larger arrays (e.g., 6, 8, 10 items), which indicates that the activity only reflects the number of items the subject can actually hold in memory at the same time. CDA

amplitude reaches an asymptotic limit for arrays of approximately 3 items, which is equivalent to the behavioral estimate of average memory capacity on this task (Figure 2a). Indeed, the precise point at which this activity reaches asymptote is different for individual subjects depending upon his or her specific memory capacity (Figure 2b). More specifically, CDA amplitude stops increasing for subjects with low memory capacity at smaller array sizes than high capacity subjects, whose CDA amplitude is much higher for large array sizes than small array sizes.

Together, these results demonstrate that the CDA follows the known psychophysical properties of visual WM and therefore is likely to specifically reflect the active representations being held in memory on a given trial rather than other more task-general processes such as arousal or general effort. Thus, this activity provides a neurophysiological confirmation of an average visual WM capacity of around 3 items. Moreover, the fact that this activity is sensitive to both the current number of items being held in memory as well as individual differences in memory capacity suggests that it holds promise as a powerful new tool for exploring the operations of visual WM.

ACKNOWLEDGMENT

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