Temporal Characteristics of Top–Down Modulations during Working Memory Maintenance: An Event-related Potential Study of the N170 Component

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Abstract

■ We investigated the top–down influence of working memory (WM) maintenance on feedforward perceptual processing within occipito-temporal face processing structures. During event-related potential (ERP) recordings, subjects performed a delayed-recognition task requiring WM maintenance of faces or houses. The face-sensitive N170 component elicited by delay-spanning task-irrelevant grayscale noise probes was examined. If early feedforward perceptual activity is biased by maintenance requirements, the N170 ERP component elicited by probes should have a greater N170 amplitude response during face relative to house WM trials. Consistent with this prediction, N170 elicited by probes presented at the beginning, middle, and end of the delay interval was greater in amplitude during face relative to house WM. Thus, these results suggest that WM maintenance demands may modulate early feedforward perceptual processing for the entirety of the delay duration. We argue based on these results that temporally early biasing of domain-specific perceptual processing may be a critical mechanism by which WM maintenance is achieved. ■

INTRODUCTION

Cognitive control is necessary for guiding complex goal-directed behavior. Selective attention and working memory (WM) are two cognitive control systems that operate via "top–down" modulation of cortical activity, in which "top" prefrontal control structures influence activity within "bottom" sensoriperceptual processing structures. The temporal characteristics of top–down modulations have been well-established in studies of selective attention using electric and magnetic recording techniques in humans (see Hopfinger, Luck, & Hillyard, 2004 for a review). Numerous studies report that selective attention modulates activity within perceptual processing sites during the first 200 msec of stimulus processing in a gain-control fashion (see Hillyard, Vogel, & Luck, 1998 for a review). That is, control operations, instantiated within the prefrontal cortex (PFC) and parietal areas (Hopfinger, Buonocore, & Mangun, 2000), increase or decrease the transmission of feedforward information during the early stages of sensoriperceptual analysis within perceptual structures. In the current study, we investigate whether WM maintenance requirements similarly result in top–down modulations at the early stages of perceptual analysis during face and house WM.

Several recent functional magnetic resonance imaging (fMRI) studies investigating the nature of top–down modulations during face and house WM have demonstrated that maintenance of these stimuli is associated with persistent activity in multiple brain regions, including the PFC and domain-specific posterior perceptual regions such as the fusiform face area (FFA) and parahippocampal place area (PPA) (Gazzaley, Cooney, McEvoy, Knight, & D'Esposito, 2005; Gazzaley, Rissman, & D'Esposito, 2004; Ranganath, Cohen, Dam, & D'Esposito, 2004; Ranganath, DeGutis, & D'Esposito, 2004). The bulk of evidence suggests that these regions do not work in isolation, but rather function in a coordinated fashion to support maintenance (Gazzaley et al., 2004; see Postle, 2006 for a review), and that this coordination may arise via oscillatory activity that synchronizes activity both across brain regions and within brain regions (Tallon-Baudry, Bertrand, & Fischer, 2001).

A recent fMRI study by Ranganath, DeGutis, et al. (2004) reported that activity within the FFA and PPA was modulated during the delay interval of delayed-recognition face and house WM tasks. Activity was greatest when the perceptual region's preferred stimulus domain was maintained relative to when the nonpreferred domain

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was maintained (e.g., greater FFA activity during face relative to house WM). Importantly, this modulation occurred in the absence of any perceptual stimulation for the entirety of the delay interval.

A key unresolved issue concerns the functional significance of delay activity within specialized perceptual modules. A prominent hypothesis is that maintenance requirements result in top–down biasing of activity within perceptual regions so that perceptual representations are maintained throughout the delay interval (Curtis & D'Esposito, 2003; Miller & Cohen, 2001). Yet, the mechanism by which maintenance requirements may influence activity within these regions is poorly understood. Specifically, previous fMRI results have been unable to clarify whether top–down biasing influences feedforward sensoriperceptual analysis. fMRI signal lacks sufficient temporal resolution to track activity within the first several hundred milliseconds of perceptual processing and is unable to distinguish between temporally early feedforward processes and later modulatory influences (see Martinez et al., 2001 for discussion).

The millisecond temporal resolution of event-related potentials (ERPs) offers an opportunity for a closer look at the level of processing at which modulations may be present. ERPs have been used to investigate the temporal characteristics of face WM's top–down influence on face processing using the N170 ERP component (e.g., Sreenivasan & Jha, 2007; Gazzaley et al., 2005). The N170 is thought to reflect early face processing (Itier & Taylor, 2004b; Bentin & Deouell, 2000; Eimer, 2000a, 2000c; Bentin, Allison, Puce, Perez, & McCarthy, 1996), and its generator site is proposed to be within face processing regions of occipito-temporal cortex (Itier & Taylor, 2004a). Recent studies have demonstrated N170 latency (Gazzaley et al., 2005) and amplitude (Sreenivasan & Jha, 2007) modulations during face WM. These studies investigated evoked activity during encoding of memoranda (Gazzaley et al., 2005) or in response to memory-confusable distractors presented during the delays of delayed-recognition tasks (Sreenivasan & Jha, 2007). Although modulations of the N170 have been reported in studies investigating attention to faces in the absence of mnemonic requirements (Holmes, Vuilleumier, & Eimer, 2003; Eimer, 2000b; but see Cauquil, Edmonds, & Taylor, 2000), to our knowledge, no studies to date have investigated whether ongoing maintenance processes modulate the N170 component in a fashion consistent with feedforward biasing of perceptual processing.

Previous studies examining top–down effects during spatial WM have reported that, similar to the effects of spatial attention on perception, top–down influences of WM modulate the early stages of perceptual processing. A study by Jha (2002) used a delay-spanning probe technique that indexed evoked activity during ongoing spatial WM maintenance. Prove-evoked early sensory responses were greater for probes appearing at memory versus nonmemory locations (see also Awh, Anllo-Vento, & Hillyard, 2000). Importantly, top–down influences may be distinct for spatial and nonspatial information (Anllo-Vento & Hillyard, 1996). Thus, it is unclear whether similar early perceptual modulations will be present during maintenance of nonspatial stimuli, such as faces and houses.

In the present study, we test the hypothesis that maintenance processes can bias feedforward perceptual activity during WM for nonspatial information. ERPs were recorded from 12 subjects as they performed a delayed-recognition task for faces and houses. The use of a delayed-recognition task allowed us to temporally segregate maintenance-related activity from encoding, retrieval, and response processes. Subjects were required to maintain an image of a face or a house (S1) over a delay period that lasted between 4300 and 6300 msec. At the end of the delay, they were presented with a test image (S2) and had to indicate with a button press whether the S2 test image matched or did not match the S1 memory image. During the delay, three probes consisting of grayscale visual noise were sequentially presented. We used the face-sensitive N170 ERP component elicited by these delay-spanning probes as an index of feedforward perceptual processing of faces (Itier & Taylor, 2004b; Bentin et al., 1996). Importantly, these probes contained only noise and no face information. N170 amplitudes evoked by similar noise-alone images were greater when subjects expected to see a face versus when they expected to see a word (Wild & Busey, 2004). Thus, noise probes are effective at eliciting N170 responses without the need to present faces or other memory-confusable images during the delay.

Our central prediction was that N170 responses evoked by presentation of noise probes during the delay will be greater in amplitude during face relative to house WM trials. Further, if feedforward modulations are, indeed, a central mechanism supporting WM maintenance processes within the perceptual cortex, this pattern of N170 modulation should be present throughout the entire period of maintenance. Our findings and their implications are presented below.

METHODS

Participants

Fifteen undergraduates (7 women, 18–21 years of age) from the University of Pennsylvania were awarded course credit for participation in this experiment. Two subjects were excluded from all analyses due to failure to follow task instructions, which led to below-chance performance. An additional subject was excluded from analyses due to an ERP recording error. All participants had normal or corrected-to-normal vision. The

University of Pennsylvania Institutional Review Board approved this study and each subject provided informed consent.

Stimuli

There were four categories of stimuli in this experiment: memory item (S1), test item (S2), delay-spanning noise probes, and noise probes presented at test (S2 probe). All stimuli were grayscale pictures and were created using Adobe Photoshop. S1 stimuli were either a face or house at 70% opacity on a background layer of grayscale speckled noise at 100% opacity. S2 stimuli were either a face or a house at 40% opacity presented on the identical noise background layer, or a noise-alone stimulus presented at 100% opacity (S2 probe trials). S1 and S2 were presented at 70% and 40% opacity, respectively, to promote the need to encode the S1 image with high fidelity. Noise probes were presented alone at 100% opacity. The noise background in S1, noise probes presented during the delay, the noise background in S2, and S2 noise probes were identical to each other and identical across trials. To minimize verbalizability, faces were cropped so that they were oval-shaped without any auxiliary features, such as hair or ears. Houses were also cropped to eliminate any peripheral landscaping or trees. All stimuli were maintained at comparable mean luminosity levels. S1, S2, and S2 probe stimuli were distinguished from noise probes by the border surround the stimulus. S1, S2, and S2 probe stimuli were surrounded by checkerboard borders, whereas noise probes were surrounded by a gray border.

Behavioral Task

Subjects performed a delayed-recognition WM task in which they had to remember faces or houses (Figure 1). Subjects sat comfortably in a sound-attenuated booth 70 cm in front of a monitor so that each stimulus subtended a visual angle of approximately $8° \times 8°$. The memory item (S1) in each trial was either a face or a house presented for 500 msec. S1 offset was followed by a delay period that was jittered from 4300 to 6300 msec. At the end of the delay period, the test item (S2) was presented centrally for 500 msec.

In one third of the trials, S2 was identical to S1 (match trials), and in another third of trials, S2 was a novel face or house (nonmatch trials). In the remaining trials, S2 was a noise probe stimulus (S2 probe trials). Subjects were instructed to determine whether S2 matched S1 and to press a button indicating a ''match'' or ''nonmatch'' response as quickly as possible without compromising accuracy. The correct response for S2 probe trials was ''nonmatch.'' Subjects were told that a face or a house would always appear at S2. The S2 probe trials were included to examine whether feedforward perceptual activity is modulated by WM retrieval processes. The intertrial interval (ITI) was jittered from 2000 to 3000 msec, with an average of 2500 msec.

During the delay period, three noise probes were presented centrally for 500 msec each. The interstimulus interval between all stimuli (between S1 and the first noise probe, between successive noise probes, and between the third noise probe and S2) was jittered between 700 and 1200 msec. A central fixation cross was presented during all interstimulus intervals, as well as during the ITI. Subjects were told that keeping the

Figure 1. Experimental paradigm. Subjects were instructed to encode the memory item (S1) and determine whether the test item (S2) was identical to S1. Presented here are two sample trials: Above is a face ''match'' trial, in which the S2 face is the same as the S1 face, and below is a house ''nonmatch'' trial, in which the S2 house is a novel house. The delay-spanning noise probes were distinguished from S1 and S2 stimuli by surrounding them with four gray bars (instead of checkered brackets for S1 and S2 stimuli). All stimuli were presented for 500 msec and interstimuli intervals were jittered from 700–1200 msec. Intertrial interval was jittered from 2000 to 3000 msec.
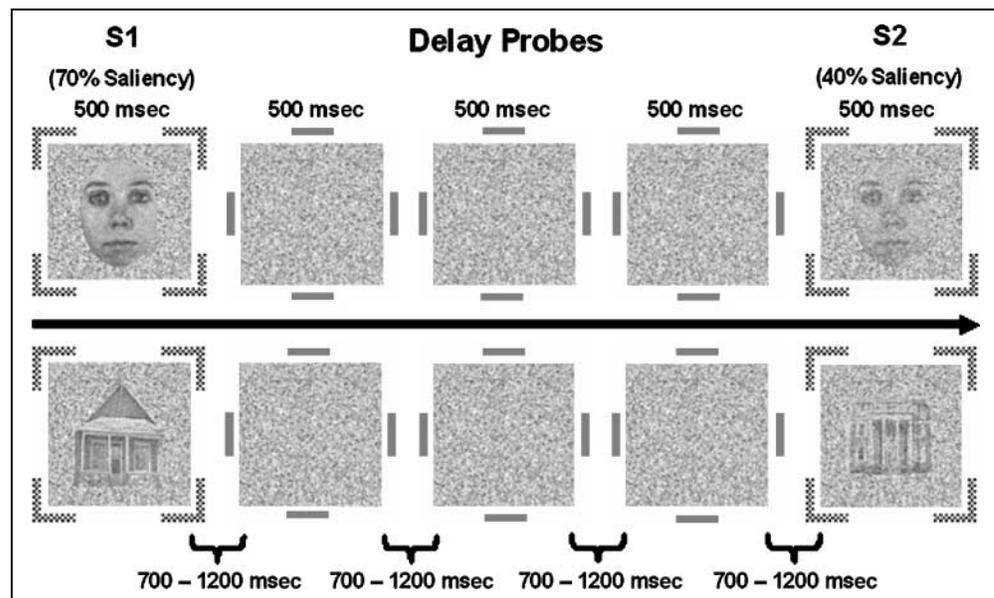
entire S1 stimulus in WM, as opposed to remembering specific features of the S1 stimulus, was the most efficient strategy for the task. Subjects were not told how many probes would appear during the delay.

Face and house WM trials were presented in separate face and house blocks. The experiment consisted of 10 blocks—5 face blocks and 5 house blocks—presented in a random order. Each block consisted of 30 trials, and trial type (match, nonmatch, and S2 probe trials) was presented randomly within each block. With the exception of the S2 match stimuli, the noise probes, and background layers, all stimuli presented during the experiment were novel.

ERP Acquisition and Analysis

Electroencephalographic (EEG) activity was recorded from 64 Ag–AgCl scalp electrodes arranged in a modified 10–20 system montage. EEG was referenced to an electrode placed on the left mastoid. Horizontal electrooculogram (HEOG) was recorded from electrodes placed at the outer canthi of both eyes to record horizontal eye movement. Vertical electrooculogram (VEOG) was recorded from electrodes placed above and below the left eye to record vertical eye movements. All channels were amplified using a pair of SynAmps amplifiers at a band-pass of 0.1–100 Hz and digitized with a 500-Hz sampling rate. Electrode impedances were kept below 5 kΩ.

Data averaging was performed after sorting by stimulus type (S1, Probe 1, Probe 2, Probe 3, S2, and S2 Probe) and WM domain (face or house). EEG and EOG were epoch-averaged from a period beginning 100 msec before stimulus onset to 700 msec following stimulus onset. Following baseline correction, eye blinks were subtracted using an eye movement reduction algorithm (Semlitsch, Anderer, Schuster, & Presslich, 1986). Epochs containing eye movement artifact larger than 500 μV or incorrect responses were excluded from averaging. Averages were filtered using a band-pass from 1 to 8 Hz (12 dB/octave).[1] The rejection rate for trials due to eye movement was less than 1%.

For all comparisons, the peak latency and average amplitude values were entered into repeated-measures analyses of variance (ANOVAs) or two-tailed paired t tests in a hypothesis-driven manner. Corrections for multiple comparisons were made where appropriate.

Behavioral Analysis

Behavioral results were obtained from all subjects. Response times (RT) and accuracy (% correct) were entered into separate two-tailed paired t tests to determine the influence of WM domain (face WM or house WM) on task performance.

RESULTS

Behavioral Results

Task accuracy (mean = 89%, standard deviation = 4%) and RT (mean = 1019 msec, SD = 290 msec) measures confirmed that subjects were able to perform the task without difficulty. In addition, separate two-tailed paired t tests were conducted for task RT and accuracy to investigate performance differences as a function of WM domain (face vs. house). Subjects were slightly more accurate for house WM trials (mean = 91%, SD = 4%) relative to face WM trials [mean = 88%, SD = 5%; $t(1, 11)$ = 2.28, p < .05]. Examination of task RT did not reveal a significant difference between face and house WM [$t(1, 11)$ = 0.89, p > .39].

ERP Results

A focal negative potential was observed in right lateral parieto-occipital electrodes (PO8, PO6, and P6) approximately 180–212 msec following stimulus onset. Based on latency and topographic distribution, this component was identified as the N170 (Bentin et al., 1996). Electrode PO8 evinced the most robust N170 across conditions; therefore we present the results from this electrode here. Similar results were found in neighboring electrodes PO6 and P6. Corresponding left lateral electrodes did not show a robust N170 in a third of subjects, and were not analyzed. This result is consistent with previous literature on face processing suggesting a right hemisphere dominance (e.g., McCarthy, Puce, Gore, & Allison, 1997) as well as studies that have found larger N170 in the right versus left hemisphere (e.g., Sagiv & Bentin, 2001).

For all statistical analyses, N170 latency was determined by finding the latency of the local minimum amplitude between 140 and 240 msec for each stimulus type (S1, probe, S2, S2 probe). N170 amplitude was defined by finding the mean N170 latency for each stimulus type and by calculating the average N170 amplitude over a specified time window equal to the mean latency ± 1 SD. For S1 and S2 stimuli, the N170 time window was 188–200 msec, and for delay probe stimuli, the time window was 184–212 msec. The N170 time window for S2 probes was 180–200 msec. Statistical analyses were performed separately for each stimulus type and are discussed below.

S1 and S2

An analysis of N170 amplitude was conducted for S1 and S2 stimuli to confirm that, similar to several previous studies demonstrating larger N170 amplitude to face relative to nonface objects (e.g., Itier & Taylor, 2004a; Bentin et al., 1996), the N170 to faces was greater in amplitude than the N170 to houses. As expected, we found that for both S1 and S2 stimuli, the N170 elicited

by faces was larger in amplitude than the N170 elicited by houses [$t(1, 11) = 4.69$ for S1; $t(1, 11) = 5.80$ for S2, $p < .01$ for both comparisons]. These results are shown in Figure 2.

Analysis of N170 latency for S1 and S2 stimuli as a function of stimulus domain (face vs. house) yielded no significant differences for S2 stimuli [$t(1, 11) = 0.77$, $p > .45$], but for S1 stimuli, the N170 to faces was significantly earlier than the N170 to houses [$t(1, 11) = 3.22$, $p < .01$]. This result is consistent with previous work that has demonstrated earlier N170 latencies to faces relative to nonface objects (Itier & Taylor, 2004a).

Delay Probes

Our primary prediction concerned the N170 elicited by delay-spanning noise probes. To ensure that our effects were not driven by subject strategies that involved systematic eye movements away from probe stimuli, we examined the eye movement channels during presentation of the delay-spanning noise probes. Analysis of eye movement channels time-locked to probe presentation indicated that EOG activity was negligible and did not differ across WM conditions [$t(1, 11) = 1.28, p > .22$ and $t(1, 11) = 0.97, p > .35$ for vertical and horizontal EOG channels respectively].

N170 elicited by noise probes was significantly smaller in amplitude than the N170 elicited by face or house S1 and S2 stimuli [$t(1, 11) > 5.9$, $p < .01$ for both comparisons]. Furthermore, although the N170 to delay probes was identified as a negative deflection in each subject, in many cases, it had an absolute positive amplitude value (see Itier & Taylor, 2004b). Importantly,
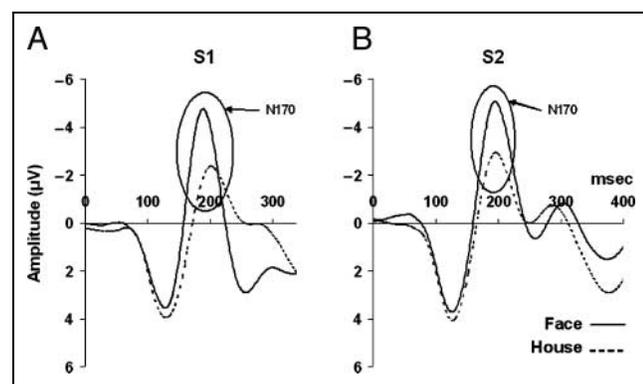
the topographic distribution indicated that the N170 was maximal in the same electrodes for delay probes and S1 and S2. In addition, these results are consistent with several findings that demonstrate smaller N170 to nonface objects than to faces (e.g., Itier & Taylor, 2004a; Bentin et al., 1996). Thus, we are confident that the component being indexed in the present analysis is the N170.

A two-factor ANOVA was conducted to examine the effects of WM domain (face vs. house) and probe order (first, second, or third noise probe) on the amplitude of the N170 to probes. There was a main effect of WM domain [$F(1, 11) = 22.37, p < .001$], indicating that the N170 amplitude elicited by probes during face WM trials was significantly greater in amplitude than the N170 elicited by probes during house WM trials. There was also a main effect of probe order [$F(2, 22) = 7.04, p < .01$]. The N170 to Probe 3 was significantly larger than the N170 to Probes 1 and 2 ($p < .05$ for both comparisons). No interaction between WM domain and probe order was observed [$F(2, 22) = 0.97, p > .39$]. Planned comparisons of WM domain on each delay probe indicate greater N170 amplitude responses to probes during face relative to house WM for all three probes, although the effect only approached significance for the third probe [two-tailed t tests; Probe 1: $t(1, 11) = 2.55, p < .05$; Probe 2: $t(1, 11) = 3.30, p < .01$, and Probe 3: $t(1, 11) = 2.11, p < .06$]. Thus, maintenance-related modulations were present throughout the delay interval. Results for the N170 to delay-spanning noise probes are depicted in Figure 3.

A second two-factor ANOVA was conducted to determine the effects of WM domain and probe order on N170 latency. We found no main effect of WM domain [$F(1, 11) = 2.35, p > .15$] or probe order [$F(2, 22) = 2.37, p > .13$], and no significant interaction [$F(2, 22) = 1.57, p > .23$].

S2 Probes

The S2 probe condition was included to explore whether perceptual processing was modulated by WM retrieval in addition to maintenance. The N170 to the S2 probe stimuli did not differ across WM domain [$t(1, 11) = 0.37, p > .71$]. Interestingly, the N170 to the S2 probes was significantly larger in amplitude than the N170 to the delay probes [$t(1, 11) = 3.78, p < .05$]. This effect was present regardless of WM domain.

Figure 2. Grand-average ERP waveform elicited by S1 and S2 stimuli. N170 amplitude to face stimuli (solid line) is significantly larger than the N170 to house stimuli (dotted line) for (A) S1 and (B) S2 stimuli ($p < .01$ for both comparisons). Mean amplitude (S1 face = −4.50 μV, *SEM* = 0.90; S1 house = −2.13 μV, *SEM* = 0.83; S2 face = −4.96 μV, *SEM* = 0.78; S2 house = −2.85 μV, *SEM* = 0.90) was calculated over the window from 188–200 msec (average peak latency for N170 to S1 and S2 ± 1 *SD*). Electrode PO8 is depicted in this figure, although results are similar for neighboring electrodes PO6 and P8.

DISCUSSION

The present study investigated the hypothesis that WM maintenance operations modulate feedforward perceptual processing in structures supporting face perception within occipito-temporal cortex. We examined the face-sensitive N170 component elicited by noise probe stimuli while manipulating the domain of the item being held in

Figure 3. Grand-average ERP waveform elicited by delay-spanning noise probes. (A) N170 amplitude to noise probes, regardless of probe number, is significantly reduced during face working memory (solid line) relative to house working memory (dotted line; $p < .001$). The pattern of larger N170 to noise probes during face relative to house working memory is significant for the (B) first and (C) second noise probes ($p < .05$ and $p < .01$, respectively) and approaches significance for the (D) third noise probe ($p < .06$). Electrode PO8 is depicted in this figure, although results are similar for neighboring electrodes PO6 and P8.
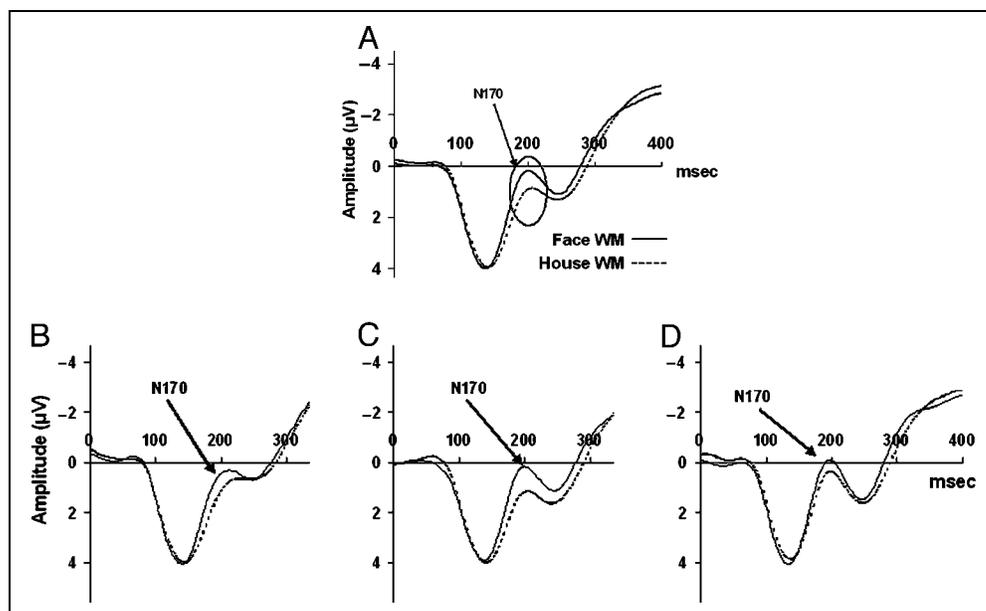
WM (face or house) and found that the N170 to noise probes was significantly greater in amplitude when subjects maintained a face relative to when they maintained a house in WM. These results suggest that activity in face-sensitive regions generating the N170 was enhanced during the earliest stages of perceptual analysis when a face was being maintained in WM. Furthermore, the pattern of greater amplitude N170 to noise probes during face WM was present for early, middle, and late probes, suggesting that modulations may play a role throughout the period of active WM maintenance. These findings are consistent with several fMRI studies demonstrating that activity in the posterior perceptual cortex is modulated by maintenance processes (Lepsien & Nobre, 2007; Fiebach, Rissman, & D'Esposito, 2006; Gazzaley et al., 2005; Ranganath, Cohen, et al., 2004; Ranganath, DeGutis, et al., 2004; Druzgal & D'Esposito, 2001b, 2003). However, the present results clarify the level at which information processing regions may be involved in maintenance operations.

Two fundamental suppositions of the present study were that the N170 represents early feedforward perceptual processing of faces and that it is capable of being modulated by top–down influences. Although there is a debate regarding the face-specificity of the N170 (e.g., Itier & Taylor, 2004b; Gauthier, Curran, Curby, & Collins, 2003), a large body of work suggests that the N170 is sensitive to holistic composition of face features (Itier & Taylor, 2004b; Eimer, 2000c; Bentin et al., 1996). Studies demonstrating that the emotional content of faces does not modulate the N170 (Holmes et al., 2003) and that the N170 is unaffected by familiarity with faces (Bentin & Deouell, 2000; Eimer, 2000a) have strengthened the case that the N170 represents early feedforward face processing. Although some have suggested that the N170 is not modulated by top–down influences, such as selective attention when perceptual load is low (Cauquil et al., 2000), there have been several convincing demonstrations of modulations in N170 amplitude (Sreenivasan & Jha, 2007; Holmes et al., 2003; Eimer, 2000b) and latency (Gazzaley et al., 2005) as a result of top–down influences. Thus, previous literature investigating the N170 component demonstrates that it is an appropriate index of feedforward perceptual processes and can be modulated in a top–down fashion.

We identify and evaluate herein alternate accounts of our observed modulations of N170 to delay probes. One possibility is that the observed modulations may be entirely due to perceptual-level effects. That is, the N170 to delay probes may have been larger in amplitude when S1 was a face versus a house because of residual perceptual activity related to processing of the S1 stimulus. As modulation of the N170 to delay probes was seen throughout the delay period, an account of the present results that relies on purely perceptual effects would suggest that S1-related perceptual activity lasts for over 5000 msec. An examination of the object processing literature renders this explanation highly unlikely. Studies recording from face- or object-sensitive inferotemporal cortical neurons in monkeys have convincingly demonstrated that neuronal activity associated with the perception of a particular class of objects returns to prestimulus levels of firing within approximately 500 msec of stimulus offset (e.g., Tsao, Freiwald, Tootell, & Livingstone, 2006; McCarthy et al., 1997; Tanaka, Saito, Fukada, & Moriya, 1991). In fact, the only context in which single-unit studies report perceptual neurons to remain active for seconds following stimulus presentation is in the context of WM tasks (Miller, Li, & Desimone, 1993), which is consistent with the current results.

An additional possibility is that the observed N170 modulations resulted from the processing of memory-*irrelevant* information that was modulated by WM load. This account relies on the fact that accuracy was significantly greater in the house WM condition relative to the face WM condition, which may have resulted from greater WM load in the face WM condition. WM load has been shown to modulate the perceptual processing of irrelevant information as measured behaviorally (Lavie, Hirst, de Fockert, & Viding, 2004) and neurally (Rose, Schmid, Winzen, Sommer, & Buchel, 2005; de Fockert, Rees, Frith, & Lavie, 2001). We examined whether our results could be explained by variations in WM load (as evidenced by accuracy differences) across condition. We divided our subject pool into subjects who were more accurate on face WM trials (face > house; $n = 5$) and subjects who were more accurate on house WM trials (house > face; $n = 7$) and performed an ANOVA of N170 amplitude to delay probes with WM domain (face or house) as a within-subjects factor and group (face > house or house > face) as a between-subjects factor. If our effect was truly driven by WM load influences on the processing of irrelevant information, then the main effect of WM domain should differ between the two groups (i.e., a significant group by WM domain interaction). We found no group by WM domain interaction [$F(1, 10) = 0.31$; $p > .86$]. Additionally, we examined the relationship between the difference in accuracy between face and house trials and the difference in N170 amplitude to the delay probes during face and house WM, and found that there was no correlation ($r^2 = -.006$). The results of these analyses strongly suggest that our results cannot be explained by WM load modulations of perceptual processing of irrelevant information.

A third intriguing possibility is that although subjects were instructed to ignore the delay probes, they may have used the probe presentation to reactivate the representation of the face or house seen at S1, and this reactivation may have resulted in the N170 modulations seen during the delay. We believe that this explanation is not functionally distinct from WM maintenance; one of the mechanisms supporting WM maintenance may be a reactivation of encoded items. Work by Johnson et al. (2005) corroborates this view. They found that brain regions activated by tasks in which subjects were explicitly instructed to "refresh" a just-activated representation had considerable overlap with regions identified in several fMRI studies as being crucial for WM maintenance.

Although the aim of the present study was to examine perceptual modulations during maintenance, the S2 probe trials allowed us to explore whether retrieval processes similarly modulated feedforward perceptual processing. Based on the results of Wild and Busey (2004), who found increased N170 to noise probes when subjects expected to see a face relative to when they expected to see a word, we predicted that the N170 to S2 probes would be greater in amplitude during face relative to house WM trials. Surprisingly, we found that N170 amplitude to S2 probes did not differ as a function of WM domain. Although it is unclear why perceptual processing did not appear to be modulated during WM retrieval in our study, our results are consistent with previous work in which WM load-dependent modulations of posterior perceptual activity were present during WM maintenance but not retrieval (Druzgal & D'Esposito, 2003).

The modulations of feedforward perceptual activity observed in our study strongly mirror feedforward modulations seen as a result of selective attention. Indeed, previous studies of spatial WM maintenance have posited that selective attention may mediate maintenance processes via early modulations of the representations of to-be-remembered locations (Jha, 2002; Awh et al., 2000). Similarly, it may be the case that the modulations in feedforward face perception observed in the present study are a result of the top–down influence of selective attention to faces. This hypothesis is consistent with behavioral results indicating that object-based attention may contribute to WM for objects (Barnes, Nelson, & Reuter-Lorenz, 2001), as well as previous work suggesting that selective attention may be responsible for input-level modulations of distractor-related activity during WM maintenance (Sreenivasan & Jha, 2007). Moreover, a recent fMRI study demonstrated that instructions to orient attention to a face or a scene that was being held in WM modulated activity in the FFA and PPA, respectively (Lepsien & Nobre, 2007). Although these results cannot specify the level of processing at which these modulations occur, in conjunction with the present study, they strongly suggest that perceptual modulations in the posterior cortex during WM maintenance are mediated by selective attention.

A related question is whether N170 modulations represent a generalized activation of face processing regions at the level of domain, or activation of a face representation at the item-specific level. Importantly, single-unit studies have demonstrated that neurons involved in perception remain active during maintenance of their preferred stimulus (Nakamura & Kubota, 1995; Miller et al., 1993; Miyashita & Chang, 1988; Fuster & Jervey, 1982), suggesting that modulations may occur at an item-specific level. In humans, evidence for modulation of item-specific perceptual processes during WM has come from the "match enhancement" literature where S2 faces that match the face being maintained in WM elicit enhanced activity within FFA relative to S2 faces that are nonmatches (Druzgal & D'Esposito, 2001a; see also Jiang, Haxby, Martin, Ungerleider, & Parasuraman, 2000). A similar instance of item-specific modulation by maintenance processes per se has not yet been demonstrated.

Although provocative, the current results are a first step in understanding the temporal characteristics of top–down influences of WM maintenance on early per-

ceptual processing. The present study was designed to maximize the number of correct trials available for ERP averaging. Thus, we lacked sufficient trial numbers to compare modulations during correct versus incorrect trials. In future studies, questions regarding the functional role of perceptual modulations on working memory task performance should be investigated (see Lepsien & Nobre, 2007). Future work should also attempt to integrate previous findings of top–down feedforward suppression of task-irrelevant distractors (Sreenivasan & Jha, 2007; Gazzaley et al., 2005; Rose et al., 2005) with the present results. Top–down enhancement of task-relevant memoranda and suppression of task-irrelevant distraction during working memory tasks may parallel gain control mechanisms of attention observed during perceptual tasks (Hillyard et al., 1998). Several neuropsychiatric conditions report the co-occurrence of disturbances in working memory and attention (e.g., ADHD, schizophrenia, depression). It may be that both of these control systems rely on similar neuromodulatory processes within the perceptual cortex that are dysfunctional during disease states.

Note

1. Rereferencing to the average of all scalp electrodes and filtering from 0.5 to 20 Hz (24 dB/octave) yielded identical results.

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