Selective Attention Supports Working Memory Maintenance by Modulating Perceptual Processing of Distractors

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Abstract

■ Selective attention has been shown to bias sensory processing in favor of relevant stimuli and against irrelevant or distracting stimuli in perceptual tasks. Increasing evidence suggests that selective attention plays an important role during working memory maintenance, possibly by biasing sensory processing in favor of to-be-remembered items. In the current study, we investigated whether selective attention may also support working memory by biasing processing against irrelevant and potentially distracting information. Event-related potentials (ERPs) were recorded while subjects ($n = 22$) performed a delayed-recognition task for faces and shoes. The delay period was filled with face or shoe distractors. Behavioral performance was impaired when distractors were congruent with the working memory domain (e.g., face distractor during working memory for faces) relative to when distractors were incongruent with the working memory domain (e.g., face distractor during shoe working memory). If attentional biasing against distractor processing is indeed functionally relevant in supporting working memory maintenance, perceptual processing of distractors is predicted to be attenuated when distractors are more behaviorally intrusive relative to when they are nonintrusive. As such, we predicted that perceptual processing of distracting faces, as measured by the face-sensitive N170 ERP component, would be reduced in the context of congruent (face) working memory relative to incongruent (shoe) working memory. The N170 elicited by distracting faces demonstrated reduced amplitude during congruent versus incongruent working memory. These results suggest that perceptual processing of distracting faces may be attenuated due to attentional biasing against sensory processing of distractors that are most behaviorally intrusive during working memory maintenance. ■

INTRODUCTION

One of the challenges of everyday life is to select and maintain relevant information in the presence of a sea of irrelevant, distracting, and competing influences. A large body of work has explored the neural mechanisms by which selective attention helps to differentiate relevant from irrelevant information during perception, but less is known about how attention may support the ability to distinguish between relevant and irrelevant information during working memory. Recently, it has been suggested that selective attention may subserve the active maintenance of information in working memory via attentional rehearsal of memoranda (for a review, see Awh, Vogel, & Oh, 2006). That is, attentional selection mechanisms, in the context of working memory, may bias prefrontal and posterior perceptual activity in favor of representations of relevant, to-be-remembered stimuli in order to ensure the high fidelity of mnemonic information over delays. Indeed, several studies of spatial working memory have demonstrated increased perceptual activity to probes appearing in memory locations throughout the entire period of working memory maintenance (Jha, 2002; Awh et al., 1999).

The concept of representational biasing via selective attention has its origins in studies of perception that suggest that the magnitude of stimulus-evoked neural activity can be modulated in a gain control fashion as a function of attention (Hillyard, Vogel, & Luck, 1998; Hillyard, Mangun, Woldorff, & Luck, 1995). By the sensory gain control account of attention, stimulus-evoked activity is amplified in attended channels relative to unattended channels. Studies of perception have also suggested that selection mechanisms may play an important role in the processing of irrelevant or distracting information. Lavie and colleagues have proposed that the degree of perceptual load present during the task influences the manner in which selection mechanisms are recruited for distractor processing (for a review, see Lavie, 2005). Under conditions of high perceptual load—when a large amount of perceptual information is present, or perceptual task demands are high—cognitive control systems, such as working memory, may recruit selective attention to bias perceptual processing against distracting information (Lavie, 2005). Several of these studies used a response-competition paradigm in which

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subjects had to respond to a target letter in the presence of peripheral distraction that was either the same or different as the target letter. Subjects were typically slower when peripheral distractors were similar to the target than when they were highly discriminable under conditions of low perceptual load. In contrast, the similarity of the distractor letter to the target had minimal effect when the perceptual load was high, indicating decreased distractor processing under conditions of high versus low load (Lavie & Cox, 1997; Lavie, 1995). Neuroimaging results provide corroborating support for reduced distractor processing during high versus low load. For example, in a functional magnetic resonance imaging (fMRI) study by Rees, Frith, and Lavie (1997), activity in the motion-sensitive middle temporal area (MT) was reduced for task-irrelevant motion distractors during high versus low load. Thus, studies investigating the role of attention in perception suggest that selective attention plays an important role in enhancing relevant and suppressing irrelevant representations.

Recently, attention's role in distinguishing relevant from irrelevant mnemonic information has been investigated during fMRI and event-related potential (ERP) studies of working memory and distraction. These studies have examined the role of the prefrontal cortex (PFC) and posterior perceptual sites in managing distraction, and have found a consistent pattern of greater prefrontal involvement associated with task-irrelevant distracting information presented during the delay of a delayed-recognition task (Postle, 2005; Jha, Fabian, & Aguirre, 2004; Sakai, Rowe, & Passingham, 2002; Chao & Knight, 1998).

The pattern of activity reported in posterior perceptual regions, however, has been inconsistent across studies. Jha et al. (2004) employed a delayed-recognition task for faces and shoes and found increased fusiform face area (FFA) activity to delay-spanning face distractors presented during face relative to shoe working memory, when the distractors were more behaviorally intrusive and impaired performance. These results were interpreted as increased hemodynamic activity related to active inhibition of face distractor processing in the FFA (Jha et al., 2004).

In contrast, Postle (2005) reported reduced activity in perceptual sites to a rapid serial visual presentation of faces when they were distracting versus when they were not distracting. These results were interpreted as down-regulation of the gain of sensory processing of irrelevant stimuli. Consistent with these results, Gazzaley, Cooney, McEvoy, Knight, and D'Esposito (2005) also report decreased activity in posterior perceptual sites to task-irrelevant stimuli. In their study, activity was recorded from the FFA and the scene-selective parahippocampal place area (PPA) during a task in which subjects viewed a memory set—a series of two faces and two scenes, followed by a memory probe, either a face or a scene. Subjects' task was to identify whether the memory

probe was part of the memory set from that trial. There were two memory conditions of interest—*remember faces/ignore scenes* and *remember scenes/ignore faces*. There was also a condition in which the two faces and two scenes were passively viewed. PPA activity was decreased in the *remember faces/ignore scenes* condition relative to the *passive view* condition, although FFA activity was not significantly reduced for the *remember scenes/ignore faces* relative to the *passive view* condition. The decreased activity in the PPA when scenes were to be ignored was taken as evidence of suppression of perceptual processing driven by top-down influences. Although provocative, these fMRI studies employed BOLD imaging techniques during which activity profiles are indirect measures of neural processing and cannot distinguish excitatory from inhibitory neural effects.

Unlike fMRI, ERPs index neural activity directly. Gazzaley et al. (2005) employed ERPs in the same task described above, and found that the face-sensitive N170 component (Bentin et al., 1996) was increased in the *remember faces/ignore scenes* relative to the *remember scenes/ignore faces* condition, but was not suppressed in the *remember scenes/ignore faces* condition relative to the *passive view condition*. Although the authors point out that N170 latency was increased to the ignored faces relative to the passively viewed faces, no previous studies have reported attentional effects as indexed by N170 latency. It may be the case that latency shifts observed by Gazzaley and colleagues are indexing effects that are functionally distinct from the amplitude modulations that have traditionally been described in the attention literature as a result of top-down attentional influences (e.g., Hillyard et al., 1998). Thus, it is unclear whether shifts in latency reflect that perceptual processing of distracting faces was attenuated when they were ignored versus passively viewed. The pattern of results described above appears to be inconsistent with a model of distractor processing in which prefrontal control areas bias recipient perceptual sites against the processing of distractors (Postle, 2005; Jha et al., 2004; Chao & Knight, 1998). However, the absence of N170 amplitude modulation to distractors may be a result of the experimental design, in which distractors (faces) were never in conflict with the to-be-remembered items (scenes). That is, although faces in the context of remembering scenes were task-irrelevant, they may not have been functionally distracting. In the present study, distraction is operationally defined as stimulus conditions that are behaviorally intrusive, and may therefore impair task performance. The question then remains: does selective attention subserve working memory maintenance by biasing sensory processing against behaviorally intrusive distractors?

To answer this question, we designed a task that allowed us to measure neural activity evoked by face distractors by indexing the face-sensitive N170 ERP component, which is thought to represent early perceptual-level face

processing (Itier & Taylor, 2004a; Eimer, 2000b; Bentin et al., 1996). The key manipulation involved varying the degree to which these face distractors were behaviorally intrusive to working memory performance. ERPs were recorded from 64 channels as subjects performed a delayed-recognition task in which the memory item (S1) was either a face or a shoe. At the end of the delay, a test item (S2) was presented, and subjects were instructed to press a button indicating whether S2 matched or did not match S1. During the delay interval of each trial, two distractor faces or two distractor shoes were presented sequentially. Distractors were either congruent with working memory domain (face distractors in the context of face working memory, or shoe distractors in the context of shoe working memory) or incongruent with working memory domain (face distractors in the context of shoe working memory, or shoe distractors in the context of face working memory). We predicted that face distractors would be more behaviorally intrusive when they were congruent relative to when they were incongruent with working memory domain, as has been shown previously in similar tasks (e.g., Jha et al., 2004). Further, we predicted that the N170 elicited by face distractors would be reduced in amplitude in the congruent working memory condition, when face distraction is behaviorally intrusive, relative to the incongruent working memory condition. This amplitude modulation would provide evidence for attentional biasing against perceptual processing of distractors during working memory maintenance.

METHODS

Participants

Twenty-two undergraduates (six women; 18–22 years of age) from the University of Pennsylvania were awarded course credit for participation in this experiment. 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.

Experimental Task

Subjects performed a delayed-recognition task in which they had to remember faces[1] and shoes (Figure 1A). Subjects were placed in a sound-attenuated booth 70 cm in front of a monitor, so that each stimulus subtended a visual angle of approximately 5.3° by 3.3°. All stimuli used in the experiment were grayscale images. The memory item (S1) in each trial was either a face or a shoe presented centrally for 750 msec. S1 offset was followed by a delay period that was jittered from 3300 msec to 5700 msec. At the end of the delay, a test item (S2) was presented centrally for 750 msec. S2 was identical to S1 on half the trials (match trials), and was a novel stimulus on the remaining trials (nonmatch 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 intertrial interval was 2000 msec. Half the trials required working memory for faces and the other half required working memory for shoes.

Subjects were instructed to keep their gaze focused on a fixation cross at the center of the screen but to ignore any items appearing during the delay period. On all trials, two task-irrelevant distractors were presented sequentially during the delay period. Distractors were either faces, shoes, or one of eight random patterns (noise masks), and were presented centrally for 750 msec. Each distractor stimulus was presented centrally and was surrounded by four gray rectangles. The gray rectangles served to differentiate distractors from S1 and S2 stimuli,

Figure 1. Experimental paradigm and main behavioral result. (A) Subjects were instructed to encode the memory item (S1), ignore the distractors (D1 and D2), and determine whether the test item (S2) was identical to S1. Presented here is a trial with face distractors and congruent (face) working memory. The task-irrelevant distractors, S1, and S2 stimuli were distinguished by surrounding them with different rectangles (gray for distractors and checkered for S1 and S2

stimuli). All stimuli were presented for 750 msec and interstimuli intervals were jittered from 600 to 1400 msec. Intertrial interval was 2000 msec. (B) Response time (RT) was impaired when working memory domain was congruent with distractor type (p = .02). This congruency effect was present for both trials with face distractors and trials with shoe distractors, although the difference was only significant for trials with face distractors (p = .05).
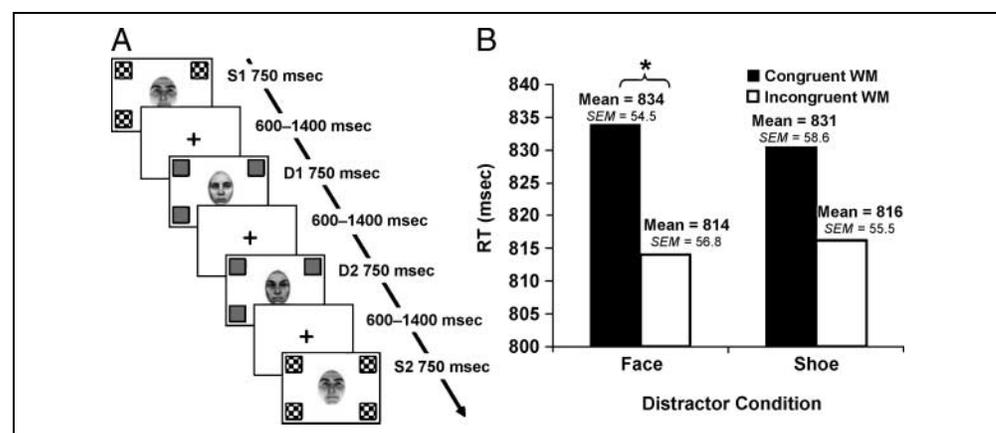
which were surrounded by rectangles with a checker-board pattern (see Figure 1A); there was therefore no ambiguity in determining which stimuli were task irrelevant. Both distractors presented during a single trial were always from the same stimulus category (e.g., two faces, or two shoes, or two masks). The interstimulus interval between all sequentially presented stimuli was jittered from 600 to 1400 msec (mean = 1000 msec). With the exception of the S2 match stimuli and the mask stimuli, no stimuli were repeated across trials. Because the question of interest for this study concerns face and shoe distractors, the mask items, which served as control stimuli for a second study (Lustig, Sreenivasan, & Jha, 2006; Sreenivasan & Jha, 2006), were excluded from all analyses, and the results from mask items will not be discussed here.

Thus, there were four main trial types: trials with face distractors congruent with the working memory domain (face working memory); trials with face distractors incongruent with the working memory domain (shoe working memory); trials with shoe distractors congruent with the working memory domain (shoe working memory); and trials with shoe distractors incongruent with the working memory domain (face working memory). All trial types occurred equiprobably and were randomly presented. Each trial type was presented 44 times over six experimental runs.

ERP Acquisition and Analysis

Electroencephalographic (EEG) activity was recorded with Ag–AgCl electrodes distributed over 64 scalp locations. 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 place 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, Distractors 1 and 2, S2) and trial type (congruent face distractor, incongruent face distractor, congruent shoe distractor, and incongruent shoe distractor). EEG and EOG were epoch-averaged to 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). Additionally, epochs containing eye movement artifact larger than 50 μV or incorrect responses were excluded from averaging. Averages were filtered using a band pass from 1 to 8 Hz (12 dB/octave).[2] The rejection rate for trials due to eye movement was about 15%. Subjects with greater than 30% of

epochs rejected due to eye movement were removed from all ERP analyses, leaving 15 subjects (four women) with useable data. The remaining subjects had an average of 66 (*SD* = 9.5) trials contributing to each average of interest (e.g., congruent face distractor).

For all comparisons, the peak latency and amplitude values were entered into separate repeated-measures analysis of variance (ANOVA) tests. In addition, planned comparisons (two-tailed paired *t* tests) were performed in a hypothesis-driven manner. Corrections for multiple comparisons were made where appropriate.

Behavioral Analysis

Behavioral results were obtained from all subjects. Response times (RTs) and accuracy (percent correct) were entered into separate repeated-measures ANOVA tests to determine the influence of distractor type (face distractor or shoe distractors) and congruency (congruent distraction or incongruent distraction). In addition, planned comparisons (two-tailed paired *t* tests) were performed for RT and accuracy in a hypothesis-driven manner. Corrections for multiple comparisons were made where appropriate.

RESULTS

Behavioral Results

Separate two-way ANOVAs were conducted for task RT and accuracy to investigate performance differences as a function of distractor domain (face vs. shoe) and congruency (congruent vs. incongruent). Similar to previous studies (Jha et al., 2004), we observed significantly slower RTs for congruent relative to incongruent trials [main effect of congruency: $F(1,21) = 6.71, p = .02$]. RTs were slower for congruent relative to incongruent trials for trials with face distractors and trials with shoe distractors. However, planned comparisons for each distractor type revealed that only trials with face distractors significantly differ as a function of congruency [$t(1,21) = 2.07, p = .05$]. This result is depicted in Figure 1B. RTs did not differ significantly as a function of distractor domain [$F(1,21) = 0.01, p > .9$], nor was there a significant interaction of distractor domain and congruency [$F(1,21) = 0.09, p > .7$].

The ANOVA for accuracy yielded no significant main effect of distractor domain [$F(1,21) = 2.39, p > .1$] and no significant main effect of congruency [$F(1,21) = 0.84, p > .3$], although a planned comparison of congruent and incongruent trials with face distractors (but not shoe distractors) indicated a near-significant trend of increased accuracy for incongruent relative to congruent trials [$t(1,21) = 1.95, p = .06$]. There was also a near-significant interaction of distractor domain and congruency [$F(1,21) = 3.64, p = .07$]. The similarity in accuracy across conditions may be due to the overall high accuracy

observed during this task (mean = 92.4% correct), suggesting that task accuracy may have been at ceiling.

ERP Results

A focal negative potential was observed in the right lateral parieto-occipital electrodes approximately 172–216 msec following stimulus onset. Based on latency and topographic distribution, this component was identified as the N170 (Bentin et al., 1996). For further analyses of the N170, the electrode that evidenced the greatest N170 amplitude, PO8, was selected for each subject, although similar results were found in neighboring electrodes PO6 and P6. In all statistical analyses, N170 amplitude was defined as the average amplitude over the range from 172 to 216 msec, which is the time range of the average peak N170 latency across subjects ±2 standard deviations.[3]

The N170 was observed to both face and shoe stimuli regardless of stimulus type (S1, distractor, S2). In accordance with numerous previous studies showing larger amplitude N170 to faces relative to other stimuli (e.g., Bentin et al., 1996), the N170 elicited by face stimuli was greater in amplitude than the N170 elicited by shoe stimuli $[t(1,14) = 2.27, p = .04]$. An analysis of peak latency indicated that the N170 to faces occurred significantly earlier than the N170 to shoes $[t(1,74) = 5.10, p < .001]$. Further statistical analyses were performed separately for each stimulus type and are discussed below.
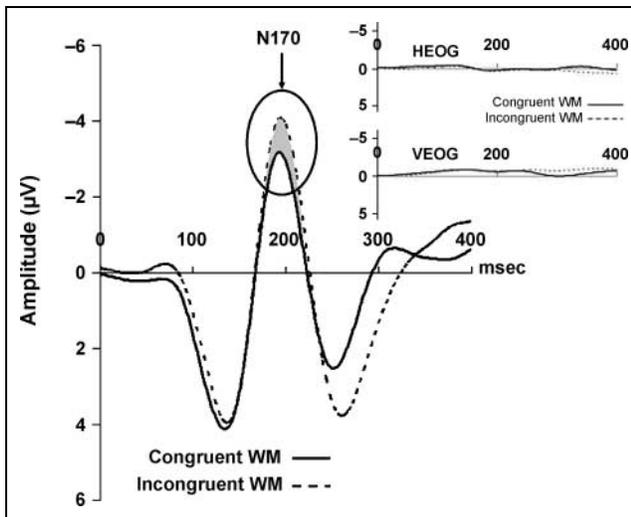
Distractors

To ensure that any effects of distractor domain and congruency were not driven by subject strategies that involved moving the eyes away from the distractor stimuli to aid working memory performance, we examined the eye movement channels during presentation of the distractor stimuli. Analysis of eye movement channels indicated that EOG activity was negligible and did not differ over any distractor or congruency conditions. EOG channels for face distractors during congruent and incongruent trials are shown in the insets in Figure 3. This result is not surprising because trials with eye movement artifact following eye movement reduction were rejected during ERP data processing.

A three-factor ANOVA was conducted to examine the effect of distractor domain (face vs. shoe), congruency (congruent vs. incongruent), and distractor number (first distractor vs. second distractor) on the amplitude of the N170 component. The N170 amplitude elicited by face distractors was significantly larger than the N170 amplitude elicited by shoe distractors [main effect of distractor domain: $F(1,14) = 6.15, p = .03$]. This result is shown is Figure 2. We also observed a significant main effect of congruency, with reduced N170 amplitude to distractors that were congruent versus incongruent with
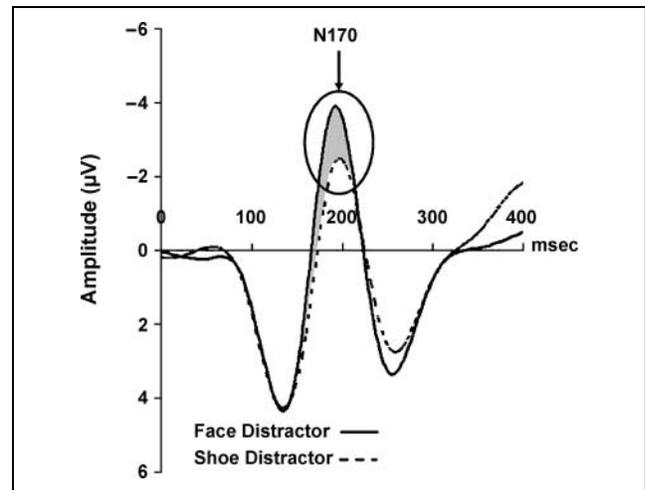
Figure 2. Grand-average ERP waveform elicited by distractor stimuli. N170 amplitude to face distractors (solid line) was significantly larger than the N170 to shoe distractors (dotted line; $p = .03$). Mean amplitude (face = −2.784 μV, SEM = 0.675; shoe = −1.583 μV, SEM = 0.741) was calculated over the window from 172 to 216 msec (average peak latency for N170 ± 2 SD). Electrode PO8 is depicted in this figure, although results are similar for neighboring electrodes PO6 and P8.

the working memory domain $[F(1,14) = 9.79, p = .007]$. Examination of the planned comparison of congruency for face distractors alone yielded a highly significant result (Figure 3), with the N170 to congruent face distractors significantly reduced relative to incongruent face distractors $[t(1,14) = 3.38, p = .004]$. The planned comparison of congruency for shoe distractors alone yielded a similar pattern of reduced N170 to congruent relative to incongruent distractors, but this result was not significant $[t(1,14) = 1.02, p > .3]$. There was no significant effect of distractor number (first vs. second) $[F(1,14) = 1.02, p > .3]$. Planned comparisons of distractor number for congruent face and shoe distractors were performed to examine the possibility that the decreased N170 amplitude to congruent distractors was due merely to a habituation effect (Woods & Elmasian, 1986). If habituation to a series of consecutive faces or shoes in congruent trials accounted for the decreased N170 to congruent distractors, we would expect to see that the N170 to the second congruent distractor (D2) is reduced relative to the first congruent distractor (D1). A paired t test comparing the N170 to the first and second congruent distractors indicated that the N170 to congruent distractors did not differ significantly as a result of distractor number [average D1 = −1.63 μV, average D2 = −2.16 μV; $t(1,14) = 1.18, p > .2$]. Examined individually, neither congruent face (average D1 = −2.02 μV, average D2 = −2.74 μV; $t(1,14) = 1.51, p > .1$) nor shoe (average D1 = −1.23 μV, average D2 = −1.58 μV; $t(1,14) = 0.55, p > .5$) distractors differed significantly in N170 amplitude between the first and second distractor. Two-way interactions of distractor domain and

Figure 3. Grand-average ERP waveform elicited by face distractor stimuli. N170 amplitude to face distractors was significantly reduced during congruent (face) working memory (solid line) relative to incongruent (shoe) working memory (dotted line; $p = .004$). Mean amplitude (congruent = -2.383 μV, *SEM* = 0.636; incongruent = -3.184 μV, *SEM* = 0.732) was calculated over the window from 172 to 216 msec (average peak latency for N170 ± 2 *SD*). Electrode PO8 is depicted in this figure, although results are similar for neighboring electrodes PO6 and P8. Horizontal (HEOG) and vertical (VEOG) electrooculogram activity is shown in the inset, demonstrating that eye movements were negligible and did not differ across conditions.

congruency, distractor domain and distractor number, and congruency and distractor number were all nonsignificant. There was a significant three-way interaction of distractor domain, congruency, and distractor number [$F(1,14) = 8.54$, $p = .01$].

A separate two-factor (distractor domain, congruency) ANOVA was conducted for peak distractor N170 latency. The peak N170 latency was significantly earlier for face distractors relative to shoe distractors (main effect of distractor domain; [$F(1,14) = 8.74$, $p = .01$]). There was no main effect of congruency [$F(1,14) = 0.00$, $p > .9$] and no significant interaction between distractor domain and congruency [$F(1,14) = 1.86$, $p > .2$].

S1 and S2

Although our predictions concerned the N170 to distractor stimuli, we describe the results for the N170 to S1 and S2 stimuli here for completeness. For the S1 stimuli, a pattern of significantly earlier N170 to faces relative to shoes was observed [$t(1,14) = 4.89$, $p < .001$]. N170 amplitude was greater to S1 faces relative to S1 shoes, although this difference did not reach significance for the S1 stimuli alone [$t(1,14) = 1.28$, $p > .2$].

Analysis of the N170 amplitude to S2 stimuli was conducted using a two-factor ANOVA, where the factors were S2 working memory domain (face vs. shoe) and congruency of preceding distractors (congruent vs. in-

congruent). S2 faces showed a nonsignificant trend of greater N170 amplitude relative to S2 shoes [$F(1,14) = 2.51$, $p > .1$]. Next, we examined whether S2 amplitude varied as a function of congruency with the distractor. Although there was an increased N170 to S2 stimuli preceded by incongruent distractors, the effect was nonsignificant [$F(1,14) = 1.66$, $p > .2$]. There was no significant interaction between working memory domain and congruency [$F(1,14) = .01$, $p > .9$].

S2 latency was analyzed separately using a two-factor ANOVA (S2 working memory domain and congruency). There was a near-significant trend of earlier S2 N170 to faces relative to shoes [$F(1,14) = 4.35$, $p = .06$]. There was no effect of congruency on N170 latency, nor was there a significant interaction between working memory domain and congruency.

Summary

As reviewed herein, N170 to faces and shoes differed significantly in both latency and amplitude, with increased amplitude and earlier latency N170 for faces vs. shoes. The N170 amplitude was significantly greater for face vs. shoe distractor stimuli, and there was a trend for increased amplitude for face relative to shoe N170 for S1 and S2 stimuli. These domain-sensitive N170 results are consistent with several previous studies (Itier & Taylor, 2004a; Bentin et al., 1996). Importantly, N170 amplitude to distractors differed as a function of the congruency of the distractor with the working memory domain. This effect was most striking for face distractors, where N170 amplitude was significantly reduced when the face distractor was in the context of congruent relative to incongruent working memory. Subsequently, we discuss possible processes reflected by the N170 modulation observed to face distractors.

DISCUSSION

In the present study, we investigated the hypothesis that selective attention may bias distractor processing in support of working memory maintenance. We hypothesized that similar to studies of distraction in the context of perceptual tasks (see Lavie, 2005), selective attention would be recruited to bias sensory processing against distractors during working memory maintenance. Specifically, we predicted that stimulus-evoked perceptual activity to task-irrelevant face distractors would be attenuated when the distractors were behaviorally intrusive to working memory performance. Behavioral intrusiveness of face distractors was manipulated by placing them in a congruent working memory context, when subjects were maintaining a face, or placing the face distractors in an incongruent working memory context, when subjects were maintaining a shoe. It has been demonstrated in similar studies (e.g., Jha et al., 2004) that congruent

distractors are more behaviorally intrusive than incongruent distractors. Indeed, response times measured in the present study indicate that behavioral performance suffered when the face distractors were in a congruent relative to incongruent task context.

Importantly, ERPs time-locked to face distractor onset demonstrated reduced amplitude N170 to face distractors in a congruent relative to incongruent working memory context. Because the N170 is a marker for early perceptual processing of faces (Itier & Taylor, 2004a; Bentin et al., 1996), we believe these results indicate attentional biasing against sensory processing of face distractors in conditions of high versus low behavioral intrusiveness. This effect may be akin to early selection operating to suppress distractor processing under conditions of high versus low perceptual load in perceptual tasks (Lavie, 2005).

Two alternative accounts for the observed attenuation in N170 to congruent relative to incongruent face distractors are that: (1) subjects looked away during congruent face distraction to avoid being distracted, resulting in reduced amplitude N170 to congruent face distractors; or (2) increased exposure to faces during congruent face distractor trials (which consist of a series of consecutive faces) relative to incongruent face distractor trials (which consist of only two consecutive faces) led to a habituation to faces and a reduced amplitude N170 to congruent face distractors. We addressed the eye movement account of these results in three ways. First, subjects were instructed to focus on the fixation cross in the center of the display for the duration of the experiment and were told not to move their eyes. Second, the eye movement reduction algorithm and artifact rejection stages of processing were designed to remove any eye movements, and subjects with excessive eye movements were excluded from all analyses. Finally, examination of EOG channels during presentation of face distractors indicates negligible eye movement, with virtually no difference in EOG activity for congruent and incongruent conditions. In addition, the P1 component, which is a component sensitive to eye position and spatial attention (Hillyard & Anllo-Vento, 1998), did not differ as a function of congruency, suggesting that there were no notable differences in spatial processing across conditions. It is therefore unlikely that subjects' strategies involving eye movements contributed to the observed results.

Short-term habituation is another possible alternative explanation for the observed results and must therefore be addressed. By this account, the N170 to face distractors may be reduced during face versus shoe working memory because face processing perceptual regions may habituate during repeated exposure to faces (S1, D1, D2). Although evidence exists for short-term habituation of early ERP components (Woods & Elmasian, 1986), recent studies suggest that the N170 may not be susceptible to habituation (Puce, Allison, & McCarthy, 1999). We addressed the habituation account by comparing the first (D1) and second (D2) congruent face distractors to see whether the N170 was reduced in amplitude to D2 relative to D1, as would be predicted by the habituation account. N170 amplitude did not differ significantly to the two congruent face distractors, suggesting that habituation cannot account for the observed results.

In addition to the N170 elicited by faces, robust N170 was also elicited by shoe stimuli. Although the N170 to faces was greater in amplitude relative to the N170 to shoes (collapsed across S1, distractor, and S2 stimuli), the N170 to faces was not significantly greater than to shoes for S1 or S2 stimuli. The N170 elicited by shoe distractors demonstrated a pattern of amplitude modulation similar to face distractors, although the congruency effect for shoe distractors was not significant. Although these results were not predicted, they were not unexpected; robust N170s have been observed in objects in several object categories, including shoes (e.g., Rossion et al., 2000), and an entire line of debate has arisen over whether the N170 reflects face-specific processing (Itier, Latinus, & Taylor, 2006; Itier & Taylor, 2004a; Eimer, 2000b; Bentin et al., 1996) or another more general process, such as processing of objects with which the observer has a certain level of expertise (Rossion, Kung, & Tarr, 2004; Gauthier, Curran, Curby, & Collins, 2003; Rossion, Gauthier, Goffaux, Tarr, & Crommelinck, 2002; Tanaka & Curran, 2001; Gauthier, Skudlarski, Gore, & Anderson, 2000; Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999). Nonetheless, it is beyond the scope of the present study to contribute to this debate, and several studies have positively demonstrated that the N170 reflects some aspect of the processing of faces and can be used as an index of early face processing (Itier & Taylor, 2004a).

In addition to N170 amplitude, N170 latency was assessed for all conditions. In accordance with previous findings (Itier & Taylor, 2004a), the N170 was significantly earlier for faces relative to shoes. This effect was robust for S1 and distractor stimuli, and near-significant for S2 stimuli ($p = .06$). We also examined latencies of the N170 elicited by distractor and S2 stimuli as a function of congruency, and found no compelling evidence that N170 latency varied across conditions. This result is inconsistent with a recent ERP study by Gazzaley et al. (2005), in which they report significant N170 latency shifts for ignored versus remembered faces.

Beyond demonstrating attenuated distractor processing as a result of working memory congruency, we sought to examine the functional significance of such attenuation by exploring differences in the suppression of distractor processing as a function of performance. Delay-period activity in prefrontal areas has previously been shown to be present during successful working memory performance, and weak or absent during incorrect working memory performance (Sakai et al., 2002). In an fMRI experiment with a paradigm almost identical

to the one in the present study, Jha et al. (2004) report that delay-period PFC activity was greater during congruent than incongruent distraction, and this congruency effect was only present for correct trials. Additionally, differential activation in the FFA for congruent relative to incongruent face distractors was found only for correct trials. One interpretation of these results is that selection failures instantiated in prefrontal and posterior activity may result in degraded working memory performance. Such an interpretation might predict that N170 amplitude to congruent face distractors observed in the present study would be more attenuated for correct relative to incorrect trials. It is important to note that although both activity in the FFA and the N170 component have been associated with face processing, the generator of the N170 is not thought to be limited to areas of the fusiform gyrus (Itier & Taylor, 2004b; Allison, Puce, Spencer, & McCarthy, 1999). We were unable to investigate this prediction in the present study due to insufficient incorrect trials (mean accuracy was 92.4%). We therefore chose an alternate means of investigating the functional significance of distractor attenuation for working memory performance. We compared the N170 to congruent face distractors in subjects with higher ($n = 7$, mean accuracy = 0.96, $SD = 0.01$) versus lower overall task accuracy ($n = 7$, mean accuracy = 0.89, $SD = 0.03$), and predicted that task success would correspond to an increased ability to attenuate face distractor processing during working memory for faces. This analysis found a near-significant trend for decreased N170 to congruent face distractors in subjects with high relative to low performance ($p = .09$). When congruent face distractors were examined separately for the first (D1) and second (D2) distractors, N170 amplitude was significantly reduced for higher relative to lower performers for D1 ($p = .03$), but not for D2. One explanation is that subjects who were able to use selective mechanisms to suppress processing of the first face distractor by attentionally biasing against face processing prior to distractor onset may have been able to subsequently prevent all distractor processing. These results are echoed by a study by Vogel et al. (2005) that suggests that abilities in selection at the level of working memory encoding may differentiate high- from low-span subjects. Although the current results are provocative, further work is necessary to elucidate the role that sensory biasing via selective attention may play in successful working memory maintenance.

Contrary to the present results, in which modulations in the N170 were observed, it has been suggested that the N170—unlike other early perceptual ERP components—is not modulated as a function of selective attention (Cauquil, Edmonds, & Taylor, 2000). It is important to keep in mind that the perceptual load in the task employed by Cauquil and colleagues was low, and early selection mechanisms may not have been invoked in this task context. Indeed, in tasks that had

a higher perceptual load, N170 amplitude was shown to be modulated by attention (Holmes, Vuilleumier, & Eimer, 2003; Eimer, 2000a). The present study suggests a correspondence between attention's role in perception and working memory maintenance. The prevailing account of perceptual studies of distractor processing is that distractor processing can be attenuated under conditions of high perceptual load, as long as there is limited loading of the cognitive control system (Lavie, Hirst, de Fockert, & Viding, 2004). Perceptual load in the present study is high because a high degree of discriminability is required to correctly identify S2 as being the same or different as S1, and cognitive load, operationalized as working memory demands, is low because only one item is to be remembered (Jha & McCarthy, 2000).

Lavie, Ro, and Russell (2003) have suggested that when the distracting items are faces, selection against distractor processing may not occur even under conditions of high perceptual load. They suggest that processing of faces may be mandatory and may not be modulated. The results of the present study are inconsistent with these findings. The perceptual processing of distracting faces was attenuated when the working memory items were congruent versus incongruent, suggesting that face processing can be modulated. Further, our results suggest that, similar to modulations with perceptual load, the degree of behavioral intrusiveness of distracting stimuli may be an important factor in determining how selection mechanisms bias distractor processing.

Most previous studies investigating distraction have not clearly delineated the stimulus features that constitute distractors. Stimuli have been labeled as distractors when they are from the same domain as the task-relevant items (e.g., Postle, 2005; Jha et al., 2004; Chao & Knight, 1998; Lavie, 1995), from a different domain as task-relevant items (e.g., Gazzaley et al., 2005), or are part of an entirely different task (e.g., Sakai et al., 2002; de Fockert, Rees, Frith, & Lavie, 2001). In the present study, faces presented during the delay were always task-irrelevant and potentially distracting, but the neural fate of these distractors changed as a function of their behavioral intrusiveness. These results caution against oversimplification of what constitutes "distracting" stimuli. In sum, the results presented here provide evidence for selective mechanisms that bias processing against the perceptual processing of behaviorally intrusive distractors, and suggest that such a mechanism may be important for working memory maintenance.

Acknowledgments

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Notes

1. Faces were created in part from a face database provided by the Max-Planck Institute for Biological Cybernetics in Tuebingen, Germany (Troje & Bulthoff, 1996).
2. Reanalysis using the following parameters—a band-pass filter from 0.5 to 20 Hz (24 dB/octave) and re-referencing off-line to an average of the scalp electrodes (Joyce & Rossion, 2005)—yielded similar results.
3. Statistical analyses performed using the peak amplitude yielded similar results.

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