

UC Riverside

UC Riverside Previously Published Works

Title

Temporal attention is not affected by working memory load

Permalink

<https://escholarship.org/uc/item/5hb8g6v5>

Authors

Zanto, Theodore P

Liu, Helen

Pan, Peter

et al.

Publication Date

2020-09-01

DOI

10.1016/j.cortex.2020.06.008

Peer reviewed



Published in final edited form as:

Cortex. 2020 September ; 130: 351–361. doi:10.1016/j.cortex.2020.06.008.

Temporal attention is not affected by working memory load

T.P. Zanto^{1,2}, H. Liu¹, P. Pan¹, A. Gazzaley^{1,2,3}

¹Department of Neurology, University of California San Francisco, San Francisco, CA 94158, USA

²Neuroscape, University of California San Francisco, San Francisco, CA 94158, USA

³Departments of Physiology and Psychiatry, University of California San Francisco, San Francisco, CA 94158, USA

Abstract

Temporal attention refers to the ability to orient attention in time, which serves to enhance performance such as target detection and discrimination and is a fundamental component of cognitive function. Although some research indicates that temporal attention ability is affected by working memory updating, it is unclear whether temporal attention is also affected by the availability of working memory stores. To address this, participants were presented a dual-task paradigm requiring zero, three, or six digits to be held in working memory while engaged in a temporally cued visual discrimination task. Results show that working memory load did not differentially affect the ability to benefit from predictive temporal cues during the visual discrimination task. This indicates that temporal attention is not affected by available working memory stores. Interestingly, posterior beta band (12–30 Hz) activity was differentially modulated by temporal attention and working memory load, such that it decreased prior to expected targets and increased with load. Analysis across participants indicated that those individuals who exhibited greater temporal attention-based modulation of beta activity (i.e., predictive < neutrally cued) displayed improved discrimination performance, but also yielded lowered working memory accuracy. Thus, the ability to benefit from temporal attention processes while multitasking comes at the cost of lowered secondary task performance. Together, these results indicate that available working memory stores do not affect temporal attention ability. Rather, limitations in divided attention ability result in a performance cost that prioritizes one task over another, which may be indexed by beta band activity.

Keywords

working memory load; temporal attention; beta band; expectation

1. Introduction

It was shown over one hundred years ago that a predictable interval between a warning and a target stimulus results in speeded responses to the target (Woodrow, 1914). The

Correspondence: Theodore Zanto, 675 Nelson Rising Ln. Box 0444, San Francisco, CA, 94158, theodore.zanto@ucsf.edu.

Declaration of Interest: None.

warning stimulus serves to cue the impending target and enables attention to be allocated in time when the cue-target interval, or foreperiod, is predictable. Whereas Woodrow (1914) demonstrated this temporal cueing effect with a consistent foreperiod duration, similar cueing effects have been observed when the cue predicts a foreperiod duration that varies on a trialwise basis (Coull and Nobre, 1998; Miniussi et al., 1999; Lange and Roder, 2006). Thus, the deployment of temporal attention to facilitate performance is under flexible cognitive control, as opposed to a rigid process with a set optimal time course. Given the limitations of cognitive control processes (Grier et al., 2003; Dux et al., 2006; Endress and Szabo, 2017), it stands to reason that temporal attention is also limited. Yet, it is unclear to what extent temporal attention may be limited by concurrent cognitive processes, such as retaining a working memory load.

Indeed, there is some evidence that a concurrent working memory load negatively affects temporal attention. During a temporally cued target detection task, participants responded faster following valid temporal cues compared to invalid cues, but this validity effect was not present when participants were given a secondary task that required updating working memory (Capizzi et al., 2012). Furthermore, the contingent negative variation (CNV), as measured by electroencephalography (EEG), was modulated by temporal attention, but exhibited less temporal-attention based modulation during the dual task condition (Capizzi et al., 2013). It is important to note that during these tasks, participants were required to update working memory. Although the ability to update working memory is related to working memory capacity (Ecker et al., 2010), it remains unclear whether temporal attention was affected by limited working memory stores or by limitations imposed by updating working memory.

Whereas working memory maintenance and updating are thought to rely on distinct mechanisms (D'Esposito et al., 1999; Miller et al., 2018), both have been related to attention control (Engle, 2018). Moreover, many researchers consider the processes involved in working memory maintenance to be, in essence, attentional processes (Cowan, 1995; Kiyonaga and Eger, 2013). Thus, it is plausible that a concurrent working memory load may interfere with temporal attention ability. To address this possibility, the current study utilized a dual task paradigm that manipulated working memory load, with no requirement to update working memory, while participants simultaneously engaged in a temporally cued visual discrimination task. It was hypothesized that if temporal attention were affected by limitations in available working memory stores, then the ability to benefit from predictive temporal cues would diminish with increasing working memory load. Similarly, it was hypothesized that if a working memory load negatively affects temporal attention, temporal attention-based modulation of neural activity will be decreased.

Temporal attention is known to modulate neural activity during the foreperiod such that EEG measures of the CNV and alpha band (8–12 Hz) activity in posterior regions decrease up to the onset of the impending target stimulus (Miniussi et al., 1999; Los and Heslenfeld, 2005; Praamstra et al., 2006; Rohenkohl and Nobre, 2011). As such, the CNV and alpha band activity during the foreperiod, prior to the target, served as our neural correlate of temporal attention. Additionally, theta band (4–8 Hz) activity was assessed because midline frontal theta oscillations have been associated with working memory maintenance (reviewed

in Hsieh and Ranganath, 2014), and this theta activity increases with an increased working memory load (Jensen and Tesche, 2002) and during multitasking performance (Anguera et al., 2013). Therefore, analysis of midline frontal theta activity will help index the extent to which participants engaged in the memory (dual) task paradigm. Finally, beta band (12–30 Hz) activity was assessed because it has been associated with both temporal attention (Roelfsema et al., 1997; Androulidakis et al., 2007; Donner et al., 2009; Bauer et al., 2014; van Ede et al., 2014) and working memory maintenance (Siegel et al., 2009)(Deiber et al., 2007; Zanto and Gazzaley, 2009; Chen and Huang, 2016). Given the sensitivity of beta band activity to both temporal attention and working memory load, beta band activity will be used as an index of the task-specific cognitive state (Engel and Fries, 2010).

It was hypothesized that if a concurrent working memory load negatively affects temporal attention, the benefits of temporally predictive cues on performance should decrease with increasing load. Concomitantly, increased load should increase frontal theta activity and lessen the temporally-cued based modulation of the CNV and alpha band activity. Similarly, because beta activity is modulated by both tasks, increased load-related beta activity should be associated with decreased temporal attention-based modulation in the beta band.

2. Methods

We report how we determined our sample size, all data exclusions (if any), all inclusion/exclusion criteria, whether inclusion/exclusion criteria were established prior to data analysis, all manipulations, and all measures in the study

2.1 Participants

Twenty-five healthy young adults (mean age, 23.4 years; range, 19 – 35 years; 16 females) gave informed consent to participate in the study approved by the Committee on Human Research at the University of California in San Francisco. All participants had normal or corrected-to-normal vision and were screened to ensure they were healthy. Additionally, all participants were required to have 12 years minimum education. Participants were instructed to maintain their normal daily routine prior to the experiment, and not ingest more caffeine than normal and refrain from excessive drinking or illicit substances 24 hours prior to the experiment.

2.2 Stimuli and experimental procedure

No part of the study procedures or analyses was pre-registered prior to the research being conducted. Stimuli were presented through E-Prime software (Psychology Software Tools) run on a Dell Optiplex GX620 with a 22" Mitsubishi Diamond Pro 2040U CRT monitor. Participants were seated in a dark room, 100 cm from the monitor, with a chin rest. A white circle with a 7 cm inner (8 cm outer) diameter was centered on a black background during the experiment. Figure 1 depicts one experimental trial. Trials were blocked according to a visual working memory load condition that required participants to remember 0, 3, or 6 digits while they performed a temporally cued target discrimination task. Each working memory load condition was presented in two blocks, for a total of 6 task blocks that were

counterbalanced across participants. Participants were instructed to fixate on a dot (0.5 cm diameter) located in the center of the circle.

The fixation period was between 1300 and 1800 ms (selected randomly) and was followed by 0, 3, or 6 numbers that were to be remembered (number load). The number load was presented for 2 sec and then a 100 ms cue appeared that contained one of three letters: S, L, or N. These letters indicated the duration of the foreperiod (S = short = 600 ms; L = long = 1400 ms; N = neutral = 600 or 1400 ms). Thus, only S and L cues predicted when the target would appear and will be referred to as PS (predictive short) and PL (predictive long), respectively. The neutral cues will be referred to as NS and NL, depending on whether the N preceded a short or long foreperiod, respectively. One of the four cue types (PS, PL, NS, NL) was selected randomly on each trial, each with a 25% probability. Following the foreperiod, a target appeared for 100 ms with either an x or a + inside the white circle, each with a 50% probability of occurrence. Participants were given a graphical depiction of the task (Figure 1), and were informed of the cue meaning, the timing of the task, and the block design. Therefore, prior to each block, participants knew in advance the amount of information to be held in working memory while engaged in the temporally cued discrimination task. Participants were instructed to respond with their thumbs as quickly and accurately as possible to the target by pressing the left button for x targets and the right button for + targets. Following the target response, if a number load was presented at the start of the trial, another number was presented until participants responded with a right button press for a match and a left button press for a non-match. Probe numbers always contained the same amount of digits as the number load. Non-matched probe stimuli (50% probability) only differed by one digit randomly selected. During each block, 160 trials were presented, yielding 40 trials for each of the four cue types per block.

2.3 Data acquisition

Data were recorded during six blocks (two per load condition) lasting ~10 min each, yielding 80 epochs of data for each cue type per condition. Electrophysiological signals were recorded with a BioSemi ActiveTwo 64-channel EEG acquisition system in conjunction with BioSemi ActiView software (Cortech Solutions). Signals were amplified and digitized at 1024 Hz with a 24-bit resolution and no on-line filter. All electrode offsets were maintained between ± 20 mV. Data and study materials are available online (<http://dx.doi.org/10.17632/j7cffjghsw.1>). Experimental stimuli and presentation code are no longer available following a hard drive crash. For access to the raw EEG data, contact the corresponding author. Per conditions of our ethics approval, access will be granted to named individuals in accordance with ethical procedures governing the reuse of sensitive data. Specifically, requestors must complete a formal data sharing agreement that provides for 1) a commitment to using the data only for research purposes and not to attempt to identify any individual participant; 2) a commitment to securing the data using appropriate computer technology; and 3) a commitment to destroying or returning the data after analyses are completed.

2.4 Data analysis

All data analyses were conducted in Matlab (Mathworks). Trials in which discrimination target responses occurred prior to stimulus onset or 2 standard deviations away from the participant's mean response time were excluded from analysis (3.4% of all trials). Two participants were excluded due to mean response times exceeding 2 standard deviations away from the group mean. Raw EEG data were referenced to the average off-line. Eye artifacts were removed through an independent component analysis by excluding components consistent with topographies for blinks, eye movements, and the electrooculogram time series. Data were segmented into epochs beginning 200 ms precue onset and ending 800 ms post-target onset. To minimize spurious peak event-related potential (ERP) measures, epochs were low-pass filtered at 30 Hz with a zero-phase shift (noncausal) finite impulse response filter. Epochs that exceeded a voltage threshold of $\pm 75 \mu\text{V}$ were rejected. A 200 ms precue baseline was subtracted from each epoch before calculating the ERP. Analysis of the ERP focused on the contingent negative variation (CNV) in a posterior region of interest (ROI) by averaging over data from five central posterior electrodes (POz, Oz, Iz, O1, O2).

Although the CNV is often reported at frontocentral regions (Brunia and Damen, 1988), it may also be observed in posterior–central regions (Simson et al., 1977; van Boxtel and Brunia, 1994), which may reflect less motor-related expectation and more perceptual anticipatory processes in the visual domain (Ruchkin et al., 1986). Importantly, the CNV is a slow wave that becomes more negative in anticipation of an impending stimulus, which can serve as an index for temporal attention processes.

Spectral activity in the theta (4–8 Hz), alpha (8–12 Hz) and beta (12–30 Hz) bands were acquired via complex Morlet wavelets (family ratio: $f_0/\sigma_f = 7$) applied to the epoched data before low-pass filtering. Spectral power was calculated from the wavelet coefficients by averaging the magnitude of spectral activity over trials, effectively ignoring phase information (Tallon-Baudry and Bertrand, 1999). Spectral power was then normalized for each participant by calculating the z-score over time from data that was concatenated across all conditions and cue types. Normalized spectral activity in the alpha and beta bands was then analyzed in two posterior ROIs averaged over five electrodes from the left (O1, PO3, PO7, P7, P9) and right (O2, PO4, PO8, P8, P10) hemispheres. Electrodes for these ROIs were selected based on previous results from the same paradigm (Zanto et al., 2011). Additional support for these posterior ROIs stem from research indicating these regions exhibit a temporal attention-based modulation of alpha and beta band activity (Roelfsema et al., 1997; Bauer et al., 2014; van Ede et al., 2014), as well as a working memory load sensitivity of beta band activity (Deiber et al., 2007; Zanto and Gazzaley, 2009). Normalized spectral activity in the theta band was analyzed in a midline anterior ROI (AFZ, FZ, FCZ, F1, F2). This region was selected for analysis due to extensive research demonstrating sensitivity of midline frontal theta activity to working memory load (reviewed in Hsieh and Ranganath, 2014). For statistical analyses of both spectral data and the CNV, data were averaged in a temporal window during the foreperiod 250 – 50 ms before target onset. Statistical analyses for EEG as well as behavioral data used a repeated-measures ANOVA with a Greenhouse–Geisser correction when appropriate.

To explore possible sources of spectral activity, data was submitted to exact low resolution electromagnetic tomography (eLORETA) as implemented through the sLORETA-Key software package (<http://www.uzh.ch/keyinst/loreta.htm>) (Fuchs et al., 2002; Pasqual-Morqui, 2002; Jurcak et al., 2007). To assess differences between conditions, a voxel-by-voxel comparison of EEG sources was performed within a time-frequency window of interest as noted above. To assess significant differences between conditions, the log of F-ratio was computed via statistical non-parametric analysis based on a permutation test (5000 iterations), which controls for multiple comparisons (Nichols and Holmes, 2002).

3. Results

3.1 Behavioral Data

All behavioral data is summarized in Table 1. Mean accuracy and response time data for the working memory task were each submitted to a repeated measures ANOVA with Load (3, 6 digits), Foreperiod (short, long), and Cue (Predictive, Neutral) as factors. Results from working memory accuracy data yielded a main effect of Load ($F(1,22) = 68.14$, $p < 0.001$, $\eta_p^2 = 0.76$) such that 3 digits ($M = 92.5\%$; $SEM = 0.9\%$) were remembered better than 6 digits ($M = 81.8\%$; $SEM = 1.2\%$). No other main effects or interactions were observed (Foreperiod: $F(1,22) = 0.16$, $p = 0.70$, $\eta_p^2 = 0.01$; Cue: $F(1,22) = 2.19$, $p = 0.15$, $\eta_p^2 = 0.09$; Load \times Cue: $F(2,44) = 0.26$, $p = 0.62$, $\eta_p^2 = 0.01$; Load \times Foreperiod: $F(2,44) = 0.19$, $p = 0.67$, $\eta_p^2 = 0.01$; Foreperiod \times Cue: $F(1,22) = 0.02$, $p = 0.88$, $\eta_p^2 = 0.001$; Load \times Foreperiod \times Cue: $F(2,44) = 0.67$, $p = 0.42$, $\eta_p^2 = 0.03$).

Results from response time data yielded main effects of Load ($F(1,22) = 58.24$, $p < 0.001$, $\eta_p^2 = 0.73$) and Foreperiod ($F(1,22) = 12.13$, $p = 0.002$, $\eta_p^2 = 0.36$) such that responses were faster for 3 digits ($M = 773$ ms; $SEM = 19$ ms) compared to 6 digits ($M = 1068$ ms; $SEM = 35$ ms) and faster following short foreperiods ($M = 902$ ms; $SEM = 31$ ms) compared to long foreperiods ($M = 939$ ms; $SEM = 33$ ms). No other main effects or interactions were observed (Cue: $F(1,22) = 0.14$, $p = 0.71$, $\eta_p^2 = 0.01$; Load \times Cue: $F(2,44) = 0.45$, $p = 0.51$, $\eta_p^2 = 0.02$; Load \times Foreperiod: $F(2,44) = 0.01$, $p = 0.91$, $\eta_p^2 < 0.001$; Foreperiod \times Cue: $F(1,22) = 0.04$, $p = 0.85$, $\eta_p^2 = 0.002$; Load \times Foreperiod \times Cue: $F(2,44) = 3.66$, $p = 0.07$, $\eta_p^2 = 0.14$). Together, these results confirm our manipulation of task difficulty such that working memory accuracies are lower and response times are slower with a high digit load.

Mean accuracy and response time data for the target discrimination task were each submitted to a similar repeated measures ANOVA, except the Load factor included an additional level (0, 3, 6 digits). Results from discrimination accuracy data yielded a main effect of Load ($F(2,44) = 11.98$; $p < 0.01$, $\eta_p^2 = 0.35$) such that, surprisingly, no working memory load ($M = 96.6\%$; $SEM = 0.4\%$) elicited lower accuracy than a working memory load with 3 digits ($M = 98.7\%$; $SEM = 0.2\%$) or 6 digits ($M = 98.3\%$; $SEM = 0.3\%$). No other main effects or interactions were observed (Foreperiod: $F(1,22) = 2.66$, $p = 0.12$, $\eta_p^2 = 0.11$; Cue: $F(1,22) = 3.13$, $p = 0.09$, $\eta_p^2 = 0.12$; Load \times Cue: $F(2,44) = 1.11$, $p = 0.34$, $\eta_p^2 = 0.05$; Load \times Foreperiod: $F(2,44) = 0.29$, $p = 0.75$, $\eta_p^2 = 0.01$; Foreperiod \times Cue: $F(1,22) = 0.28$, $p = 0.60$, $\eta_p^2 = 0.01$; Load \times Foreperiod \times Cue: $F(2,44) = 2.06$, $p = 0.14$, $\eta_p^2 = 0.09$).

Results from response time data yielded a main effect of Load ($F(2,44) = 40.79$, $p < 0.001$, $\eta_p^2 = 0.65$) such that target discrimination responses were slower with no concurrent working memory load ($M = 506$ ms; $SEM = 9$ ms) compared to 3 digits ($M = 433$ ms; $SEM = 10$ ms; $t(22) = 3.87$, $p < 0.001$) or 6 digits ($M = 442$ ms; $SEM = 10$ ms; $t(22) = 3.22$, $p = 0.003$) in working memory. No response time difference was observed between 3 and 6 digits held in working memory ($t(22) = 1.71$, $p = 0.10$). Furthermore, a main effect of Cue ($F(1,22) = 11.23$, $p = 0.003$, $\eta_p^2 = 0.34$) indicated responses were faster when the cue was predictive ($M = 455$ ms; $SEM = 8$ ms) compared to neutral ($M = 465$ ms; $SEM = 8$ ms). Importantly, an interaction between Cue and Foreperiod ($F(1,22) = 16.06$, $p < 0.001$, $\eta_p^2 = 0.42$) replicated our previous findings that response times were modulated by cue type only for short (NS > PS; $t(22) = 4.05$; $p < 0.001$), but not long (NL = PL; $t(22) = 0.27$; $p = 0.79$), foreperiod durations (Figure 2). In other words, response times were faster following short foreperiod durations that were cued (PS) compared to neutrally cued (NS), whereas no difference in response times were observed between cue types following a long foreperiod duration (NS = PS). The cueing effect has been previously observed to be exclusive to short, but not long, foreperiod durations because when a neutral cue is presented, it is understood that the foreperiod duration is long if the target does not appear after the short foreperiod duration (Miniussi et al., 1999; Zanto et al., 2011). Thus, all cueing effects were expected to occur during the short foreperiods. No other main effects or interactions were observed (Foreperiod: $F(1,22) = 3.13$, $p = 0.09$, $\eta_p^2 = 0.12$; Load \times Cue: $F(2,44) = 1.22$, $p = 0.31$, $\eta_p^2 = 0.05$; Load \times Foreperiod: $F(2,44) = 1.28$, $p = 0.26$, $\eta_p^2 = 0.06$; Load \times Foreperiod \times Cue: $F(2,44) = 1.13$, $p = 0.33$, $\eta_p^2 = 0.05$).

Together, the behavioral results indicate that working memory performance declines with an increasing digit load, and such increased task difficulty actually improves target discrimination performance, presumably due to increased task engagement. Although Load did not interact with Cue, an ad-hoc analysis assessing the cue effect (predictive versus neutral) was conducted for each Load level during short foreperiod durations. In other words, NS was compared to PS for each of the three load conditions. This was conducted to ensure that load did not alter the cueing effect. Results confirmed the cueing effect (NS > PS) at each Load level (each $p < 0.01$) and, therefore, provided additional evidence that the ability to benefit from temporal attention was not affected by working memory load.

3.2 Contingent Negative Variation

To assess the CNV, posterior CNV amplitudes were submitted to a repeated measures ANOVA with Load (0, 3, 6 digits), Foreperiod (short, long), and Cue (Predictive, Neutral) as factors. Results showed a main effect of Foreperiod ($F(1,22) = 16.00$; $p < 0.001$, $\eta_p^2 = 0.42$) such that the CNV was more negative during short foreperiods compared to long foreperiods. Additionally, an interaction between Cue and Foreperiod was observed ($F(1,22) = 4.89$; $p = 0.04$, $\eta_p^2 = 0.18$; Supplementary Figure 1a). Ad-hoc analysis of this interaction showed that the CNV was modulated by Cue (i.e., predictive more negative than neutral) more during short compared to long foreperiod durations ($t(22) = 2.21$; $p = 0.04$; Supplementary Figure 1b), as previously observed (Miniussi et al., 1999; Zanto et al., 2011). No other main effects or interactions were observed. Importantly, the main effect of Load ($F(2,44) < 0.01$; $p > 0.99$, $\eta_p^2 < 0.001$) and the interaction between Load and Cue ($F(2,44)$

= 0.72; $p = 0.49$, $\eta_p^2 = 0.03$) as well as Load \times Cue \times Foreperiod ($F(2,44) = 0.83$; $p = 0.44$, $\eta_p^2 = 0.04$) were not significant. Furthermore, it should be noted that Load did not exhibit a main effect or any interactions when assessing the CNV in more fronto-central regions. Thus, a concurrent working memory load did not alter temporal attention processes as indexed by the CNV.

3.3 Alpha Band Activity

Normalized posterior alpha band activity prior to the target was submitted to the same ANOVA as the CNV with the addition of ROI (left, right hemisphere) as a fourth factor. A main effect of Cue ($F(1,22) = 12.06$, $p = 0.002$, $\eta_p^2 = 0.35$; Supplementary Figure 2) was observed such that alpha activity was more negative following a predictive compared to neutral cue. The main effect of ROI was trending toward significance (ROI: $F(1,22) = 4.05$; $p = 0.06$, $\eta_p^2 = 0.16$), indicating greater alpha activity in the left, compared to right, hemisphere. No other main effects or interactions were observed (Foreperiod: $F(1,22) = 2.40$; $p = 0.14$, $\eta_p^2 = 0.10$; Load \times Foreperiod: $F(2,44) = 0.11$; $p = 0.90$, $\eta_p^2 = 0.005$; Foreperiod \times Cue: $F(1,22) = 2.89$; $p = 0.10$, $\eta_p^2 = 0.12$; Load \times ROI: $F(2,44) = 1.27$; $p = 0.29$, $\eta_p^2 = 0.05$; Cue \times ROI: $F(1,22) < 0.01$; $p = 0.98$, $\eta_p^2 < 0.001$; Foreperiod \times ROI: $F(1,22) = 0.45$; $p = 0.51$, $\eta_p^2 = 0.02$; Load \times Cue \times ROI: $F(2,44) = 0.26$; $p = 0.77$, $\eta_p^2 = 0.01$; Load \times Foreperiod \times ROI: $F(2,44) = 0.50$; $p = 0.61$, $\eta_p^2 = 0.02$; Foreperiod \times Cue \times ROI: $F(1,22) = 0.36$; $p = 0.55$, $\eta_p^2 = 0.02$; Load \times Foreperiod \times Cue \times ROI: $F(2,44) = 0.39$; $p = 0.68$, $\eta_p^2 = 0.02$). Most notably, the main effect of Load ($F(2,44) = 0.69$; $p = 0.51$, $\eta_p^2 = 0.03$) and the interaction between Load and Cue ($F(2,44) = 0.28$; $p = 0.76$, $\eta_p^2 = 0.01$) as well as Load \times Cue \times Foreperiod ($F(2,44) = 0.09$; $p = 0.91$, $\eta_p^2 = 0.004$) were not significant. Thus, a concurrent working memory load also did not alter temporal attention processes as indexed by alpha band activity.

3.4 Theta Band Activity

Normalized anterior theta band activity prior to the target was submitted to the same ANOVA as the CNV. A main effect of Foreperiod ($F(1,22) = 15.93$, $p < 0.001$, $\eta_p^2 = 0.42$) was observed such that theta activity was greater during short, compared to long, foreperiods. Additionally, an interaction between Load and Cue ($F(2,44) = 4.82$, $p = 0.01$, $\eta_p^2 = 0.18$) was observed. Post-hoc analysis of the interaction indicated that theta activity was greater following neutral, compared to predictive, cues when there was no working memory load ($t(22) = 2.49$, $p = 0.02$). However, no theta activity differences were observed between cue types with a concurrent working memory load (both $p > 0.35$). Interestingly, no differences between load levels were observed when comparing within cue type (e.g., predictive 0 load vs predictive 6 load; all $p > 0.12$). No other main effects or interactions were observed (Cue: $F(1,22) = 0.27$; $p = 0.61$, $\eta_p^2 = 0.01$; Load \times Foreperiod: $F(2,44) = 0.28$; $p = 0.76$, $\eta_p^2 = 0.01$). Of note, the main effect of Load ($F(2,44) = 0.31$; $p = 0.73$, $\eta_p^2 = 0.01$), the interaction between Cue and Foreperiod ($F(1,22) = 2.81$; $p = 0.11$, $\eta_p^2 = 0.11$) as well as the Load \times Cue \times Foreperiod interaction ($F(2,44) = 0.51$; $p = 0.61$, $\eta_p^2 = 0.02$) were not significant. The absence of a Load main effect coupled with the lack of a systematic difference between load levels within the Load \times Cue interaction suggests theta was not sensitive to a concurrent working memory load. Moreover, Cue and Foreperiod did not interact as would be expected if theta activity were involved in temporal attention

processes. Therefore, midline frontal theta activity does not appear to provide much insight into the relationship between working memory load and temporal attention processes.

3.5 Beta Band Activity

Normalized posterior beta band activity prior to the target was submitted to the same ANOVA as the alpha band activity. A main effect of Load ($F(2,44) = 3.23$, $p = 0.05$, $\eta_p^2 = 0.13$) was observed such that beta activity increased with increasing digit load (Figure 3). Additionally, a main effect of Cue ($F(1,22) = 14.57$, $p < 0.001$, $\eta_p^2 = 0.40$) and an interaction between Cue and Foreperiod ($F(1,22) = 6.04$, $p = 0.02$, $\eta_p^2 = 0.22$) was observed. Ad-hoc analysis of the interaction showed that beta activity was modulated by Cue (i.e., neutral > predictive) only for short ($t(22) = 3.46$; $p = 0.002$), but not long ($t(22) = 0.50$; $p = 0.62$), foreperiod durations (Figure 4). Thus, beta activity was differentially modulated by temporal attention and working memory load, such that it decreased prior to expected targets and increased with load. No other main effects or interactions were observed (Foreperiod: $F(1,22) = 0.90$; $p = 0.35$, $\eta_p^2 = 0.04$; ROI: $F(1,22) = 1.89$; $p = 0.19$, $\eta_p^2 = 0.08$; Load \times Foreperiod: $F(2,44) = 1.16$; $p = 0.32$, $\eta_p^2 = 0.05$; Load \times ROI: $F(2,44) = 1.00$; $p = 0.37$, $\eta_p^2 = 0.04$; Cue \times ROI: $F(1,22) = 0.45$; $p = 0.51$, $\eta_p^2 = 0.02$; Foreperiod \times ROI: $F(1,22) = 0.12$; $p = 0.73$, $\eta_p^2 = 0.006$; Load \times Cue \times ROI: $F(2,44) = 0.18$; $p = 0.84$, $\eta_p^2 = 0.008$; Load \times Foreperiod \times ROI: $F(2,44) = 0.42$; $p = 0.66$, $\eta_p^2 = 0.02$; Foreperiod \times Cue \times ROI: $F(1,22) = 0.64$; $p = 0.43$, $\eta_p^2 = 0.03$; Load \times Foreperiod \times Cue \times ROI: $F(2,44) = 0.31$; $p = 0.74$, $\eta_p^2 = 0.01$). Most notably, the interaction between Load and Cue ($F(2,44) = 2.36$; $p = 0.11$, $\eta_p^2 = 0.10$) as well as Load \times Cue \times Foreperiod ($F(2,44) = 0.97$; $p = 0.39$, $\eta_p^2 = 0.04$) were not significant. As such, similar to the other neural metrics of temporal attention, working memory load did not affect temporal attention-based modulation of beta activity.

To address whether the cue-based modulation of beta activity affected discrimination performance, a regression analysis was conducted between the magnitude of beta modulation (neutral short – predictive short (NS – PS)) and the cued performance gains in discrimination response time following the short foreperiod durations (NS – PS), averaged over load. Results showed that participants who modulated beta band activity the most (NS > PS) exhibited the greatest benefit from predictive cues ($r = 0.53$, $p = 0.009$; Figure 5A). Based on the topographical distribution, this beta band modulation appears to arise largely from parieto-occipital regions (Supplementary Figure 3A), rather than from frontal or motoric regions. Source localization of beta band activity supports this assertion, and indicates cuneus/precuneus as the most likely source of this modulatory effect (Supplementary Figure 3B). Although the comparison of beta sources between NS and PS conditions was only trending toward significance (NS > PS, $p = 0.10$, Supplementary Figure 3B), topographies and source localization data both support the assertion that cue-based modulation of beta activity arises from posterior regions.

As it was shown that beta activity increased with an increasing working memory load, it may be hypothesized that the magnitude of beta modulation during short foreperiods (NS – PS) reflect differences in working memory engagement, such that increased beta activity prior to expected targets indicates an engagement of working memory processes while decreased beta activity reflects a disengagement. Thus, increased beta modulation

(NS > PS) may reflect the difference in engagement / disengagement with working memory processes. To address this, participants were grouped by a median split of those who exhibited high (NS > PS) and low (NS \approx PS) beta modulation averaged over load. Within group comparisons showed that those participants who exhibited high beta modulation (NS > PS) yielded lowered working memory accuracy following predictive cues compared to neutral cues (NS > PS, $t(22) = 2.25$, $p = 0.03$; Figure 5B), but this relationship was not observed in participants with low beta modulation (NS \approx PS, $t(22) = 0.53$, $p = 0.60$; Figure 5B). Although between group comparisons of working memory differences (NS – PS) did not reach significance ($p = 0.11$), this is most likely due to limited statistical power after dividing participants into subgroups. Overall, these results indicate that participants with high beta modulation disengaged working memory processes prior to discrimination. Thus, participants who exhibited greater beta modulation were able to enhance discrimination performance (Figure 5A) at the expense of working memory accuracy (Figure 5B). This indicates that the ability to utilize predictive cues is limited by divided attention ability, which prioritizes one task over another.

Together, results from beta band activity are similar to response time performance in that both are modulated by temporal attention and working memory load. The magnitude of beta modulation was related to performance such that those participants who modulated beta band activity in response to temporally predictive cues benefitted the most during the discrimination task, but exhibited declines in working memory performance. This suggests that the ability to utilize predictive cues is sensitive to divided attention ability, which yields a trade-off in performance as indexed by beta band activity.

4. Discussion

Here it was shown that a concurrent working memory load did not detrimentally affect temporally cued discrimination performance or neural markers of temporal attention as indexed by CNV and pre-stimulus alpha and beta band activity in posterior regions. These results indicate temporal attention ability is not affected by the availability of working memory stores. However, posterior beta band activity during the foreperiod was differentially modulated by temporal attention and working memory load, such that it decreased prior to expected targets and increased with load. Furthermore, participants who exhibited the greatest temporal attention-based modulation of beta activity displayed the greatest cue-based benefits in discrimination performance, but also exhibited lower working memory accuracy. Together, these results suggest that participants optimized discrimination performance at the expense of the secondary working memory task by disengaging working memory processes as indexed by anticipatory beta band activity. Thus, temporal attention appears to be sensitive to cognitive limitations, such as divided attention, but this is not due to limitations in available working memory stores.

Previous research has demonstrated that updating working memory disrupts temporal attention ability (Capizzi et al., 2012, 2013). Here, it was assessed whether a concurrent working memory load would similarly alter neural signatures of temporal attention as indexed by the CNV, alpha, and beta band activity during the foreperiod, but this was not observed. Although both working memory maintenance and working memory

updating have been related to attention control (Engle, 2018), they are thought to rely on distinct mechanisms (D'Esposito et al., 1999; Miller et al., 2018). As such, it is possible that temporal attention only shares cognitive resources with working memory updating processes. However, previous research into beat-based timing mechanisms have indicated temporal attention is not affected by working memory updating (Cutanda et al., 2015). Therefore, additional research will be required to ascertain the role of working memory updating in temporal attention processes.

Although beat-based timing mechanisms are thought to differ from duration-based timing mechanisms (Teki et al., 2011) as implemented in the current study, Cutanda et al. (2015) also demonstrated that the ability to benefit from predictive, beat-based timing cues was not affected by working memory load, in line with our current results. Thus, both beat-based and duration-based timing mechanisms likely do not share cognitive resources underlying working memory maintenance. As such, previous reports of age-related declines in utilizing duration-based (Zanto et al., 2010; Bollinger et al., 2011; Zanto et al., 2011; Padgaonkar et al., 2017) or beat-based (Zanto et al., 2019) timing information may not be fully attributed to limitations in available working memory stores. It is possible that temporal attention is a fundamental component of cognition, and as such, may either require little working memory resources or perhaps may be resistant to capacity limitations. Yet, a recent study using rhythmic sequences demonstrated that consecutive time intervals are allocated working memory resources, and memory for such intervals decline with increasing load (Teki and Griffiths, 2014). Therefore, it could be hypothesized that the ability to utilize temporal attention is not influenced by a concurrent working memory load when the contents are irrelevant to timing processes. However, when working memory stores are filled with timing-based information, capacity limitations may influence timing abilities.

The current data supports previous research indicating beta band sensitivity to working memory load (Deiber et al., 2007; Zanto and Gazzaley, 2009; Chen and Huang, 2016) and temporal attention processes (Roelfsema et al., 1997; Androulidakis et al., 2007; Donner et al., 2009). It could be argued that the observed modulation of beta activity by the current task demands reflects a measure of alertness, cognitive load, or a more general measure of cognitive state. Indeed, these results support a previously established relationship between increased beta oscillations and speeded response times (Kaminski et al., 2012), which were previously interpreted as a measure of alertness. In the current task, beta activity increased with working memory load, which resulted in speeded response times. As such, the increased beta activity could be interpreted as increased alertness, perhaps as an indication of an urgency to quickly finish the discrimination task in order to complete the working memory task before the contents were forgotten. However, this interpretation does not account for the beta modulation by the cues, where beta increased following NS cues, resulting in slowed response times.

Alternatively, it may be hypothesized that the increased beta activity during the neutrally cued short foreperiod may reflect increased cognitive load, as cognitive demand is thought to increase with increased temporal uncertainty (Vallesi et al., 2014). This would explain why beta activity was modulated as a function of temporal uncertainty (i.e., NS > PS) and also explain why beta activity increased with increasing working memory load. However, this

does not account for why participants with high beta modulation prior to the discrimination target exhibited lower working memory accuracy following predictive cues compared to neutral cues. If lowered beta activity following a predictive cue indicates lowered cognitive load, then it would be expected that working memory performance would be increased, not decreased as it was observed.

A more likely interpretation for the observed beta activity comes from research suggesting it reflects maintenance of cognitive state. Notably, pre-stimulus beta power has been associated with general control processes that can facilitate temporal integration based on expectation (Geerligs and Akyurek, 2012), which may help integrate subsequent audio-visual stimuli (Hipp et al., 2011; Keil et al., 2012). Given the various sensorimotor and cognitive control functions evoking beta band activity, it has been hypothesized that beta activity reflects maintenance of current cognitive state (Engel and Fries, 2010). In this light, the observed decrease of beta activity prior to discriminating expected targets may index a cognitive state that releases the contents of working memory in order to minimize the integration (or maximizing the segregation) of the stimuli from the two tasks. This is evidenced by decreased beta activity associated with lower working memory load as well as an inverse relationship of beta modulation between the discrimination and working memory tasks. This interpretation is modestly supported by source localization, which indicated that beta activity in cuneus/precuneus is lowered when anticipating a discrimination target. Given the role of cuneus/precuneus in working memory maintenance (van Snellenberg et al., 2015; Daniel et al., 2016), it is therefore not surprising that subsequent working memory declined when this region was disengaged. Indeed, the cuneus/precuneus is involved in working memory for relational (abstract) information that is not tied to the original sensory percept (Blacker and Courtney, 2016). Thus, beta activity modulation more likely reflects changes in cognitive state that disengages the relational content between tasks, rather than an indication of cognitive load or alertness.

It has been suggested that predictive timing operates by organizing low and mid-frequency oscillations (delta, theta, and beta activity) and by dissolving activity in the alpha band (Arnal and Giraud, 2012). The phase entrainment of low-frequency oscillations to external sensory cues can serve as an important and flexible mechanism for enhancing sensory processing (Cravo et al., 2013) and that temporal attention may utilize these low-frequency oscillations to modulate higher frequencies in the beta band (Cravo et al., 2011). Although the current analyses did not address potential cross-frequency coupling effects, these results contribute to a growing literature indicating beta band activity is a signature of cognitive state and that modulation of this beta activity may reflect engagement/disengagement processes associated with managing more than one task goal. Nonetheless, this interpretation is speculative and additional research will be required to confirm our results and help understand the role of beta oscillations in temporal attention and cognitive control more broadly.

As another means to explore the influence of working memory load on temporal attention ability, midline frontal theta activity was assessed. Results showed that theta activity was not systematically modulated by load as expected. Previous research has demonstrated that theta activity typically increases with an increasing working memory load (reviewed in

Hsieh and Ranganath, 2014). Although we observed a numerical increase in theta activity as load increased from zero to six items, this load sensitivity was not strong enough to reach significance. It could be argued that the lack of theta sensitivity to working memory load may stem from the blocked design, because prior research observing this effect often varies load on a trial-wise basis. However, block designs are capable of modulating midline frontal theta activity as a function of load (Gevins et al., 1997; Krause et al., 2000; Brookes et al., 2011). A more plausible explanation for the lack of theta modulation by load may be attributed to task prioritization. If participants made the discrimination task a higher priority than the working memory task, then working memory load would not affect the ability to capitalize on predictive cues, as observed. Furthermore, if the discrimination task were a higher priority, then contents in working memory would not have been maintained strongly, resulting in decreased sensitivity of theta activity to load, as observed. However, to fully ascertain whether this was the case, a single task version of the working memory task would be required in order to show that this task and these participants were capable of modulating theta based on load, and that the load-based modulation is decreased with the introduction of another task.

Conclusions

In summary, the current results indicate that temporal attention ability is not affected by a concurrent working memory load, at least when the contents are irrelevant to the timing of the discrimination task. This was evidenced by speeded response times following predictive temporal cues as well as cue-based modulation of the posterior CNV, alpha, and beta band activity, regardless of the concurrent working memory load. However, in anticipation of a discrimination target, posterior beta band activity was differentially modulated by temporal attention and working memory, such that beta decreased prior to expected targets and increased with a concurrent working memory load. Importantly, participants who exhibited the greatest temporal attention-based modulation of beta activity capitalized the most from the temporal cues via speeded responses to predicted discrimination targets. Yet, those benefits in discrimination performance came with a cost to performance on the secondary task, as evidenced by lowered working memory accuracy. Thus, decreased beta activity following predictive cues appears to disengage working memory mechanisms in lieu of a cognitive state that supports discrimination performance. Additional research will be required to understand what aspect of divided attention ability limits performance and drives participants to prioritize one task over another.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

Acknowledgements

This work was supported by the National Institutes of Health grants 4F32AG030249-03 and 5R01AG030395. We thank Martine Van Schouwenburg, Peter Wais, and Jyoti Mishra for their insightful comments on the manuscript.

References

- Androulidakis AG, Doyle LM, Yarrow K, Litvak V, Gilbertson TP, Brown P (2007) Anticipatory changes in beta synchrony in the human corticospinal system and associated improvements in task performance. *European Journal of Neuroscience* 25:3758–3765.
- Anguera JA, Boccanfuso J, Rintoul JL, Al-Hashimi O, Faraji F, Janowich J, Kong E, Larraburo Y, Rolle C, Johnson E, Gazzaley A (2013) Video game training enhances cognitive control in older adults. *Nature* 501:97–101. [PubMed: 24005416]
- Arnal LH, Giraud AL (2012) Cortical oscillations and sensory predictions. *Trends Cogn Sci* 16:390–398. [PubMed: 22682813]
- Bastos AM, Usrey WM, Adams RA, Mangun GR, Fries P, Friston KJ (2012) Canonical Microcircuits for Predictive Coding. *Neuron* 76:695–711. [PubMed: 23177956]
- Bauer M, Stenner MP, Friston KJ, Dolan RJ (2014) Attentional modulation of alpha/beta and gamma oscillations reflect functionally distinct processes. *J Neurosci* 34:16117–16125. [PubMed: 25429152]
- Blackler KJ, Courtney SM (2016) Distinct neural substrates for maintaining locations and spatial relations in working memory. *Frontiers in Human Neuroscience* 10:594. [PubMed: 27932963]
- Bollinger J, Rubens MT, Masangkay E, Gazzaley A (2011) An expectation-based memory deficit in aging. *Neuropsychologia* 49:1466–1475. [PubMed: 21272595]
- Brookes MJ, Wood JR, Stevenson CM, Zumer JM, White TP, Liddle PF, Morris PG (2011) Changes in brain network activity during working memory tasks: A magnetoencephalography study. *Neuroimage* 55:1804–1815. [PubMed: 21044687]
- Brunia CHM, Damen EJP (1988) Distribution of slow brain potentials related to motor preparation and stimulus anticipation in a time-estimation task. *Electroencephalography and Clinical Neurophysiology* 69:234–243. [PubMed: 2450004]
- Capizzi M, Sanabria D, Correa A (2012) Dissociating controlled from automatic processing in temporal preparation. *Cognition* 123:293–302. [PubMed: 22397820]
- Capizzi M, Correa A, Sanabria D (2013) Temporal orienting of attention is interfered by concurrent working memory updating. *Neuropsychologia* 51:326–339. [PubMed: 23085375]
- Chen YG, Huang XT (2016) Modulation of alpha and beta oscillations during an n-back task with varying temporal memory load. *Frontiers in Psychology* 6:2031. [PubMed: 26779113]
- Coull JT, Nobre AC (1998) Where and when to pay attention: The neural systems for directing attention to spatial locations and to time intervals as revealed by both PET and fMRI. *J Neurosci* 18:7426–7435. [PubMed: 9736662]
- Cravo AM, Rohenkohl G, Wyart V, Nobre AC (2011) Endogenous modulation of low frequency oscillations by temporal expectations. *J Neurophysiol* 106:2964–2972. [PubMed: 21900508]
- Cravo AM, Rohenkohl G, Wyart V, Nobre AC (2013) Temporal Expectation Enhances Contrast Sensitivity by Phase Entrainment of Low-Frequency Oscillations in Visual Cortex. *J Neurosci* 33:4002–4010. [PubMed: 23447609]
- Cowan N (1995) *Attention and memory: An integrated framework*. Oxford Psychology Series, No. 26. New York: Oxford University Press.
- Cutanda D, Correa A, Sanabria D (2015) Auditory Temporal Preparation Induced by Rhythmic Cues During Concurrent Auditory Working Memory Tasks. *Journal of Experimental Psychology-Human Perception and Performance* 41:790–797. [PubMed: 25893682]
- Daniel TA, Katz JS, Robinson JL (2016) Delayed match-to-sample in working memory: A BrainMap meta-analysis. *Biological Psychology* 120:10–20. [PubMed: 27481545]
- Deiber MP, Missonnier P, Bertrand O, Gold G, Fazio-Costa L, Ibanez V, Giannakopoulos P (2007) Distinction between perceptual and attentional processing in working memory tasks: A study of phase-locked and induced oscillatory brain dynamics. *J Cogn Neurosci* 19:158–172. [PubMed: 17214572]
- D’Esposito M, Postle B, Ballard D, Lease J (1999) Maintenance versus manipulation of information held in working memory: An event-related fMRI study. *Brain and Cognition* 41:66–86. [PubMed: 10536086]

- Donner TH, Siefel M, Fries P, Engel AK (2009) Buildup of choice predictive activity in human motor cortex during perceptual decision making. *Curr Biol* 19:1581–1585. [PubMed: 19747828]
- Dux P, Ivanoff J, Asplund C, Marois R (2006) Isolation of a central bottleneck of information processing with time-resolved fMRI. *Neuron* 52:1109–1120. [PubMed: 17178412]
- Ecker UKH, Lewandowsky S, Oberauer K, Chee AEH (2010) The Components of Working Memory Updating: An Experimental Decomposition and Individual Differences. *Journal of Experimental Psychology-Learning Memory and Cognition* 36:170–189.
- Endress A, Szabo S (2017) Interference and memory capacity limitations. *Psychological Review* 124:551–571. [PubMed: 28414490]
- Engle AK (2018) Working memory and executive attention: A revisit. *Perspectives on Psychological Science* 13:190–193. [PubMed: 29592654]
- Engel AK, Fries P (2010) Beta-band oscillations - signalling the status quo? *Current Opinion in Neurobiology* 20:156–165. [PubMed: 20359884]
- Fuchs M, Kastner J, Wagner M, Hawes S, Ebersole JS (2002) A standardized boundary element method volume conductor model. *Clin Neurophysiol* 113:702–712. [PubMed: 11976050]
- Fuster JM (1990) Inferotemporal units in selective visual attention and short-term memory. *J Neurophysiol* 64:681–697. [PubMed: 2230917]
- Geerligs L, Akyurek EG (2012) Temporal integration depends on increased prestimulus beta band power. *Psychophysiology* 49:1632–1635.
- Gevins A, Smith ME, McEvoy L, Yu D (1997) High-resolution EEG mapping of cortical activation related to working memory: Effects of task difficulty, type of processing and practice. *Cerebral Cortex* 7:374–385. [PubMed: 9177767]
- Grier RA, Warm JS, Dember WN, Matthews G, Galinsky TL, Parasuraman R (2003) The vigilance decrement reflects limitations in effortful attention, not mindlessness. *Human Factors* 45:349–359. [PubMed: 14702988]
- Hipp JF, Engel AK, Siegel M (2011) Oscillatory Synchronization in Large-Scale Cortical Networks Predicts Perception. *Neuron* 69:387–396. [PubMed: 21262474]
- Hsieh LT, Ranganath C (2014) Frontal midline theta oscillations during working memory maintenance and episodic encoding and retrieval. *Neuroimage* 85:721–729. [PubMed: 23933041]
- Jensen O, Tesche CD (2002) Frontal theta activity in humans increases with memory load in a working memory task. *European Journal of Neuroscience* 15:1395–1399.
- Jurcak V, Tsuzuki D, Dan I (2007) 10/20, 10/10, and 10/5 systems revisited: their validity as relative head-surface-based positioning systems. *Neuroimage* 15:1600–1611.
- Kaminski J, Brzezicka A, Gola M, Wrobel A (2012) Beta band oscillations engagement in human alertness process. *Int J Psychophysiol* 85:125–128. [PubMed: 22155528]
- Keil J, Muller N, Ihssen N, Weisz N (2012) On the Variability of the McGurk Effect: Audiovisual Integration Depends on Prestimulus Brain States. *Cerebral Cortex* 22:221–231. [PubMed: 21625011]
- Kiyonaga A, Egnér T (2013) Working memory as internal attention: Toward an integrative account of internal and external selection processes. *Psychonomic Bulletin & Review* 20:228–242. [PubMed: 23233157]
- Krause CM, Sillanmaki L, Koivisto M, Saarela C, Haggqvist A, Laine M, Hamalainen H. (2000) The effects of memory load on event-related EEG desynchronization and synchronization. *Clin Neurophysiol* 111:2071–2078. [PubMed: 11068244]
- Lange K, Roder B (2006) Orienting attention to points in time improves stimulus processing both within and across modalities. *J Cogn Neurosci* 18:715–729. [PubMed: 16768372]
- Los SA, Heslenfeld DJ (2005) Intentional and unintentional contributions to nonspecific preparation: Electrophysiological evidence. *Journal of Experimental Psychology-General* 134:52–72. [PubMed: 15702963]
- Los SA, Kruijne W, Meeter M (2014) Outlines of a multiple trace theory of temporal preparation. *Frontiers in Psychology* 5: 1058. [PubMed: 25285088]
- Miller EK, Lundqvist M, Bastos AM (2018) Working memory 2.0. *Neuron* 100:463–475. [PubMed: 30359609]

- Miniussi C, Wilding EL, Coull JT, Nobre AC (1999) Orienting attention in time - Modulation of brain potentials. *Brain* 122:1507–1518. [PubMed: 10430834]
- Moran J, Desimone R (1985) Selective attention gates visual processing in the extrastriate cortex. *Science* 229:782–784. [PubMed: 4023713]
- Nichols TE, Holmes PA (2002) Nonparametric permutation tests for functional neuroimaging: A primer with examples. *Human Brain Mapping* 15:1–25. [PubMed: 11747097]
- Padgaonkar NT, Zanto TP, Bollinger J, Gazzaley A (2017) Predictive cues and age-related declines in working memory performance. *Neurobiology of Aging* 49:31–39. [PubMed: 27736673]
- Pascual-Marqui RD (2002) Standardized low-resolution brain electromagnetic tomography (sLORETA): technical details. *Methods Find Exp Clin Pharmacol* 24D:5–12.
- Praamstra P, Kourtis D, Kwok HF, Oostenveld R (2006) Neurophysiology of implicit timing in serial choice reaction-time performance. *J Neurosci* 26:5448–5455. [PubMed: 16707797]
- Redick TS (2014) Cognitive control in context: Working memory capacity and proactive control. *Acta Psychologica* 145:1–9. [PubMed: 24240136]
- Roelfsema PR, Engel AK, Konig P, Singer W (1997) Visuomotor integration is associated with zero time-lag synchronization among cortical areas. *Nature* 385:157–161. [PubMed: 8990118]
- Rohenkohl G, Nobre AC (2011) Fluctuations of anticipatory neural oscillations according to temporal expectations. *J Neurosci* 31:14076–14084. [PubMed: 21976492]
- Ruchkin DS, Sutton S, Mahaffey D, Glaser J (1986) Terminal CNV in the absence of motor response. *Electroencephalography and Clinical Neurophysiology* 63:445–463. [PubMed: 2420561]
- Siegel M, Warden MR, Miller EK (2009) Phase-dependent neuronal coding of objects in short-term memory. *Proc Natl Acad Sci U S A* 106:21341–21346. [PubMed: 19926847]
- Simson R, Vaughan HG, Ritter W (1977) Scalp topography of potentials in auditory and visual gong tasks. *Electroencephalography and Clinical Neurophysiology* 43:864–875. [PubMed: 73454]
- Tallon-Baudry C, Bertrand O (1999) Oscillatory gamma activity in humans and its role in object representation. *Trends Cogn Sci* 3:151–162. [PubMed: 10322469]
- Teke S, Griffiths TD (2014) Working memory for time intervals in auditory rhythmic sequences. *Frontiers in Psychology* 5: 1329. [PubMed: 25477849]
- Teke S, Grube M, Kumar S, Griffiths TD (2011) Distinct Neural Substrates of Duration-Based and Beat-Based Auditory Timing. *J Neurosci* 31:3805–3812. [PubMed: 21389235]
- Vallesi A, Arbula S, Bernardis P (2014) Functional dissociations in temporal preparation: Evidence from dual-task performance. *Cognition* 130:141–151. [PubMed: 24291265]
- van Boxtel GJM, Brunia CHM (1994) Motor and nonmotor components of the contingent negative variation. *Int J Psychophysiol* 17:269–279. [PubMed: 7806470]
- van Ede F, Szebenyi S, Maris E (2014) Attentional modulation of somatosensory alpha, beta and gamma oscillations dissociate between anticipation and stimulus processing. *Neuroimage* 97:134–141. [PubMed: 24769186]
- van Snellenberg JX, Slifstein M, Read C, Weber J, Thompson JL, Wager TD, Shohamy D, Abi-Dargham A, Smith EE (2015) Dynamic shifts in brain network activation during supracapacity working memory task performance. *Human Brain Mapping* 36:1245–1264. [PubMed: 25422039]
- Woodrow H (1914) The Measurement of Attention. *Psychological Monographs* 17:1–158.
- Zanto TP, Gazzaley A (2009) Neural suppression of irrelevant information underlies optimal working memory performance. *J Neurosci* 29:3059–3066. [PubMed: 19279242]
- Zanto TP, Gazzaley A (2014) Attention and aging. In: *Handbook of Attention* (Nobre AC, Kastner S, eds), pp 927–971. Oxford: Oxford University Press.
- Zanto TP, Hennigan K, Ostberg M, Clapp WC, Gazzaley A (2010) Predictive knowledge of stimulus relevance does not influence top-down suppression of irrelevant information in older adults. *Cortex* 46:561–574.
- Zanto TP, Pan P, Liu H, Bollinger J, Nobre AC, Gazzaley A (2011) Age-Related Changes in Orienting Attention in Time. *J Neurosci* 31:12461–12470. [PubMed: 21880908]
- Zanto TP, Padgaonkar NT, Nourishad A, Gazzaley A (2019) A tablet-based assessment of rhythmic ability. *Frontiers in Psychology* 10:2471. [PubMed: 31736843]

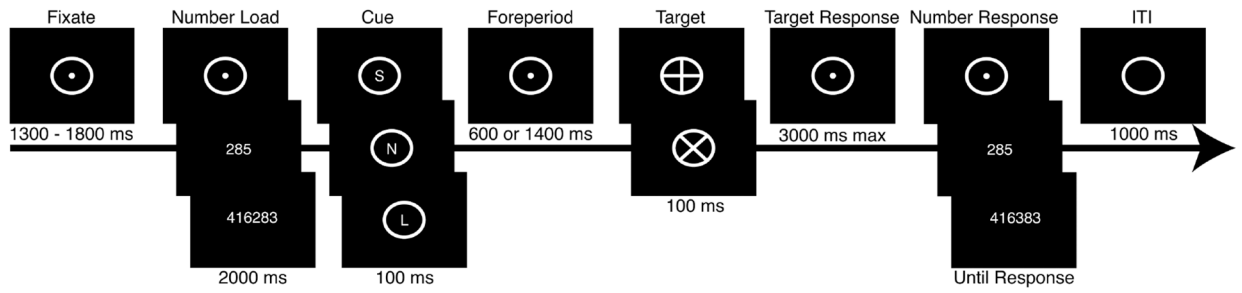


Figure 1.

Experimental paradigm. Participants were given either zero, three, or six numbers to hold in working memory while engaged in a cued discrimination task. Cues indicated whether the foreperiod would be short (S), long (L), or neutral (N).

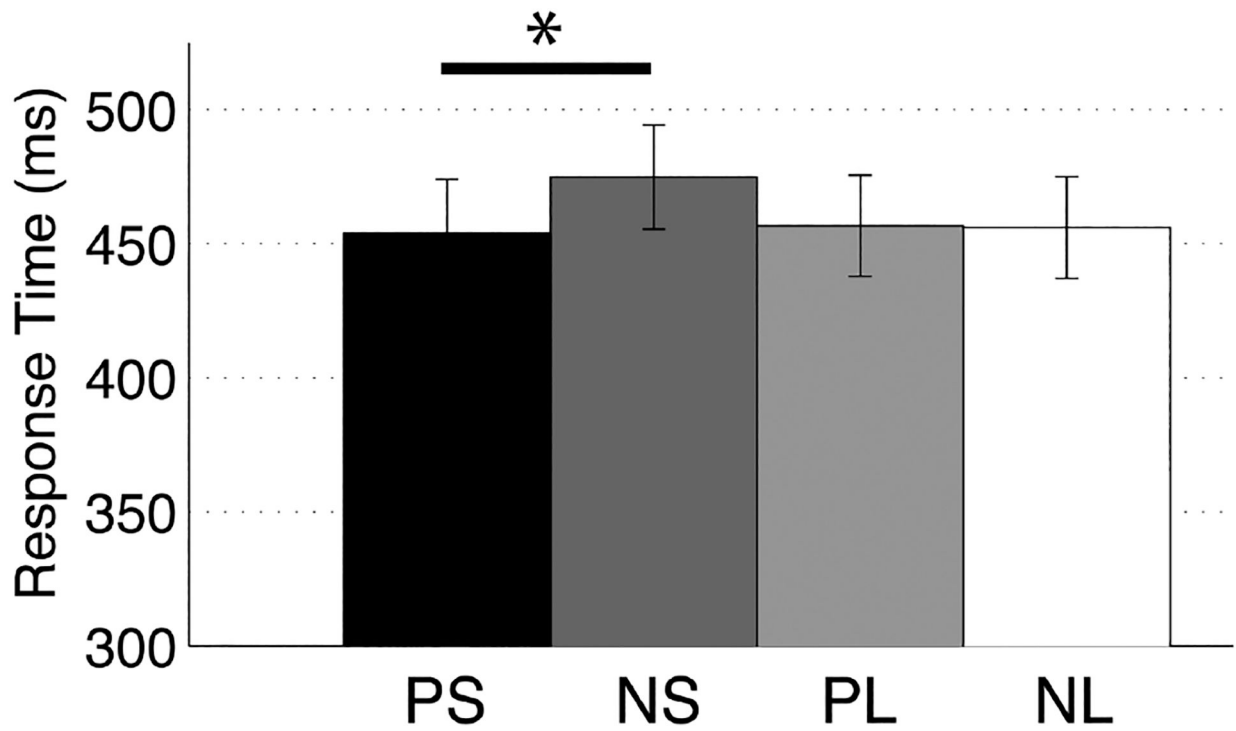


Figure 2. Discrimination task response times. Following short foreperiods, participants exhibited faster response times when given a predictive (PS) compared to neutral (NS) cue. Following long foreperiods, no differences were observed between predictive (PL) and neutral (NL) cues. Asterisk indicates $p < 0.05$. Error bars indicate standard error of the mean.

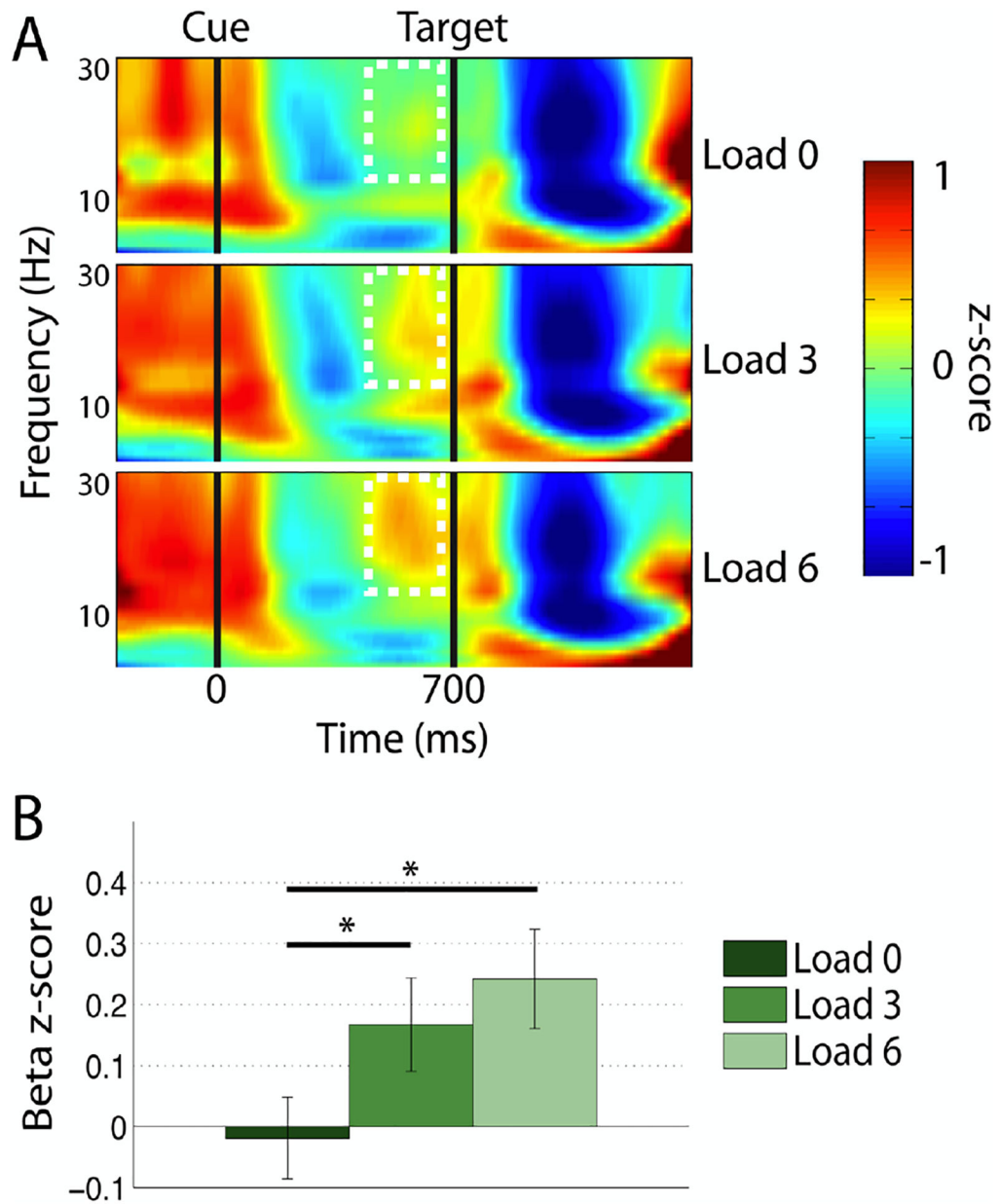


Figure 3. Effects of working memory load on beta band activity. (A) Beta activity prior to stimulus onset (white box) displayed for short foreperiods, (B) which increased with working memory load regardless of foreperiod duration. Asterisk indicates $p < 0.05$. Error bars indicate standard error of the mean.

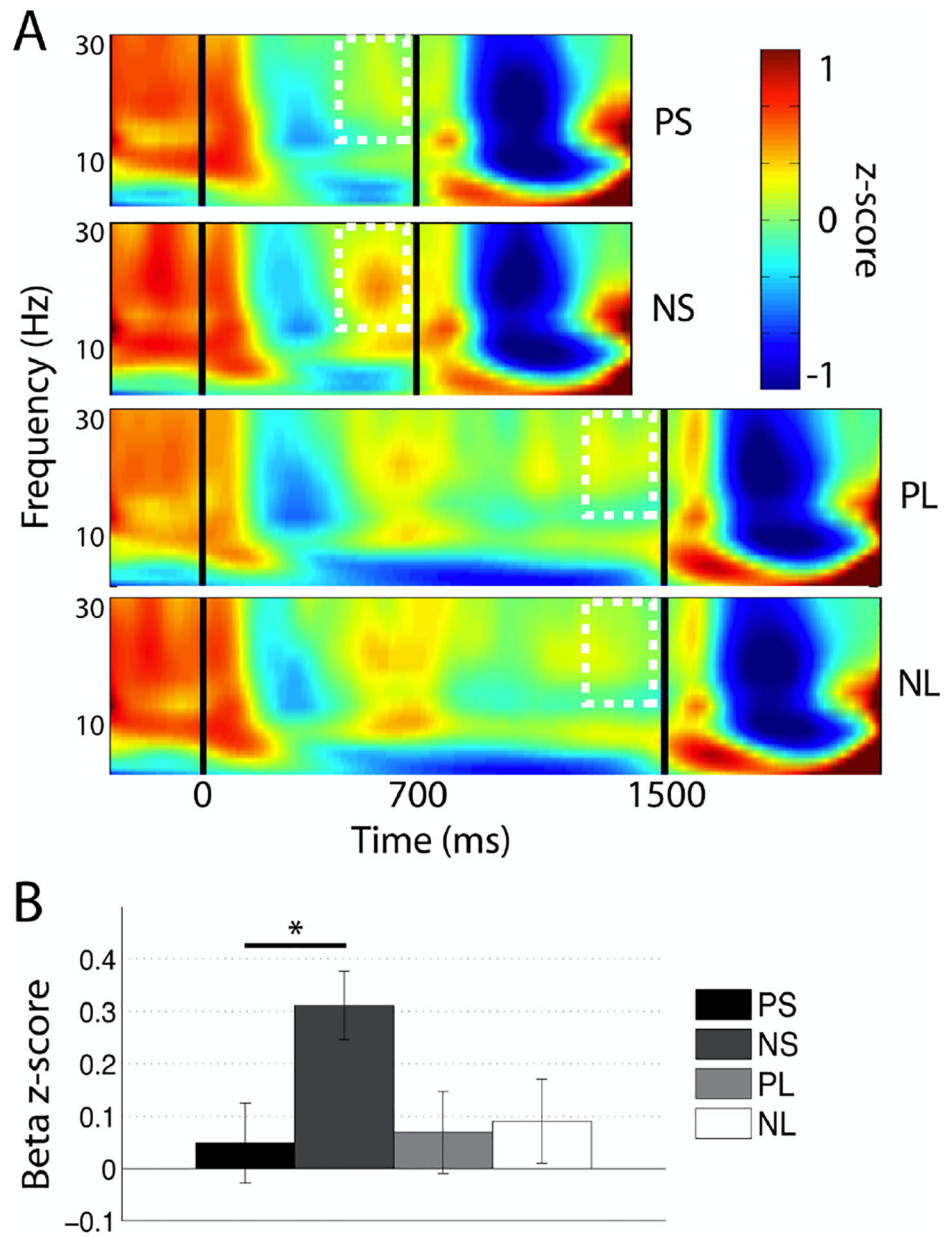


Figure 4. Effects of cue on beta band activity. (A) Beta activity prior to stimulus onset (white box) (B) decreased during short foreperiods following a predictive (PS) compared to neutral (NS) cue. No difference was observed during long foreperiods between predictive (PL) and neutral (NL) cues. Asterisk indicates $p < 0.05$. Error bars indicate standard error of the mean.

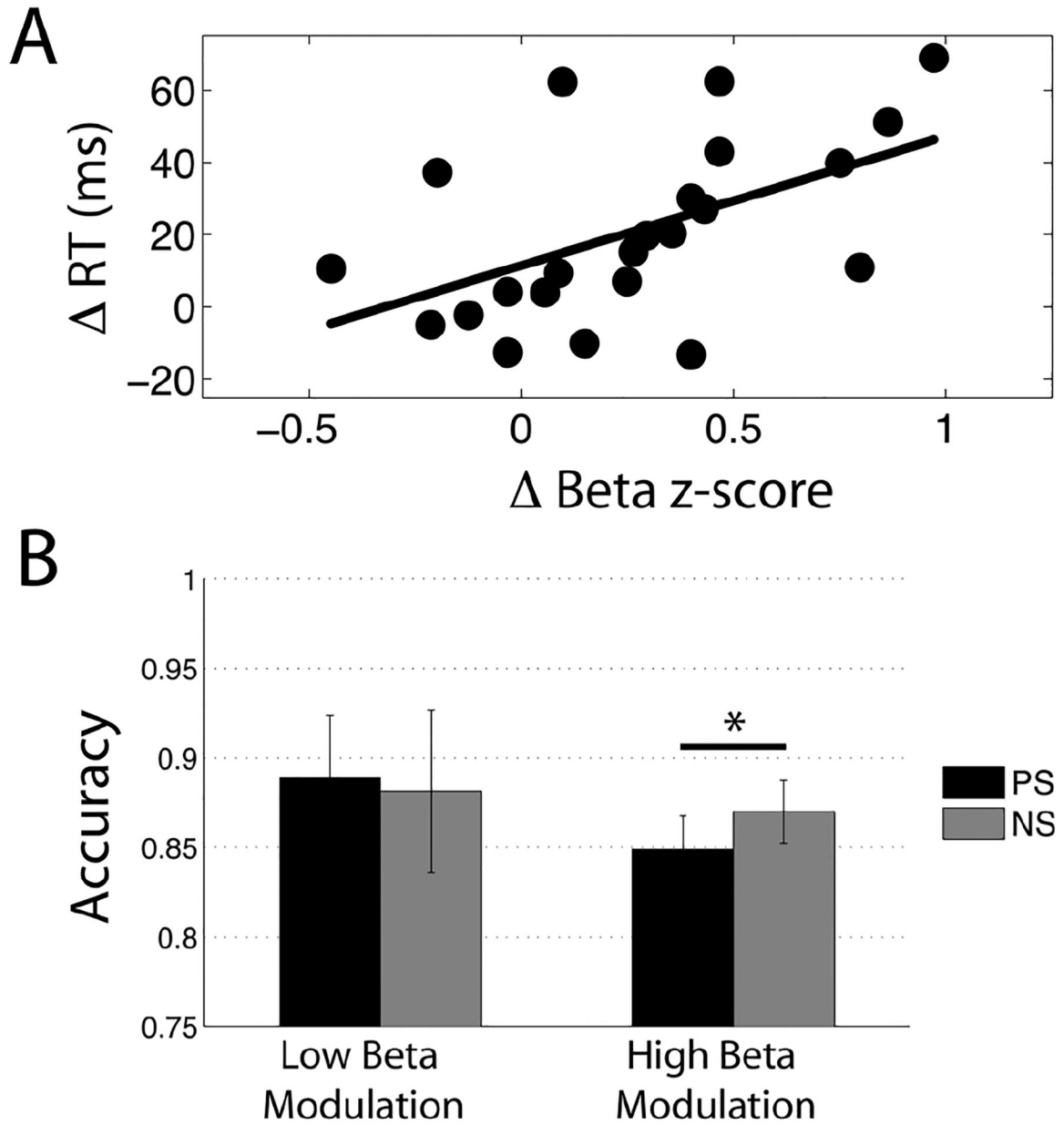


Figure 5. Relationship between beta activity and performance. (A) Discrimination response time (RT) benefit from predictive cues was greatest in participants who exhibited the greatest beta activity modulation (i.e., $\Delta = NS - PS$; $r = 0.53$, $p = 0.009$). (B) A median split of participants based on beta modulation shows that those who modulated beta activity the most (i.e., $NS > PS$) exhibited differences in working memory accuracy. Thus, participants who modulated beta activity based on cued information enhanced discrimination performance at the expense of working memory performance. Asterisk indicates $p < 0.05$. Error bars indicate standard error of the mean.

Table 1.

Mean performance metrics. Numbers in parentheses represent standard error of the mean. PS = predictive cue, short foreperiod, NS = neutral cue, short foreperiod, PL = predictive cue, long foreperiod, NL = neutral cue, long foreperiod.

		PS	NS	PL	NL
Working memory accuracy (%)	<i>Load 0</i>	--	--	--	--
	<i>Load 3</i>	92.1 (1.7)	92.5 (2.4)	91.9 (1.8)	93.6 (1.3)
	<i>Load 6</i>	81.0 (2.4)	82.5 (2.4)	81.9 (2.4)	81.7 (2.6)
Working memory RT (ms)	<i>Load 0</i>	--	--	--	--
	<i>Load 3</i>	760 (35)	750 (33)	787 (39)	794 (46)
	<i>Load 6</i>	1041 (65)	1058 (71)	1089 (72)	1084 (74)
Discrimination accuracy (%)	<i>Load 0</i>	96.3 (0.7)	96.6 (0.6)	96.3 (1.0)	97.4 (0.7)
	<i>Load 3</i>	98.3 (0.6)	98.8 (0.4)	98.9 (0.3)	98.8 (0.3)
	<i>Load 6</i>	97.8 (0.7)	98.3 (0.5)	98.8 (0.4)	98.5 (0.6)
Discrimination RT (ms)	<i>Load 0</i>	499 (17)	519 (17)	502 (19)	505 (19)
	<i>Load 3</i>	424 (21)	446 (20)	434 (20)	427 (20)
	<i>Load 6</i>	438 (22)	460 (21)	434 (18)	437 (19)