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Working memory templates are maintained as feature-specific perceptual codes

Kartik K. Sreenivasan, Deepak Sambhara, and Amishi P. Jha

Center for Cognitive Neuroscience, University of Pennsylvania, Philadelphia, Pennsylvania

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Sreenivasan KK, Sambhara D, Jha AP. Working memory templates are maintained as feature-specific perceptual codes. *J Neurophysiol* 106: 115–121, 2011. First published April 20, 2011; doi:10.1152/jn.00776.2010.—Working memory (WM) representations serve as templates that guide behavior, but the neural basis of these templates remains elusive. We tested the hypothesis that WM templates are maintained by biasing activity in sensoriperceptual neurons that code for features of items being held in memory. Neural activity was recorded using event-related potentials (ERPs) as participants viewed a series of faces and responded when a face matched a target face held in WM. Our prediction was that if activity in neurons coding for the features of the target is preferentially weighted during maintenance of the target, then ERP activity evoked by a nontarget probe face should be commensurate with the visual similarity between target and probe. Visual similarity was operationalized as the degree of overlap in visual features between target and probe. A face-sensitive ERP response was modulated by target-probe similarity. Amplitude was largest for probes that were similar to the target, and decreased monotonically as a function of decreasing target-probe similarity. These results indicate that neural activity is weighted in favor of visual features that comprise an actively held memory representation. As such, our findings support the notion that WM templates rely on neural populations involved in forming percepts of memory items.

visual short-term memory; sensory recruitment; ERP; match enhancement

WORKING MEMORY (WM) REPRESENTATIONS, which consist of recently encountered information that is maintained in an active state, as well as activated long-term representations (Baddeley 1986; Cowan 1993; Lewis-Peacock and Postle 2008; Oberauer 2002; Ruchkin et al. 2003), are critical for directing top-down attention and other memory-guided behaviors (Chelazzi et al. 1998; Downing 2000; Duncan and Humphreys 1989). A recent conceptualization of WM, termed the “sensory recruitment model”, posits that the same neural circuits involved in perception of an item are recruited to maintain the item in the form of a memory template (D’Esposito 2007; Pasternak and Greenlee 2005). Prefrontal control signals are thought to heighten activity in neurons that code for the perceptual features of the memory item, such that population activity within sensoriperceptual cortex is tuned in favor of those perceptual features (Desimone and Duncan 1995; Duncan and Humphreys 1989; Reddy et al. 2009). Given the high resolution with which WM representations can be encoded (e.g., Zhang and Luck 2008), an essential prediction of the sensory recruitment model is that sensoriperceptual activity supporting WM templates should be

selective for the perceptual features that comprise the memory item. Thus far, evidence in support of this prediction has been lacking. The present study was designed to investigate the selectivity of sensory recruitment during WM for complex visual items.

Participants viewed a series of faces and responded to faces that matched a target face held in WM. If actively maintaining the target face in WM preferentially weights visual neurons in favor of target-specific features, then neural population response should be selectively enhanced during target presentation relative to nontarget presentation. Moreover, the response to a nontarget probe face should reflect the degree to which visual features of the target are present in the probe. Prior single-unit and functional MRI (fMRI) studies have reported greater activity in inferior temporal cortex (ITC) for probes that match the target information relative to nonmatching probes (“match enhancement”; Druzgal and D’Esposito 2001; Miller and Desimone 1994). Yet, it is unclear whether match enhancement is sensitive to the perceptual features of the probe, as predicted by the sensory recruitment model.

To investigate the feature sensitivity¹ of WM templates, we employed a morphing technique to create a set of probe faces with facial features that were composed of parametrically varying degrees of the corresponding target facial features. As shorthand, we operationally define “similarity” as the degree of overlap in specific facial features between the target and probes. Event-related potentials (ERPs) time-locked to face presentation indexed face-evoked neural activity. Our analysis focused on the face-sensitive N250 ERP response, which is the earliest electrophysiological marker of face perception that is reliably influenced by memory for individual faces (Tanaka et al. 2006) and is generated within face-processing regions of ITC (Kaufmann et al. 2009; Schweinberger et al. 2002). Our prediction was that probe-evoked N250 would scale with the similarity to the target, with the highest amplitude responses evoked by the target itself, and monotonic amplitude reductions as similarity to the target decreased.

MATERIALS AND METHODS

Participants

Nineteen volunteers (eight female; 18–27 years of age) from the University of Pennsylvania community (Philadelphia, PA) took part in this experiment, which was approved by the University of Pennsyl-

Address for reprint requests and other correspondence: A. P. Jha, Dept. of Psychology, Univ. of Miami, 5665 Ponce de Leon, Coral Gables, FL 33146 (e-mail: ajha@psy.miami.edu).

¹ It is important to distinguish our use of the term “feature sensitivity” from the well-accepted notion that faces are recognized in a holistic—as opposed to a feature-based—manner (Tanaka and Farah 1993). Feature sensitivity in the current context is meant to connote the idea that two items that share many features will evoke more similar neural responses in high-level visual regions than will two items that share very few features (e.g., Tsunoda et al. 2001).

vania Institutional Review Board. Participants were neurologically normal, had normal or corrected-to-normal vision, and provided informed consent. Analyses focused on data from 15 participants (five female; 18–27 years of age) after four individuals were excluded due to excessive eye movement or inability to follow task instructions.

Stimuli

One hundred two unique faces were assembled from a set of black-and-white drawings of face features (eyes, noses, and mouths) from the Mac-a-Mug Pro software package (Shaherazam Software, Milwaukee, WI). One face was arbitrarily chosen as the target face. A second face, hereafter referred to as the control face, was chosen such that these two faces consisted of a unique set of features (i.e., the nose, eyes, and mouth of the target were different than the nose, eyes, and mouth of the control face). The remaining 100 faces were designated as novel faces.

We manipulated stimulus similarity as follows. The target face and control face were loaded into the Morph 2.5 package (Gryphon Software, Canada), which can be used to create a series of images that defines a transformation of a start image into a target image. Four intermediate probe images were saved for each 20% increment toward the control face. The probe faces were designated as the 80%, 60%, 40%, and 20% faces, indicating the percentage of target features present in each probe face. Critically, the fact that individual features of each probe retained a percentage of each corresponding original target feature allowed us to examine how face processing was influenced by target-probe similarity. At the same time, each feature of a probe face was qualitatively different from the corresponding features of the other probe faces. The face stimuli are depicted in Fig. 1A.

Experimental Design

Participants performed a continuous target detection (CTD) task, in which they responded to the presentation of the target face, which was learned through a brief encoding session. The encoding session and the CTD occurred within a single experimental session, during which participants were seated ~70 cm in front of a computer monitor inside a dimly lit, sound-attenuated booth.

Encoding session. Two brief matching tasks familiarized participants with the target and helped them discriminate between target and probes. Prior to the first matching task, participants studied a paper copy of the image of the target for 5 min.

In the first task, two faces (each 4.5° by 5° of visual angle) were presented simultaneously on the screen, 9.4° to the left and right of fixation. The face on the left was always the target, and the face on the right was either the target (50% of trials) or the 80%, 60%, or 40%

face (each presented on 16.7% of trials). The target was presented on each trial to facilitate encoding. Participants responded with a button press indicating whether the two faces were identical (match) or different (nonmatch). The face pairs were present on the screen for 1,500 ms. Following a 750-ms delay, feedback was presented for 1,750 ms. The intertrial interval (ITI) was jittered from 800 to 1,200 ms (mean = 1,000 ms).

The second matching task was identical to the first, except that both faces varied on each trial. Match trials consisted of two targets or two 80%, 60%, or 40% faces. Nonmatch trials consisted of the target and the 80%, 60%, or 40% face. Each stimulus type was equally likely to appear to the right or the left of the fixation cross. During the encoding session, participants viewed a total of 720 faces, one-half of which were targets, and the remaining one-half of which were divided evenly among 80%, 60%, and 40% faces.

CTD. The CTD task consisted of a series of centrally presented faces (4.5° by 5° of visual angle). To minimize response-related artifact during ERP recording, participants only responded to the appearance of a target with a button press. No feedback was given. Each face was presented for 750 ms, followed by an ITI of variable duration (800–1,200 ms; mean = 1,000 ms; see Fig. 1B). The CTD was divided into seven runs of <3 min each. Each run was followed by a brief period of rest. Target (80%, 60%, 40%, 20%), control, and novel faces were each presented 100 times over the course of the experiment. Presentation order was counterbalanced for sequence effects. The target was not repeated on consecutive trials.

The CTD was designed to encourage participants to maintain an active representation of the target throughout the task to distinguish targets from probe faces. Previous investigations of memory-guided target identification have employed versions of a delayed match-to-sample task, which can be performed using familiarity-based cues (see Miller and Desimone 1994). Importantly, active maintenance, whether it involves recently encountered information or activated portions of long-term memory (Cowan 1993; Lewis-Peacock and Postle 2008), may rely on different neural substrates than those recruited by passive, familiarity-based strategies (Speer et al. 2003). Active maintenance was promoted by the high degree of similarity across stimuli, which necessitated a high-resolution memory template for the target. Furthermore, all stimuli, with the exception of novel faces, were familiar to participants, precluding them from using a sense of familiarity to distinguish targets from probes. Consistent with our aim of promoting active maintenance, postexperiment debriefing—asking participants to reveal any strategies that may have been used—indicated that participants did not consciously use familiarity as a strategy.

To distinguish our predicted effects of active maintenance from bottom-up neural modulations due to repeated stimulus presentations (see Grill-Spector et al. 2006 for a review; Jiang et al. 2000; Miller et

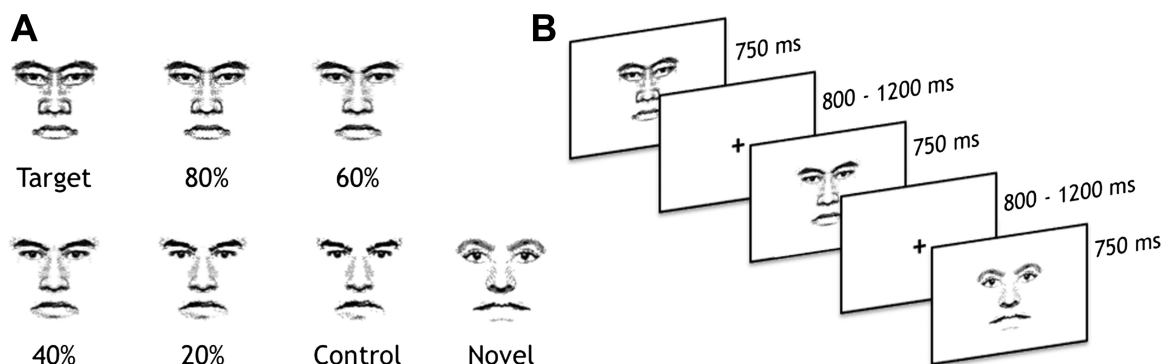


Fig. 1. Face stimuli and timeline of the continuous target detection (CTD). *A*: the target face was maintained in working memory. Nontarget probe faces contained a percentage of target facial features (80%, 60%, 40%, and 20%, respectively), whereas the control and novel faces were composed of facial features that were distinct from target facial features (see MATERIALS AND METHODS for details). The novel face shown here is an example of the 100 novel faces that were presented over the course of the CTD. *B*: each face was presented centrally for 750 ms, followed by a variable intertrial interval (800–1,200 ms). Participants responded to the presentation of the target face.

al. 1991, 1993), we compared the N250 elicited by the control and novel faces. Control and novel faces were both novel at the start of the CTD, but the control face was repeatedly presented throughout the CTD, whereas novel faces were presented only once each. The comparison of these two conditions provided us with an index of repetition-based modulation for faces that did not contain task-relevant target features.

ERP Acquisition and Analysis

EEG activity was recorded from a custom cap with Ag-AgCl electrodes distributed over 64 scalp locations in a modified 10–20 montage. EEG was referenced to an electrode placed on the left mastoid. Horizontal and vertical electrooculograms (EOGs) were recorded from electrodes placed at the outer canthi of both eyes and above and below the left eye to record horizontal and vertical eye movement, respectively. All channels were amplified using a pair of SynAmps amplifiers (Neuroscan, El Paso, TX) at a band-pass of 0.1–100 Hz and digitized with a 500-Hz sampling rate. Electrode impedances were kept below 5 k Ω .

Prior to segmentation, all channels were re-referenced offline to an average of all scalp electrodes. Next, EEG and EOG were epoch-averaged to a period beginning 100 ms before stimulus onset to 700 ms following stimulus onset. Following baseline correction, epochs containing eye-movement artifact larger than 100 μ V or associated with incorrect behavioral responses were removed from analysis (Itier and Taylor 2004). Additionally, epochs following target presentation were removed to avoid motor contamination. Data averaging was performed after sorting by stimulus type. Averages were filtered using a band-pass from 0.15 to 30 Hz (24 dB/octave).

Data from three participants were excluded from further analysis due to excessive eye movements (between 19% and 53% of epochs rejected). An additional participant was excluded from all analyses due to an inability to follow task instructions. For the remaining 15 participants, the rejection rate for epochs due to excessive eye movements was 5.8% (SD = 5.3%), and the mean number of segments contributing to each average was 78.6 (range = 53–99; SD = 9.1).

Data analysis focused on the N250 component, which is thought to index memory for individual faces (Tanaka et al. 2006). Previous work has suggested that this component is involved in face processing (Nasr and Esteky 2009), has a right-lateralized topography consistent with face processing (Schweinberger et al. 1995), and has been localized to face-processing regions (Kaufmann et al. 2009; Schweinberger et al. 2002). An earlier, face-sensitive component, the N170, has also been shown to be influenced by WM control processes (Banko and Vidnyanszky 2010; Clapp et al. 2010; Jongen and Jonkman 2010; Sreenivasan and Jha 2007; Sreenivasan et al. 2007) and may be involved in individuating faces (Jacques and Rossion 2006; Jemel et al. 2003), although this finding is not consistent across studies (Bentin and Deouell 2000; Eimer 2000a). Given evidence that the N170 is thought to reflect structural processing of faces (Bentin et

al. 1996; Carmel and Bentin 2002; George et al. 1996), which is face general (Bentin and Deouell 2000; Eimer 2000a), we did not expect N170 to be modulated by target-probe similarity. Nonetheless, we analyzed N170 amplitude for the sake of completeness. For each component, peak component latency across participants and conditions served as the center of a 40-ms window over which mean amplitude was calculated separately for each participant and each condition. Amplitude values were entered into a repeated-measures ANOVA to determine how target-probe similarity modulated component amplitude. Separate ANOVAs were run for N250 and N170. To test the selectivity of the memory template for the target, a planned pairwise contrast compared N250 elicited by the target with N250 elicited by the 80% face. Planned pairwise contrasts among 80%, 60%, and 40% faces were used to test feature sensitivity while holding familiarity constant; these three faces were presented an equal number of times across encoding and CTD sessions.

RESULTS

Behavioral Results

Hit rate (mean = 92.9%; SD = 6.5%) and false alarm (FA) rate (mean = 2.2%; SD = 1.7) indicated that participants encoded the target faithfully and were able to distinguish the target from the other faces.

ERP Results

Focal-negative potentials were observed in lateral parieto-occipital electrodes 184 ms and 288 ms following face onset (Fig. 2). Based on latency and topographic distribution, these components were identified as the N170 (Bentin et al. 1996; Bentin and Deouell 2000; Itier and Taylor 2004) and the N250 (Schweinberger et al. 2004). Both components showed consistent topographic distribution across all stimulus types (see Supplemental Fig. 1).

The N170 was lateralized to the right hemisphere, as has been noted previously (Sagiv and Bentin 2001). The grand average topographic map indicated a focus in electrode PO8 (Fig. 2). The focus of the N170 was consistent across participants; data from electrode PO8 were therefore used for all N170 analyses.

N250 was observed bilaterally but was more robust in the right hemisphere. The grand average topographic map indicated a focus in electrode PO8 (Fig. 2), but there was considerable variability in peak electrode across participants. We therefore employed an electrode-of-interest (EOI) approach (Downing et al. 2001; Liu et al. 2000): for each participant, we pooled data across the two parietal or occipital electrodes

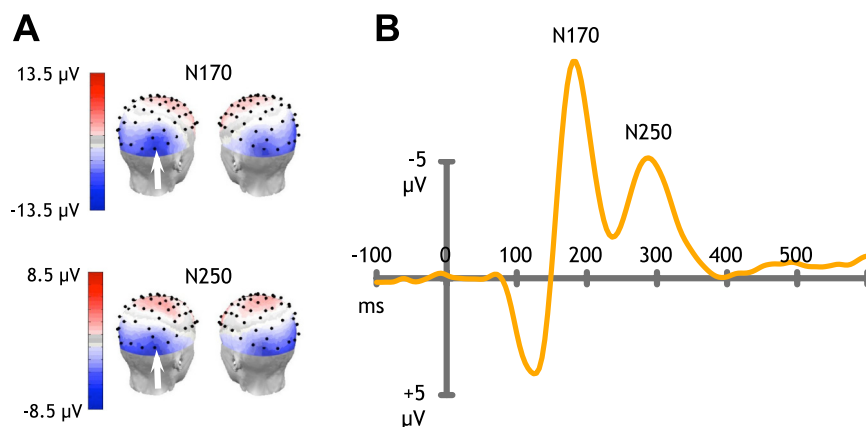


Fig. 2. Grand average of the face-evoked response, averaged across participants and all stimulus types. *A*: the topographic voltage distribution maps for the N170 (top) and N250 (bottom). Data are from the peak of each component (184 ms for N170 and 288 ms for N250). Both components had a focus in right parieto-occipital electrode PO8 (indicated by the white arrows), but the peak N250 electrode varied considerably across participants. *B*: the grand average event-related potential (ERP) waveform from electrode PO8 shows the time course and amplitude of the N170 and N250.

showing the most prominent N250 across all stimuli (data from individual parietal and occipital electrodes evinced the same pattern of results; see Supplemental Fig. 2).

N170. A repeated-measures ANOVA with stimulus type (target, 80%, 60%, 40%, and 20%) as a single factor indicated that N170 amplitude was insensitive to our manipulation of similarity [$F(4,56) = 1.15$; $P > 0.3$; $\eta_p^2 = 0.08$]. Individual pairwise contrasts confirmed that N170 amplitude did not significantly differ across any conditions (all $P > 0.6$; see Figs. 3 and 4).

N250. The analogous ANOVA of N250 amplitude yielded a significant effect of stimulus type [$F(4,56) = 44.28$; $P < 0.001$; $\eta_p^2 = 0.76$]. Polynomial contrasts [significant linear effect, $F(1,14) = 56.26$; $P < 0.001$; $\eta_p^2 = 0.80$; significant quadratic effect, $F(1,14) = 59.26$; $P < 0.001$; $\eta_p^2 = 0.81$] indicated a monotonic decrease in N250 amplitude with diminishing target-probe similarity. Grand average waveforms elicited by target and probe faces are displayed in Fig. 3. The N250 to the target face was significantly enhanced compared with N250 to the 80% face (paired t -test; $P < 0.001$), suggesting that WM for the target selectively biased neurons coding for target features. Enhanced N250 to the target could not be explained by the fact that participants viewed the target more frequently than the 80% face during the encoding session. Our control comparison (control vs. novel) exhibited repetition-related attenuation, with decreased N250 to the control (repeated 100 times) relative to novel faces (presented once each; $P < 0.05$; Fig. 4, and see Supplemental Fig. 3), suggesting that increased repetition of the target would have, if anything, led to a decrease in N250 amplitude in the target relative to the 80% face condition. Individual pairwise comparisons substantiated our prediction that N250 amplitude to equally familiar probes would be sensitive to target-probe similarity; N250 amplitude significantly differed across 80%, 60%, and 40% faces (all $P < 0.02$; Bonferroni corrected for multiple comparisons; see Fig. 4).

Control analyses confirmed that the pattern of N250 modulation could not be attributed to endogenous processing reflecting the discrimination difficulty. First, behavioral performance was poorest for the 80% face (87.8% accuracy vs. 93.1% for the target), yet the N250 was largest to the target for every participant. Second, the difference in amplitude between target and 80% faces was similar ($P > 0.6$) for participants who performed better on the 80% face relative to the target ($n = 6$) and participants who performed better on the target relative to

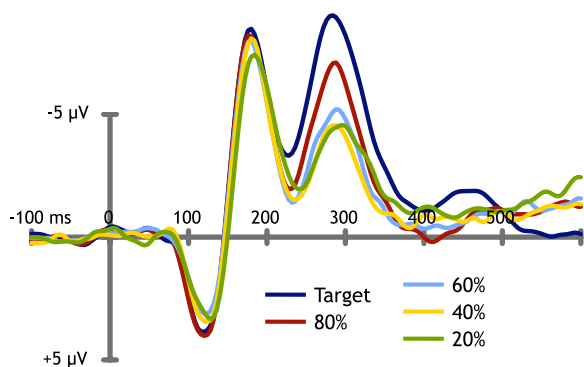


Fig. 3. ERP waveform as a function of target-probe similarity. N250 was largest to the target face and decreased monotonically as a function of decreasing target-probe similarity. Waveforms were generated from data averaged across the individual participant electrodes identified in the electrode-of-interest analysis.

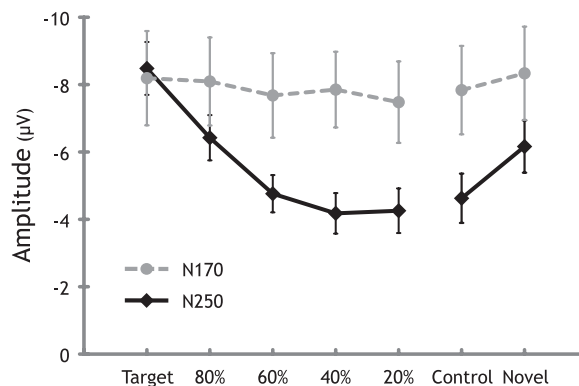


Fig. 4. Average N170 and N250 amplitude for each stimulus type. N170 amplitude (gray circles) did not differ across conditions. N250 amplitude (black diamonds) was largest for targets and decreased progressively for 80%, 60%, and 40% faces. N250 was reduced for the control face compared with novel faces, indicating passive, repetition-based effects.

the 80% face ($n = 9$). Finally, we analyzed ERPs recorded during the second matching task from the encoding session, when participants viewed two faces and indicated whether they were identical. Data from the encoding session were available for eight of the 15 participants². Behavioral performance confirmed that discriminating between two similar faces (target vs. 80%, 80% vs. 60%, or 60% vs. 40%) was more difficult ($P < 0.01$) than discriminating between two less-similar faces (target vs. 60%, 40%, or 20%; 80% vs. 40% or 20%; 60% vs. 20%). N250 amplitude measures were calculated using an EOI analysis and subjected to a repeated-measures ANOVA with similarity as the main factor. If the N250 reflected discrimination difficulty, amplitude should be largest when participants viewed two faces that were highly similar. However, there was no main effect of similarity [$F(3,21) = 0.75$; $P > 0.5$; $\eta_p^2 = 0.10$], and none of the individual pairwise comparisons was significant (all $P > 0.4$). These analyses confirm that the N250 is insensitive to discrimination difficulty, suggesting that N250 modulations observed in the CTD reflect activation of the target memory template.

To further ensure that N250 modulations were due to WM mechanisms, rather than a learned (be it intentional or unintentional) strategy, which evolved over the course of the experiment, we repeated the above ANOVA with the factor of stimulus type and the additional factor of experiment half (first one-half of the CTD vs. second one-half of the CTD). We found no main effect of experiment half and no interaction, indicating that the pattern of N250 amplitude was stable across the experiment.

DISCUSSION

Searching for a face in a crowd is a common experience. We examined the neural correlates of this process—one that requires holding an activated memory trace of a face in WM and comparing it with faces in the environment. By requiring participants to compare the memory trace of a target face with faces that varied in their similarity to the target, we demonstrated that face-sensitive N250 amplitude was closely related to the degree of similarity between a task-relevant face main-

² We repeated the main N250 analysis with the CTD data from the eight participants who also had ERP data from the encoding session. The results were identical to those found with all 15 participants [main effect of stimulus type [$F(4,28) = 32.98$; $P < 0.001$; $\eta_p^2 = 0.83$]].

tained as a memory template and a visually presented face. Our data corroborate critical predictions of the sensory recruitment model: that WM templates bias perceptual activity with a high degree of selectivity for the memory item, and that templates weight population response in favor of visual features corresponding to features of the memory item. These results support the emerging view that memory templates and visual percepts are supported by the same neural circuitry (Awh and Jonides 2001; D'Esposito 2007; Pasternak and Greenlee 2005; Postle 2006).

The present results complement two recent studies in which fMRI pattern classification techniques were used to identify stimulus-specific activation patterns in early visual areas during WM maintenance (Harrison and Tong 2009; Serences et al. 2009). In both studies, participants retained simple visual objects (grating and Gabor stimuli) in WM. Classifiers were trained to distinguish activation patterns in early visual areas during the delay period when no stimuli were present. In both cases, the classifiers were able to accurately predict the identity of the item being held in WM based on activations during the delay period. Although these studies did not investigate the feature sensitivity of early visual delay-period activity, their results indicate that early visual neurons, which encode simple visual features, are involved in forming memory templates. Our study demonstrates that WM templates for more complex stimuli are similarly maintained in a feature-sensitive code and confirms, via N250 sensitivity, that WM processes engage temporally early stages of processing, presumably within face-sensitive regions of ITC (Kaufmann et al. 2009; Schweinberger et al. 2002).

Unlike previous electrophysiological studies of WM, which measure activity during a blank maintenance interval (Sreenivasan et al. 2007; Vogel and Machizawa 2004; Vogel et al. 2005), we chose to infer maintenance processes from probe-induced activity. The advantage of this approach is that it allowed us to index feature-specific perceptual biases. Human electrophysiological measures cannot identify feature-specific perceptual activity during delay intervals, and fMRI investigations of stimulus-specific delay period activity have thus far been limited to simple gratings (Harrison and Tong 2009; Serences et al. 2009). Furthermore, traditional WM delay tasks can often be solved using a sense of familiarity or recency. Our design discouraged the use of familiarity strategies that recruit neural circuits that are distinct from those recruited by active maintenance (Speer et al. 2003). One limitation of our design is that probe onset likely initiates multiple operations, including exogenous processes such as perceptual processing of the probe (the focus of the current study) and endogenous processes such as stimulus evaluation and response. It is therefore important to consider which of these operations was being measured by the N250, which is well established as being sensitive to face presentation and is thought to reflect the perceptual analysis of faces (Kaufmann et al. 2009; Schweinberger et al. 2002). We argue that modulations of this component reflect the top-down influence of ongoing WM maintenance operations. Similar logic has previously been used to infer top-down WM effects from modulations of perceptual processing (Awh et al. 2000; Gazzaley et al. 2005; Jha 2002; Morgan et al. 2008; Sreenivasan et al. 2007). Consistent with this interpretation, the N250 is not modulated by postperceptual processes such as semantic associations (Kaufmann et al. 2009) and is elicited by face presentation in the absence of explicit WM requirements or implicit activations of face representations by stimulus repetition

(e.g., Sreenivasan et al. 2009), suggesting that it is perceptual in nature. Furthermore, we observed N250 modulations as a function of our perceptual manipulation while controlling for factors, such as familiarity, which can modulate endogenous decisional processes. Finally, previously described ERP components indexing domain-general, endogenous selection processes are characterized by central or more broadly distributed topographic distributions and long-lasting durations (Eimer 2000b; Harter and Aine 1984; Hillyard et al. 1998; Senkowski and Herrmann 2002; Smid et al. 1999) and demonstrate sensitivity to the difficulty of the discrimination (Senkowski and Herrmann 2002; Vogel and Luck 2000), all of which dissociate these components from the N250 measured in the current experiment.

Another issue to consider is the generalizability of our findings across various WM contexts. Our task required generation and maintenance of a memory template of an item that was well learned through the encoding session. As such, we cannot rule out the possibility that our results may be exclusive to representations that are well learned prior to being maintained in WM. Several studies have shown that even brief experience discriminating between hard-to-discriminate stimuli can lead to neural plasticity that is relatively long lasting (see Goldstone 1998). As a consequence, neurons in high-level visual regions may become more sharply tuned for task-relevant features (e.g., Saarinen and Levi 1995). While we postulate that similar biasing mechanisms likely characterize memory templates when the memory item is not well learned, a direct comparison of the feature sensitivity of memory templates for well-learned and novel items may be necessary to clarify this issue.

Finally, our results may offer insight into why occasional lapses in WM may occur. We found that the perceptual response to currently attended stimuli is modulated by the degree of feature overlap with activated memory templates. Neural activity of attended stimuli may need to pass a threshold for subsequent decision-making processes to deem the stimulus as a "match". If memory templates are of poor resolution, nontarget stimuli may erroneously reach this threshold, leading to incorrect target identification. Alternatively, incorrect target identification may also occur if the perceptual signal of currently attended items is of poor quality (e.g., looking for your friend in a dimly lit room or without your glasses on). While the low FA rate in the current study precluded us from conducting an in-depth analysis of errors, future investigations elaborating on these concepts must probe the relationship between stimulus-specific coding, the integrity of memory templates, and behavioral decisions.

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Present addresses: K. K. Sreenivasan, Helen Wills Neuroscience Institute, University of California Berkeley, Berkeley, CA 94720-3192 (ksreenivasan@berkeley.edu); D. Sambhara: University of Illinois, College of Medicine at Urbana-Champaign, 190 Medical Sciences Bldg., MC-714, 506 S. Mathews Ave., Urbana, IL 61801 (e-mail: dsambh2@uic.edu).

GRANTS

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

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