Working memory load for faces modulates P300, N170, and N250r

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Abstract

We used event-related potential (ERP) methodology to examine neural activity associated with visual working memory (WM) for faces. There were two main goals. First, to extend previous findings of P300 load modulation to WM for faces. Second, to examine whether N170 and N250r are also influenced by WM load. Between one and four unfamiliar faces were simultaneously presented for memory encoding. After a one second delay, a target face appeared, and participants had to judge whether this face was part of the previous face array. P300 amplitude decreased as WM load increased, and this P300 suppression was observed at both encoding and retrieval. WM load was also found to modulate other ERPs. The amplitude of the N170 elicited by the target face decreased with load, and this N170 decrease levelled off at load two, reflecting the behavioural WM capacity of around two faces. In addition, the N250r, observed as an ERP difference for target faces that were present in the encoding array relative to target faces that were absent, was also reduced for higher WM loads. These findings extend previous work by showing that P300 modulation by WM load also occurs for faces. Furthermore, we show, for the first time, that WM load affects the N250r and the early visual N170 component. This suggests that higher visual areas play an important role in WM for faces.

Introduction

Working memory (WM) refers to the system of temporary memory stores and control processes that facilitate the maintenance and manipulation of information that is no longer physically available (Baddeley, 1992). The focus of the current study is on the maintenance component of WM. WM can be divided into separate verbal and visual subsystems (see Logie, 1995), each of which has a severely limited storage capacity. The limits of WM capacity can be determined by varying WM load; that is, the number of items which must be simultaneously maintained in WM. In the visual domain, WM capacity is limited to around four objects (Cowan, 2001; Luck & Vogel, 1997; Vogel, Woodman, & Luck, 2001).

However, it appears that the capacity of visual WM may also depend on the nature of the stored objects. For example, studies of change detection have shown that WM capacity is higher for simple objects, such as coloured squares and letters, compared to more visually complex objects, such as shaded cubes and faces (Alvarez & Cavanagh, 2004; Eng, Chen, & Jiang, 2005), suggesting that visual WM capacity is influenced by the complexity of objects. Other work has shown that WM capacity is reduced when the stimuli in the task belong to the same object category compared to when different categories of object are used (Olsson & Poom, 2005).

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Recent work suggests that visual WM capacity may also depend on the nature of object perception processes. In particular, upright faces are processed more configurally than inverted faces or other objects (e.g. Maurer, Le Grand, & Mondloch, 2002). Curby and Gauthier (2007) suggested that this configural face processing allows more faces to be stored in WM than other objects of similar visual complexity. In support of this idea, they found that visual WM capacity was larger for upright faces compared to inverted faces, while perceptual limitations were controlled for by providing sufficient time for encoding[1]. Furthermore, the detrimental effect of inversion on WM capacity was significantly larger for faces compared to cars. At a long encoding duration, capacity for upright faces was greater than for upright cars, whereas there was no difference in capacity for inverted faces and cars. It appears that visual WM has a close relation to the perceptual processes engaged when seeing visual objects.

Event-related potentials (ERPs) provide a powerful means for examining the neural mechanisms underlying WM for faces. ERP studies have shown that the P3b subcomponent of the P300 is strongly associated with memory processes. For example, Fabiani, Karis, & Donchin (1986) found that the P3b elicited by stimuli in an incidental memory paradigm was larger for stimuli that were subsequently recalled compared to stimuli that were not recalled. They suggested that the P3b reflects a "context-updating" process (Donchin, 1981), in which WM representations are updated or reorganised to accommodate incoming information. An alternative interpretation of P3b suggested that it may reflect 'closure' of perceptual events (e.g. Verleger, 1988).

P3b amplitude appears to be sensitive to the allocation of processing resources (see Kok, 2001). For example, in dual task studies, increases in the difficulty (and hence resource requirements) of the primary task were found to be associated with increased amplitude of the P3b for stimuli in the primary task and reduced amplitude of the P3b elicited by events in the secondary task (e.g. Sirevaag, Kramer, Coles, & Donchin, 1989). Of most relevance here, a considerable amount of research has shown that P3b amplitude decreases as WM load increases (see Kok, 2001). For example, McEvoy, Smith, and Gevins (1998) found that, when participants had to indicate whether or not a target stimulus matched a stimulus presented either 1, 2, or 3 (WM loads 1-3) trials previously, the amplitude of the P3b elicited by the target stimulus was reduced with increasing WM load. They proposed that as WM load increases, more processing resources are allocated to WM maintenance processes so that fewer resources are available for stimulus evaluation, resulting in attenuation of the P3b at higher WM loads.

Recent work suggests that the P3b may consist of different subcomponents reflecting functionally and anatomically distinct neural processes (see Linden, 2005). When participants had to perform a simple oddball task, the P3b to the oddball consisted of only one peak, which fMRI-based source analysis localised to generators in inferior temporal cortex (IT), inferior parietal lobe, and posterior parietal cortex (PPC) (Bledowski et al., 2004). Subsequent work (Bledowski et al., 2006) examined fMRI and ERP measures of neural activity during a delayed recognition task, in which either one or three novel objects were sequentially presented for memory encoding, then after a delay of several seconds, a test stimulus requiring a match/mismatch response appeared. When this more complex task was used, the P3b elicited by the test stimulus was divided into two peaks with different neural generators. The early P3b subcomponent (366 ms) was generated in IT, left temporoparietal junction, and PPC, similar to the single P3b peak found in the simple oddball task (Bledowski et al., 2004), whereas the later subcomponent (585 ms) was generated mainly in PPC and ventrolateral prefrontal cortex (VLPFC). Sustained PPC

[1]Note that WM capacity for faces was still very limited (between 1.5 and 3 faces).

activity over the time range of both P3b subcomponents was assumed to indicate a crucial role for this region in memory storage operations that are required for stimulus evaluation. Of most interest, the second subcomponent of the P3b was influenced by WM load, with reduced amplitude for a WM load of three objects compared to a WM load of one object. Bledowski et al. (2006) proposed that the early P3b subcomponent is related to stimulus evaluation processes, whereas the later subcomponent reflects memory search processes in the VLPFC which access a posterior parietal storage buffer. They suggested that this VLPFC memory search process is only necessary in complex WM tasks, whereas stimulus evaluation in posterior parietal areas is sufficient for more simple tasks.

If WM capacity is influenced by the processes underlying object perception, it is possible that neural effects of WM load may also be observed at earlier stages of processing. As already noted, behavioural studies have shown that WM capacity for faces depends on the nature of face perception mechanisms. Other work suggests that storage of visual information in WM involves the cortical areas involved in processing visual signals (see Pasternak & Greenlee, 2005). Of particular interest, recent work found that fusiform gyrus activity produced by a to-be-remembered face was maintained across three separate delay intervals and intervening faces, suggesting that this region is necessary for the storage of faces in WM (Postle, Druzgal, & D'Esposito, 2003). Indeed, another study found that activity in the fusiform face area (FFA) increased linearly with WM load during an encoding period in which between 1 and 4 faces were simultaneously presented, and also during a delay period in which the encoded faces had to be maintained (Druzgal & D'Esposito, 2003). These findings suggest that higher visual areas play an important role in WM processes.

Therefore, WM load might affect face-sensitive ERP components. ERP studies have shown that face perception elicits a large negative deflection over bilateral occipito-temporal scalp regions, peaking around 170ms after face onset (e.g. Bentin, Allison, Puce, Perez, et al., 1996). This N170 is often larger for faces than for other types of visual stimuli (e.g. Bentin et al., 1996; Carmel & Bentin, 2002), and is thought to index an early perceptual stage of face processing, such as processing of relational configuration. For example, the N170 is sensitive to the removal of features from a face (e.g. Eimer, 2000b), and is typically delayed and enhanced for inverted faces relative to upright faces (e.g. Bentin et al., 1996; Itier & Taylor, 2002, 2004; Latinus & Taylor, 2006; Rossion et al., 2000), which is assumed to reflect disruption of configural processing.

ERP source analyses have shown that the N170 for faces originates in occipito-temporal cortex (e.g. Latinus & Taylor, 2006; Schweinberger, Pickering, Jentzsch, Burton, & Kaufmann, 2002b), and combined fMRI and ERP recordings have shown significant correlations between N170 amplitude and the BOLD signal in bilateral fusiform gyrus, suggesting that activity in this region contributes to N170 (Horovitz, Rossion, Skudlarski, & Gore, 2004; Iidaka, Matsumoto, Haneda, Okada, & Sadato, 2006). Interestingly, similar to N170, fMRI activity in fusiform gyrus has also been found to be sensitive to face inversion (Yovel & Kanwisher, 2005) and face configuration (Schiltz & Rossion, 2006). WM for faces appears to involve face-specific visual processes, such as configural processing (Curby & Gauthier, 2007), and FFA activity can be modulated by WM load for faces (Druzgal & D'Esposito, 2003). Taken together, these findings suggest the possibility that the N170 may also be influenced by WM load.

Indeed, there is considerable evidence to suggest that the N170 is sensitive to top down factors. For example, the N170 elicited by two shapes was larger in amplitude if the shapes were previously seen as the eyes in a schematic face compared to when there was no perceptual context associated with the shapes (Bentin, Sagiv, Mecklinger, Friederici, & von Cramon, 2002). Similarly, other work has shown that N170 amplitude can be modulated by

emotional affect associated with faces (Pizzagalli et al., 2002) and memory retrieval of emotional context (Galli, Feurra, & Viggiano, 2006). The N170 may also be influenced by attention in some circumstances, with larger amplitude for attended faces than for unattended faces (Eimer, 2000a; Holmes, Vuilleumier, & Eimer, 2003; but see Lueschow et al., 2004). These top-down influences on N170 amplitude are consistent with the idea that the N170 may be modulated by WM load.

Another ERP of interest is the N250r or early repetition effect. The N250r for faces is a relative negativity over temporal sites and relative positivity over frontal sites for repeated compared to new faces (Pfütze, Sommer, & Schweinberger, 2002; Schweinberger, Pfütze, & Sommer, 1995). This N250r is usually thought to reflect facilitated processing for repeated faces at the level of long-term memory representations of familiar faces (for reviews see Boehm & Paller, 2006; Schweinberger & Burton, 2003), so-called face recognition units (FRUs; Bruce and Young, 1986). The relation of the N250r to activity at the level of FRUs is suggested by at least two groups of findings. Firstly, for unfamiliar faces, which do not have FRUs, the N250r is much reduced or even absent (Pfuetze et al., 2002, Schweinberger et al. 1995). Secondly, the scalp topographies of the N250r are different for faces compared to items from other visual domains which contain representations similar to FRUs, such as words (Boehm, Sommer, & Lueschow, 2005; Pfuetze et al., 2002). Such differences are usually considered to indicate the involvement of different neurocognitive processes, and one can thus infer the domain-specificity of the underlying representations.

Source analysis suggests that the N250r for faces may originate from the fusiform gyrus (Schweinberger et al., 2002b). This corresponds to fMRI work showing that face repetition modulates activity in FFA (e.g. Gauthier et al., 2000). The N250r survives only a few intervening items and is not observed for longer lags (Schweinberger, Pickering, Burton, & Kaufmann, 2002a; but see Graham & Dawson, 2005). This suggests that the N250r may be related to WM processes, such as the maintenance of face representations in WM, and that it may be sensitive to WM load.

The present study had two main goals. First, to extend previous findings of P3b load modulation to WM load for faces. Second, to examine whether the face-related N170 and N250r are influenced by WM load. Previous work has found WM load modulations of P3b in a memory search paradigm using sequential presentation at encoding, but this study did not examine effects of WM load on N170 and N250r (Schweinberger & Sommer, 1991). The current study used a delayed-recognition task, which allowed the separate ERP investigation of the encoding and retrieval phases. As already noted, the focus of the current study is WM maintenance. Unlike n-back tasks or tasks using sequential presentation at encoding, the use of a delayed-recognition task enabled the examination of WM maintenance in the absence of executive processes such as WM updating. Between one and four faces (WM loads 1-4) were simultaneously presented for memory encoding. Then, after a short delay, a test face appeared and participants had to indicate whether this face matched one of the faces in the previous encoding display. A small stimulus set was used and faces repeated multiple times to control for co-occurring episodic memory and priming processes[2].

Based on the results of previous work (Bledowski et al., 2006), the P3b elicited by the test face was expected to contain two subcomponents, and it was predicted that the amplitude of the second P3b peak would decrease with increasing WM load. Similarly, recent work has shown that the reduction in P3b amplitude for increasing WM loads occurs during memory

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[2]Note that, because faces were identical at study and test, it is possible that this task could be performed using picture, rather than face, recognition.

encoding of simultaneously presented items as well as during memory retrieval (Busch & Herrmann, 2003). However, that study measured the mean amplitude over the entire time window of the P3b and did not distinguish between the two P3b subcomponents. Therefore, it is not clear which P3b subcomponent is affected by WM load during encoding. If the late P3b peak reflects memory search operations in the VLPFC, as suggested by Bledowski et al. (2006), then it may not be influenced by WM load because memory search processes are not engaged at encoding. Alternatively, other VLPFC-mediated cognitive processes may be required for memory encoding, leading to load-related modulation of the late P3b subcomponent during encoding.

It was expected that the N170 would be modulated by WM load at encoding because of differences in the number of faces present in the display. However, in the retrieval phase only a single face was presented for all load conditions. Therefore, an effect of WM load on the N170 at retrieval would indicate the influence of top down WM processes. It is not known whether the N250r is influenced by WM load. However, if the N250r reflects WM processes related to temporary activation of face recognition units, then the N250r elicited by the test face may be modulated by WM load.

Method

Participants

19 students (10 males, 9 females) from the University of Wales, Bangor participated in the experiment in return for course credits or money. Participants were aged between 19 and 28 (mean age 20) and had normal or corrected-to-normal vision. All participants reported normal neurological and psychiatric health.

Stimuli and Procedure

Stimuli were presented on a 19 inch TFT monitor using E-Prime software running on a PC. Responses were registered using keys 'A' and 'L' on a standard computer keyboard. Stimuli appeared on a white background. There were 6 male faces, each of which subtended a visual angle of 3° vertically by 2.5° horizontally. The faces were black and white face photographs drawn from the neutral face set in the Ekman and Friesen (1976) series. Each face had a neutral expression and was seen in a frontal view with the eyes looking directly ahead. The encoding display consisted of four stimuli presented around a central black fixation cross (0.2°), with the centre of each stimulus 2° away from the fixation cross. Between one and four (WM loads 1-4) of these stimuli were photographs of faces, and the remaining stimuli were scrambled face photographs. The locations of the faces in the encoding display were randomised. The retrieval display consisted of one face presented in the centre of the screen. The face in the retrieval display either matched one of the faces in the encoding display (50% of trials) or did not match any of the faces in the encoding display (50% of trials).

The sequence of events in a trial was as follows. The central fixation cross turned red for two seconds to indicate the start of the trial. Then the encoding display was presented for 2 seconds and participants had to memorise the faces while fixating on the central cross (participants reported no difficulty maintaining fixation during encoding and no signs of eye movements during encoding were detected in the EOG). This was followed by a 1 second delay, during which participants had to maintain fixation on the cross. Then a test face appeared for 2 seconds and participants had to make a 'yes' or 'no' response, based on whether or not the test face matched one of the faces in the encoding array. Participants had 2 seconds from the onset of the test face to make a response. The intertrial interval was between 3 and 6 seconds (average 4.5 seconds). Figure 1 shows an example of a typical trial.

The experiment contained 320 trials (80 in each WM load condition), divided into 8 blocks of 40 trials each. Each block contained an equal number of the four WM load conditions. For each load condition in each block half of the target faces were matching and half were mismatching. The order of conditions was randomised. Each block lasted for almost 8 minutes, and participants were given a short rest between each block. In addition, to improve efficiency of eye artifact correction during EEG analysis, participants performed an eye-movement task between the fourth and fifth blocks. This consisted of 20 leftward saccades, 20 rightward saccades, 20 upward saccades, 20 downward saccades, and 20 eyeblinks. The eye-movement task lasted for approximately 4 minutes.

EEG recording and analysis

The experiment took place inside a Faraday cage to minimize electrical interference. The electroencephalogram (EEG) was recorded from 64 ring electrodes using Abralyt Light (FMS, Munich) as a conducting agent. An elastic cap (Easy Cap; FMS, Munich) was used to place the electrodes in the following 10-10 positions (American Encephalographic Society, 1994): Nz, FP1, FPz, FP2, AF7, AFz, AF8, F9, F7, F5, F3, F1, Fz, F2, F4, F6, F8, F10, FT9, FT7, FC3, FC1, FCz, FC2, FC4, FT8, FT10, T7, C5, C3, C4, C6, T8, TP9, TP7, CP3, CP1, CPz, CP2, CP4, TP8, TP10, P9, P7, P5, P3, P1, Pz, P2, P4, P6, P8, P10, PO9, PO7, POz, PO8, PO10, O1, Oz, O2, Iz. Two infraorbital channels (IO1 and IO2) were located vertically below each eye. All channels were referenced during recording to a reference electrode positioned at Cz, and an electrode positioned at AF4 served as ground. Electrode impedances were kept below 5 kΩ. The EEG was recorded with two BrainAmps DC amplifiers (Brain Products, Munich) and sampled at 500 Hz with a 250 Hz low-pass filter.

EEG data were re-referenced offline to the average reference. The EEG for correct-response trials was separated into epochs of 5 seconds duration, starting 1 second before the onset of the face array and ending 1 second after the onset of the target face. Eye artifact correction was accomplished separately for each participant by subjecting the EEG data recorded during the eye movement task to independent components analysis (ICA; Makeig et al., 1999), identifying components related to eye artifacts by their topography and association with triggers indicating saccades or eyeblinks, and removing these components from the experimental data. The data were visually inspected and trials containing any other artifacts were excluded from subsequent analyses. On average 92% of trials were retained after the artifact rejection. Baseline correction was performed on the interval 500 ms prior to the onset of the face array. The data were filtered (0.5-20 Hz), and all artifact-free epochs for correct-response trials were averaged into ERPs for each channel and each WM load.

ERP components were identified by their scalp topographies and peak latencies. Peak amplitudes in the encoding phase (the face array) and the retrieval phase (the single face) were measured relative to the prestimulus baseline (i.e. the 500 ms period before the onset of the face array). Peaks were determined as the local maxima or minima within the time segment 90 to 140 ms after the onset of the face array or single face for P1, 140 to 210 ms for N170, 300 to 400 ms for the early P3b subcomponent, and 450 to 700 ms for the late P3b subcomponent. Peak amplitudes were taken at PO7 and PO8 for P1, at P7, PO7, P8, and PO8 for N170, and at P5, Pz, and P6 for P3b. Peak latency was measured at P7 (for P1), PO8 (for N170), and Pz (for P3b). The amplitudes of the other electrodes were measured at those latencies.

For each component, peak latencies were submitted to repeated-measures analyses of variance (ANOVA) with the factor WM load (1, 2, 3, or 4). P1 peak amplitudes were entered into a 4×2 ANOVA with the factors load and hemisphere, and N170 peak amplitudes were entered into a $4 \times 2 \times 2$ ANOVA with the factors load, hemisphere, and electrode (P7/8 or PO7/8). For the analysis of early and late P3b subcomponents mean

amplitudes of the 50 ms time window around the peak were submitted to a 4×3 ANOVA with the factors load and electrode (P5, Pz, and P6). Significant effects of WM load were examined further using planned comparisons of the amplitude difference between consecutive levels of load. Greenhouse-Geisser corrections were applied where appropriate to correct for violations of the assumption of sphericity.

Behavioural Results

As can be seen in Table 1, accuracy decreased as working memory load increased. As a measure of WM capacity, each participant's maximum Cowan's K value (K-max) across the four levels of load was obtained[3]. K-max ranged from 1.24 to 3.40, with an average of 2.01, showing that average WM capacity for faces in this task was around 2 faces.

To examine the effect of WM load on accuracy, d' scores were submitted to a repeated-measures analysis of variance (ANOVA) with the factor WM load (1, 2, 3, or 4). This analysis revealed a significant effect of memory load, $F(3, 54) = 91.6$, $p < .001$. Planned comparisons of the d' difference between consecutive levels of load found that d' was higher for load 1 than for load 2, $F(1, 18) = 50.2$, $p < .001$, and higher for load 2 than for load 3, $F(1, 18) = 57.1$, $p < .001$, however the d' difference between loads 3 and 4 did not reach significance, $F(1, 18) = 3.1$, $p < .1$.

A repeated-measures ANOVA on the median reaction time (RT) data for correct-response trials found a significant effect of memory load, $F(3, 54) = 161.8$, $p < .001$. Planned comparisons found that RTs were faster for load 1 than for load 2, $F(1, 18) = 100.1$, $p < .001$, faster for load 2 than for load 3, $F(1, 18) = 76.7$, $p < .001$, and marginally faster for load 3 than for load 4, $F(1, 18) = 4.1$, $p = .06$.

Electrophysiological Results

The face array (encoding phase) and the single face (retrieval phase) both elicited a positive wave (P1) at 118 ms (encoding) and 128 ms (retrieval) with maximum peak amplitude at PO7 and PO8 (Figures 2 and 3). This was followed at 184 ms (for encoding and retrieval) by a negative deflection (N170) which was maximal over the parieto-occipital electrodes (P7, PO7, P8, and PO8). The N170 was followed by a large ERP response over parietal electrodes corresponding to the P3b component. This P3b response was divided into two peaks at 354 ms and 512 ms during the encoding phase and at 356 ms and 550 ms during the retrieval phase.

ERP Latencies

The only significant effect of WM load on latency was found for the P1 at encoding, $F(3, 54) = 5.0$, $p = .009$. Follow-up tests revealed that the P1 occurred significantly later in load 2 than in load 4, $p = .016$, but no other latency differences between load conditions were significant. No effect of WM load on latency was found for any other components at encoding or retrieval ($F < 2.1$).

ERP Amplitudes

Encoding

P1: There was a main effect of hemisphere, $F(1, 18) = 4.8$, $p = .04$, with a larger P1 on the left than on the right, and a main effect of load, $F(3, 54) = 5.6$, $p = .002$. However, there

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[3]Cowan's K was calculated for each participant using the formula $K = S \times (H - F)$, where K is memory capacity, S is set size (i.e. working memory load), H is the hit rate, and F is the false alarm rate.

was no interaction between hemisphere and load, $F(3, 54) = 0.8$, ns. Planned comparisons showed that P1 amplitude increased significantly only from load 1 to load 2, $F(1, 18) = 12.0$, $p = .003$, whereas the amplitude increases from load 2 to load 3 and from load 3 to load 4 did not reach significance.

N170: The N170 was significantly larger over the right hemisphere, $F(1, 18) = 9.5$, $p = .006$, and there was also a main effect of load, $F(3, 54) = 16.9$, $p < .001$. There was no effect of electrode, $F(1, 18) = 0.3$, ns, and no interactions were significant. Planned comparisons showed that N170 amplitude was larger for load 2 than for load 1, $F(1, 18) = 13.6$, $p = .002$, and larger for load 3 than for load 2, $F(1, 18) = 10.7$, $p = .004$. There was no amplitude difference between loads 3 and 4.

Early P3b: There was a main effect of electrode, $F(2, 36) = 7.9$, $p = .001$; amplitude was significantly higher at P6 compared to P5 ($p = .002$) and Pz ($p = .05$). There was no effect of load, $F(3, 54) = 0.2$, ns, and no interaction between electrode and load, $F(6, 108) = 1.6$, ns.

Late P3b: There was a main effect of electrode, $F(2, 36) = 30.1$, $p < .001$, with larger amplitude at Pz than at P5 ($p < .001$) and P6 ($p = .005$), and larger amplitude at P6 than P5 ($p = .002$). There was also a main effect of load, $F(3, 54) = 18.8$, $p < .001$, and no interaction, $F(6, 108) = 0.9$, ns. Planned comparisons showed that late P3b amplitude decreased significantly from load 1 to load 2, $F(1, 18) = 16.2$, $p = .001$, and from load 2 to load 3, $F(1, 18) = 6.7$, $p = .02$. There was no significant amplitude difference between loads 3 and 4, $F(1, 18) = 0.7$, ns.

The effects of WM load on the early ERP components during encoding may be explained by perceptual differences in the encoding displays for the different load conditions. That is, as WM load (i.e. the number of intact faces in the display) increased, the number of scrambled faces decreased. Therefore, the modulation of P1 by WM load may reflect the different spatial frequencies of scrambled faces and intact faces. Similarly, the N170 increase with WM load may be due to the increasing number of intact faces in the encoding display. The early P3b subcomponent was largest over the right hemisphere, whereas the late P3b subcomponent was largest at Pz. Of most interest, only the late P3b was modulated by WM load at encoding. In accordance with other findings (Busch et al., 2003), amplitude decreased as WM load increased.

Retrieval

P1: There was no effect of hemisphere, $F(1, 18) = 0.1$, ns, or load, $F(3, 54) = 0.3$, ns, and no interaction, $F(3, 54) = 1.5$, ns.

N170: There was a significant effect of load, $F(3, 54) = 8.4$, $p < .001$. The N170 was larger over the right hemisphere, and this difference was marginally significant, $F(1, 18) = 3.7$, $p = .07$. There was a main effect of electrode, $F(1, 18) = 5.5$, $p = .03$, with larger amplitude at P7/P8 than at PO7/PO8. There was also an interaction between hemisphere and electrode, $F(1, 18) = 4.3$, $p = .05$; follow-up analyses showed that the effect of electrode was significant over the left hemisphere, $F(1, 18) = 8.6$, $p = .009$, but not over the right hemisphere, $F(1, 18) = 1.4$, ns. No other interactions were significant. Contrary to the encoding phase, N170 amplitude decreased as load increased. Planned comparisons found that N170 amplitude was significantly larger for load 1 than for load 2, $F(1, 18) = 9.4$, $p = .007$, whereas N170 amplitude did not significantly differ between loads 2 and 3 or between loads 3 and 4.

Early P3b: There were main effects of load, $F(3, 54) = 6.0$, $p = .001$, and electrode, $F(2, 36) = 19.3$, $p < .001$, and no interaction, $F(6, 108) = 1.5$, ns. Amplitude was smaller at P5

than at Pz, $(p < .001)$ and P6 $(p < .001)$, whereas there was no amplitude difference between Pz and P6. Planned contrasts found significantly reduced amplitude for load 2 compared to load 1, $F(1, 18) = 10.2$, $p = .005$, and for load 4 compared to load 3, $F(1, 18) = 4.8$, $p = .04$.

Late P3b: There was a main effect of load, $F(3, 54) = 4.8$, $p = .005$, a main effect of electrode, $F(2, 36) = 56.1$, $p < .001$, and a significant interaction between electrode and load, $F(6, 108) = 3.4$, $p = .014$. Overall, amplitude was larger at Pz compared to P5 $(p < .001)$ and P6 $(p < .001)$, and larger at P6 compared to P5 $(p = .004)$. The electrode $\times$ load interaction was examined by comparing the effects of load at each electrode. There was no effect of load at P6, $F(3, 54) = 1.5$, ns. At P5 there was a main effect of load, $F(3, 54) = 4.7$, $p = .005$, and planned comparisons showed that P5 amplitude decreased significantly only from load 1 to load 2, $F(1, 18) = 6.4$, $p = .02$. There was also a main effect of load at Pz, $F(3, 54) = 9.0$, $p < .001$. Planned comparisons showed that the decrease in Pz amplitude with increasing load was significant only between loads 2 and 3, $F(1, 18) = 12.1$, $p = .003$.

In summary, the N170 elicited by the test face at retrieval was modulated by WM load; N170 amplitude decreased as load increased. The N170 load effects cannot be explained by load differences at baseline or P1, as no effect of load was observed at P1. As expected, P3b amplitude decreased as WM load increased.

Match versus mismatch analysis

To further examine the effects of WM load on ERPs at retrieval, the waveforms for faces that matched a face in the previous encoding array (the match condition) were compared to the waveforms for faces that did not match any of the faces in the encoding array (the mismatch condition). As before, this analysis was carried out on correct-response trials only. Amplitudes of the P1, N170, and P3b components were analysed as above with the additional factor of match/mismatch and with the electrode factor omitted to simplify the analyses. For the N170 analysis, a 4 (load) $\times$ 2 (hemisphere) $\times$ 2 (match/mismatch) ANOVA was performed on the peak amplitudes at P7 and P8, as the previous analysis showed that the N170 was largest at these electrodes. For the P3b, a 4 (load) $\times$ 2 (match/mismatch) ANOVA was performed on the mean amplitude at Pz.

P1—There was no effect of match/mismatch, $F(1, 18) = 1.0$, ns, and match/mismatch did not interact with any other variables.

N170—There was a significant effect of match/mismatch, $F(1, 18) = 4.4$, $p = .05$, and a significant interaction between match/mismatch and hemisphere, $F(1, 18) = 5.8$, $p = .03$. There were no other significant effects involving match/mismatch. Follow-up analyses found a significant effect of match/mismatch over the left hemisphere, $F(1, 18) = 8.7$, $p = .009$, with reduced N170 amplitude in the match condition compared to the mismatch condition. In contrast, there was no effect of match/mismatch over the right hemisphere, $F(1, 18) = 0.3$, ns.

Early P3b—There was a main effect of match/mismatch, $F(1, 18) = 5.1$, $p = .04$, with larger amplitude in the match condition than in the mismatch condition. However, there was no interaction between match/mismatch and load, $F(3, 54) = 1.5$, ns.

Late P3b—There was no main effect of match/mismatch, $F(1, 18) = 1.4$, ns, and no interaction between match/mismatch and load, $F(3, 54) = 0.2$, ns.

N250r—The N250r was revealed by an increased negativity at temporo-parietal sites and increased positivity at fronto-central sites for matching faces compared to mismatching faces

in the latency range between 200 to 400 ms following face onset. The N250r was analysed by calculating match minus mismatch difference waveforms for each load condition (see Figure 4). Because the peak of the N250r was not always clearly detectable in the individual difference waveforms, particularly at higher memory loads, a formal latency analysis of N250r was not conducted. The peak latency (320 ms) was identified by visual inspection of the grand-averages, and mean amplitudes from a 50 ms window around the peak latency were then obtained from the difference waves for each participant.

Mean amplitudes at P9 and P10 (which showed the largest negative deflection) were submitted to a 2×4 ANOVA with the factors hemisphere and load. There was a significant main effect of load, $F(3, 54) = 11.3$, $p < .001$, and no interaction between hemisphere and load, $F(3, 54) = 1.4$, ns. Planned comparisons showed that N250r amplitude decreased significantly from load 1 to load 2, $F(1, 18) = 10.6$, $p = .004$, and from load 2 to load 3, $F(1, 18) = 8.7$, $p = .009$.

A one-way ANOVA with the factor load was also performed on the mean amplitudes at FCz. Again, there was a main effect of load, $F(3, 54) = 8.4$, $p < .001$, and planned comparisons found a significant decrease in FCz amplitude from load 1 to load 2, $F(1, 18) = 4.5$, $p = .049$, and from load 2 to load 3, $F(1, 18) = 11.2$, $p = .004$. In contrast to the temporoparietal sites, there was also a significant amplitude increase from load 3 to load 4, $F(1, 18) = 6.4$, $p = .02$.

WM Capacity Analysis

To examine the effects of individual WM capacity on the ERP load modulations described previously, participants were divided into a high capacity group (N = 9), in which K-max ranged from 2 to 3.4 (mean = 2.5), and a low capacity group (N = 10), in which K-max ranged from 1.2 to 1.8 (mean = 1.5). Planned comparisons of the amplitude difference between consecutive levels of load were performed for low and high capacity participants.

Encoding

N170: In high capacity participants the increase in N170 amplitude with increasing WM load was only significant between loads 2 and 3, $F(1, 8) = 7.1$, $p = .03$, whereas in low capacity participants the amplitude increase was only significant between loads 1 and 2, $F(1, 9) = 15.1$, $p = .004$.

Early P3b: As noted above, there was no effect of load on early P3b amplitude. However, over all levels of load early P3b amplitude at encoding was significantly higher for the high capacity group than for the low capacity group, $F(1, 17) = 6.4$, $p = .02$. This is consistent with previous work showing that P3b amplitude at encoding indicates whether an item will be subsequently remembered (Fabiani et al., 1986).

Late P3b: The decrease in amplitude with increasing WM load was significant only between loads 1 and 2 for high capacity participants, $F(1, 8) = 6.0$, $p = .04$. By contrast, low capacity participants showed significant amplitude decreases from load 1 to load 2, $F(1, 9) = 10.6$, $p = .01$, and also from load 2 to load 3, $F(1, 9) = 7.4$, $p = .02$.

Retrieval

N170: The amplitude decrease from load 1 to load 2 was significant for the high capacity group, $F(1, 8) = 6.1$, $p = .04$, whereas the low capacity group showed a smaller amplitude decrease, which did not reach significance, $F(1, 9) = 3.7$, $p = .09$.

Early P3b: No significant amplitude differences between WM load levels were observed for high capacity participants, whereas low capacity participants showed a reduction in early P3b amplitude between loads 1 and 2, F (1, 9) = 7.8, p = .02.

Late P3b: No capacity differences were found for late P3b.

N250r—In the high capacity group the decrease in N250r amplitude as WM load increased was only significant between loads 2 and 3, $F(1, 8) = 11.2$, $p = .01$ (P9/P10), $F(1, 8) = 20.5$, $p = .002$ (FCz). By contrast, low capacity participants showed a significant amplitude decrease only from load 1 to load 2, $F(1, 9) = 9.3$, $p = .01$ (P9/P10), $F(1, 9) = 5.9$, $p = .04$ (FCz).

Discussion

The first goal of this study was to explore whether the WM load modulation of the P3b (e.g. Kok, 2001) also applies to WM for faces. The P3b was divided into two subcomponents at both encoding and retrieval. The amplitude of the late P3b subcomponent decreased as WM load increased at both encoding and retrieval, whereas the amplitude of the early P3b subcomponent was only suppressed by WM load at retrieval. Therefore, as expected, these findings show that the P3b is modulated by WM load for faces, with distinct effects of WM load for the early and late subcomponents.

It is thought that P3b amplitude may be suppressed at higher WM loads either because the increased cognitive demands of the task leave fewer resources available for stimulus evaluation (e.g. McEvoy et al., 1998), or because P3b overlaps with slow negative waves that are associated with the difficulty of complex cognitive processes (e.g. Mecklinger, Kramer, & Strayer, 1992). These explanations are not mutually exclusive and the P3b suppression observed in the current study may reflect a combination of different factors.

In addition, the two P3b subcomponents may reflect different WM processes. As already noted, the early P3b subcomponent is thought to reflect stimulus evaluation (Bledowski et al., 2006). The finding that the early P3b subcomponent observed in the current study was larger on the right is consistent with this idea, because faces are processed more in the right hemisphere (e.g. Kanwisher, McDermott, & Chun, 1997). The WM load modulation of the early P3b subcomponent only at retrieval is compatible with a resource-based account of P3b suppression (e.g. McEvoy et al., 1998). For example, if the early P3b subcomponent reflects stimulus evaluation, then it may not be affected by WM load at encoding because sufficient resources are available, whereas at retrieval the increased cognitive demands of maintaining more items in WM may leave fewer resources available for stimulus evaluation, resulting in a reduced early P3b subcomponent.

It has been suggested that the late P3b subcomponent reflects memory search operations mediated by the PFC (Bledowski et al., 2006). Indeed, the late P3b subcomponent did not show the right lateralisation that was observed for the early P3b, suggesting that this subcomponent reflects a higher-level WM process that occurs after stimulus evaluation. However, the finding that the late P3b subcomponent was modulated by load at encoding does not support Bledowski et al.'s (2006) view that this subcomponent indexes memory search, because these operations are not necessary at encoding. Kok (2001) suggested that WM tasks may require control mechanisms which rely on a different neural system from the mechanisms underlying event categorisation. Therefore, the late P3b subcomponent observed in the current study may reflect more general WM control processes that are necessary for both encoding and retrieval. In support of this idea, recent fMRI work found that PFC, which plays a role in the generation of the second P3b subcomponent (Bledowski

et al., 2006), was activated during WM encoding of 1-4 faces, and this PFC activity increased with WM load after load 2, suggesting that higher cognitive processes, such as chunking and compressing information, may be recruited when WM reaches capacity (Druzgal & D'Esposito, 2003).

The second goal of this study was to examine whether ERP components associated with face processing are influenced by WM load, as suggested by recent work showing that WM for faces involves face-specific visual processes, such as configural processing (Curby & Gauthier, 2007). At encoding, N170 amplitude increased as the number of faces increased, and this N170 increase varied according to WM capacity. That is, for participants with a WM capacity of less than two faces the N170 increase was significant only between loads 1 and 2, whereas participants with a WM capacity of two or more faces showed an N170 increase from load 2 to load 3. At retrieval, the N170 elicited by the test face decreased in amplitude as WM load increased. Importantly, this N170 amplitude decrease was significant between loads 1 and 2, but then levelled off after load 2. This corresponds to the behavioural data, in which average WM capacity was found to be 2 faces. As already noted, the N170 is thought to reflect configural processing of faces (e.g. Bentin et al., 1996; Eimer, 2000b; Itier & Taylor, 2004; Latinus & Taylor, 2006). Therefore, the modulation of N170 by WM load shows that WM capacity limits are reflected in early stages of face processing.

There is evidence to suggest that limited-capacity resources are required for the configural processing underlying recognition of facial identity (see Palermo & Rhodes, 2007). For example, performance on tasks involving face recognition is impaired if more than one face is presented at a time (Bindemann, Burton, & Jenkins, 2005; Boutet & Chaudhuri, 2001; Palermo & Rhodes, 2002). Jenkins, Lavie, & Driver (2003) found that interference from irrelevant distractor faces in a name categorisation task was reduced by adding another distractor face to the display, but not by adding a nonface object. In contrast, distractor interference from nonface objects was reduced by adding any type of visual stimulus to the display. Based on these findings, Jenkins et al. (2003) suggested that the face processing system has its own face-specific capacity limits. In support of this idea, other work has shown that the N170 elicited by a target face is reduced when a distractor face is present (Jacques & Rossion, 2004, 2006). As noted previously, visual WM storage may involve sensory cortical areas (Pasternak & Greenlee, 2005), and face-specific visual areas may play a role in WM maintenance of faces (Postle, Druzgal, & D'Esposito, 2003). Therefore, the reduction in N170 amplitude with increasing WM load at retrieval may reflect the limited processing capacity of visual areas involved in face processing.

In the current study, maintenance of the to-be-remembered faces would require more neural resources in face processing regions as the number of faces in the encoding array increased, leaving fewer resources available for processing the test face. This would result in a reduced N170 for higher loads. If the processing capacity of face-specific visual areas was reached at WM loads of two faces, as suggested by the behavioural data, then there would be fewer neural resources available for processing the test face at WM loads of two or more faces compared to a WM load of one face, but no major differences across the higher load conditions. This is consistent with the large reduction in N170 amplitude between loads 1 and 2, but no significant N170 decrease between loads 2-4. Interestingly, the amplitude decrease between loads 1 and 2 was only significant for high capacity participants. This may be because the capacity limits of visual areas were reached earlier for low capacity participants. That is, the average WM capacity of the low capacity group was 1.5 faces, so maintenance of just one face in WM would leave insufficient resources for processing the test face.

Alternatively, the effect of load on the N170 may be due to more general resource limits. As already noted, N170 is sometimes reduced for unattended faces (Eimer, 2000a; Holmes et al., 2003; but see Lueschow et al., 2004). It is possible that the N170 elicited by the test face in the current study was reduced for higher WM loads because attentional resources were reallocated from target processing to maintaining face representations in WM. That is, at higher WM loads, more attention may be required for WM maintenance processes, resulting in less attention being allocated to the test face. This explanation would be similar to resource-based accounts of P3b attenuation with increasing WM load (e.g. McEvoy et al., 1998).

It could be argued that the N170 reduction with increasing WM load may be due to other factors, such as adaptation of the face processing mechanisms reflected in the N170. Recent work using adaptation paradigms, in which prolonged viewing of a stimulus leads to visual after-effects, has shown that the N170 evoked by a face is reduced and delayed following adaptation to a different face (Kovacs et al., 2006; Schweinberger et al., 2007). Therefore, the N170 amplitude reduction with increasing WM load in the current study may reflect increased adaptation when more faces are presented at encoding, leading to a greater reduction in N170 for the test face. However, this account does not seem particularly relevant here, as there is no evidence to suggest that increasing the number of faces in the encoding array would increase the neural effects of adaptation. In sum, although the precise mechanisms of the N170 modulation by WM load are thus not yet clear, the results of the present study support other work showing that N170 is modulated by top down factors (Bentin et al., 2002; Eimer, 2000a; Galli et al., 2006; Holmes et al., 2003; Pizzagalli et al., 2002) by providing the first evidence that the N170 is affected by WM load.

The presence or absence of the test face in the previous encoding display had a significant effect on N170 and the early P3b subcomponent elicited by the test face. N170 amplitude, independent of WM load, was reduced when the test face matched one of the faces in the encoding display. Note that this effect is unlikely related to priming or episodic memory, as all faces had been presented many times over the course of the experiment; the amplitude reduction of N170 for matching versus nonmatching faces instead seems to represent a very short-lived effect of face repetition. This is similar to other work showing a reduction in N170 amplitude for repeated faces (Campanella et al., 2000; George et al., 1997; Guillaume & Tiberghien, 2001; Heisz et al., 2006a, 2006b; Itier & Taylor, 2002, 2004). The early P3b subcomponent was larger for matching compared to mismatching faces, which is consistent with the results of other studies (e.g. McEvoy et al., 1998). However, this may simply be due to carry-over effects of the N170 reduction for matching faces. Interestingly, the match effects on N170 and P3b were not modulated by memory load. That is, WM load had a similar influence on processing of both matching and mismatching faces at retrieval.

Immediate face repetition produced an N250r, measured as an ERP difference between matching and mismatching faces. Importantly, the amplitude of the N250r decreased as WM load increased, and this decrease levelled off after load 2, corresponding to the behavioural WM capacity limit of two faces. Also, this N250r decrease with load varied according to individual WM capacity; low capacity participants showed an N250r decrease between loads 1 and 2, whereas for high capacity participants the N250r decreased between loads 2 and 3. The modulation of the N250r with WM load suggests that the facilitated processing of repeated faces is weaker under higher WM loads. Like the N170, this effect may also reflect limits in processing resources. For example, at higher memory loads, the limited neural resources available for WM maintenance would be distributed across more individual face representations, so that fewer resources would be allocated to each face. A matching face would therefore cause a weaker activation increase of its corresponding representation at higher WM loads than at lower WM loads, resulting in a smaller N250r. Mutually

suppressive interactions (e.g. Desimone & Duncan, 1995; Kastner & Ungerleider, 2001) between face representations at higher loads may also contribute; indeed, inhibitory interconnections are a central part of cognitive models of face recognition (Burton, Bruce, & Johnston, 1990). Although further work is needed to determine the precise mechanisms underlying the WM load modulation of the N250r, the current results clearly indicate a strong relationship between the processes reflected in the N250r and working memory, for example the temporary maintenance of face recognition units in working memory.

Finally, it should be noted that, because the encoding display was presented for a fixed length of time (2 seconds) for all levels of WM load, the study time available per face decreased as WM load increased. Therefore, WM capacity limits for faces observed in this study may be partly due to limited encoding time for larger WM loads. This may have caused a decrease in the quality of face representations, resulting in more errors when comparing the test face to the remembered faces. It is possible, therefore, that the WM load modulation of N170 and N250r may reflect differences in representational quality of faces, rather than the number of faces in WM, and future work should examine this idea.

In conclusion, the current study extends previous findings of P3b attenuation with increasing WM load by showing that this P3b modulation also occurs for faces. The early P3b subcomponent, which is thought to reflect stimulus evaluation, was modulated by WM load only at retrieval. By contrast, the late P3b subcomponent, which may be related to higher cognitive control processes, was modulated by WM load at both encoding and retrieval. Furthermore, the results of this study provide the first evidence to show that WM load for faces is reflected in the amplitudes of the N170 and N250r. Although further work is needed to establish the precise mechanisms underlying WM load modulation of face sensitive ERPs, these findings suggest that higher visual areas play an important role in WM for faces.

Acknowledgments

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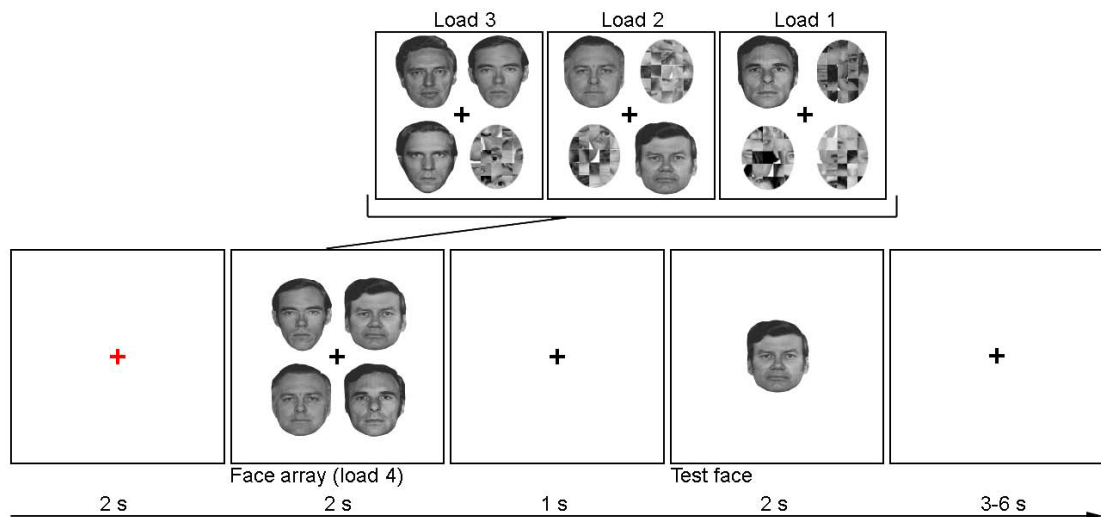
Figure 1.

The sequence of events in a trial. The fixation cross turned red for 2 seconds to indicate the start of the trial. Then a memory encoding array consisting of 1 – 4 faces was presented for 2 seconds. This was followed by a 1 second delay, then a test face appeared for 2 seconds. During these 2 seconds, participants had to indicate whether or not the test face matched one of the faces in the encoding array. The intertrial interval was between 3 and 6 seconds.
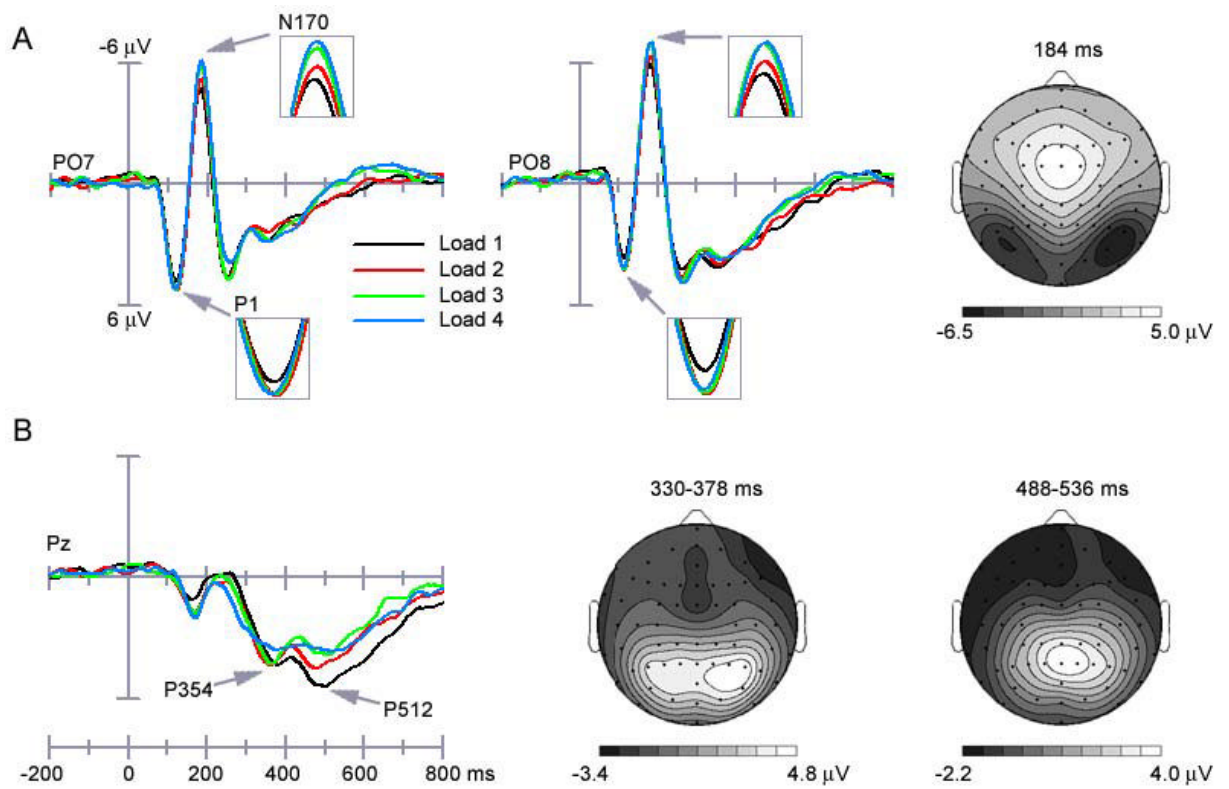
Figure 2.
ERP responses elicited by the face array at encoding. Panel A shows grand average waveforms at PO7 and PO8 and a topographical map of N170 scalp voltage. Panel B shows grand average waveforms at Pz and voltage maps of the two P3b peaks.
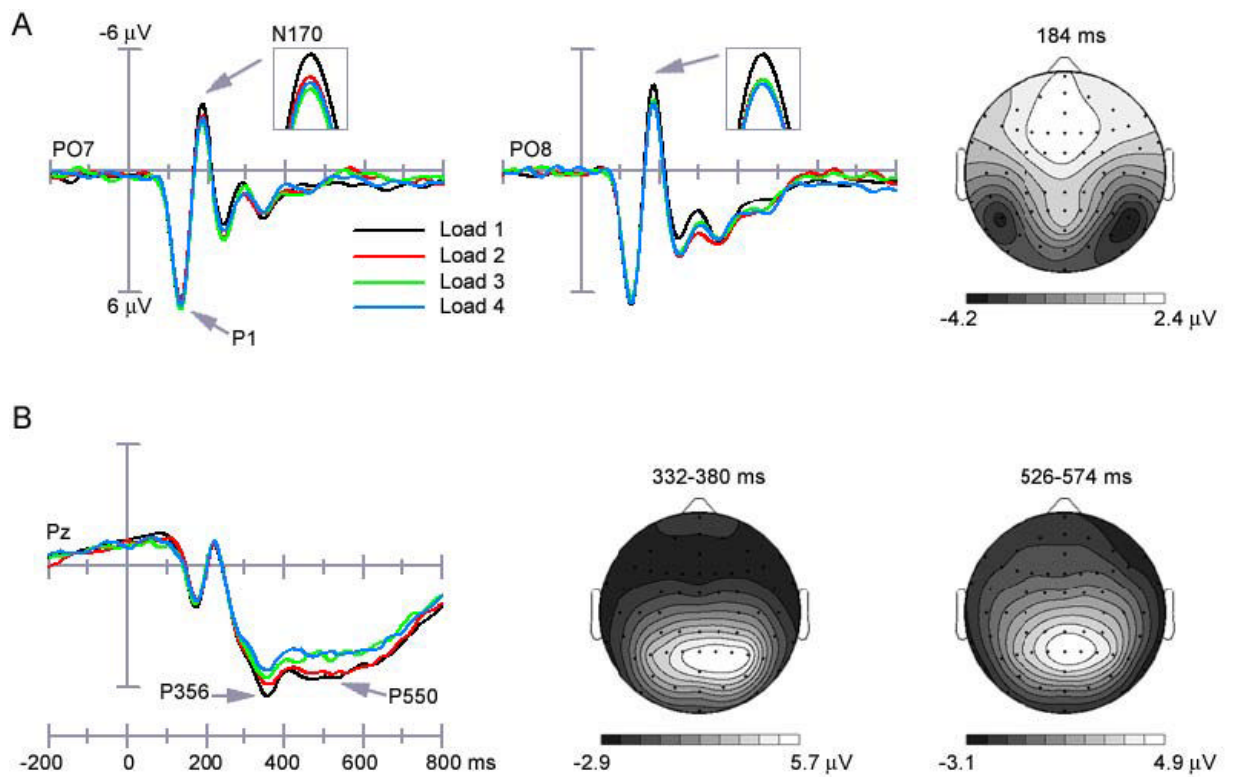
Figure 3.
ERP responses elicited by the test face at retrieval. Panel A shows grand average waveforms at PO7 and PO8 and a topographical map of N170 scalp voltage. Panel B shows grand average waveforms at Pz and voltage maps of the two P3b peaks. Note that a pre-encoding interval was used as the baseline for retrieval ERPs (see methods).
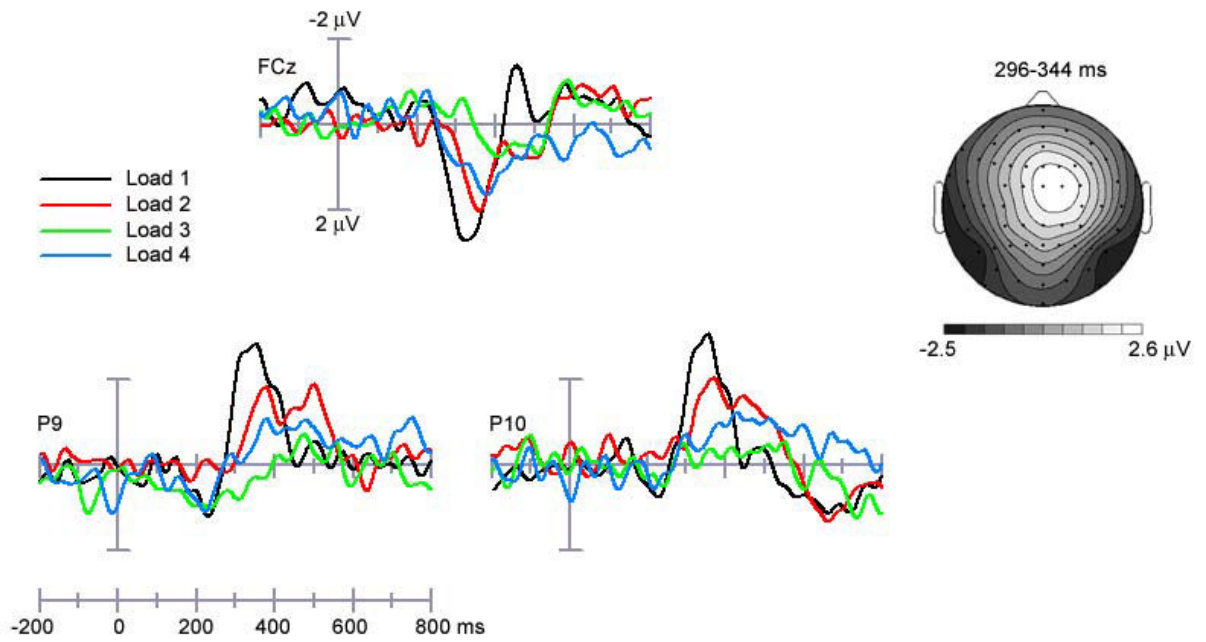
Figure 4.
Difference waves match vs. nonmatch at FCz, P9, and P10, and a topographical map of N250r scalp voltage at load 1. Note that a pre-encoding interval was used as the baseline for retrieval ERPs (see methods).

Table 1

Median RT, mean hit rate (proportion of 'yes' responses on target present trials), and mean false alarm rate (proportion of 'yes' responses on target absent trials) as a function of working memory load. Standard error is shown in parentheses. Accuracy is shown by d-prime, which was obtained from mean hit and false alarm rates.

	Load 1	Load 2	Load 3	Load 4
Median RT	725 (22)	831 (26)	928 (31)	952 (28)
Hit rate	0.96 (0.01)	0.85 (0.02)	0.74 (0.04)	0.75 (0.04)
False alarm rate	0.02 (0.01)	0.09 (0.02)	0.19 (0.03)	0.28 (0.04)
d-prime	3.69	2.45	1.49	1.22