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Interhemispheric ERP asymmetries over inferior parietal cortex reveal differential visual working memory maintenance for fearful versus neutral facial identities

PAOLA SESSA,[a] ROY LURIA,[a] ALEX GOTLER,[b] PIERRE JOLICŒUR,[c] AND
ROBERTO DELL'ACQUA[a,d]
[a]Department of Developmental Psychology, University of Padova, Padova, Italy
[b]Department of Behavioral Sciences, Ben-Gurion University of the Negev, Israel
[c]Centre de Recherche en Neuropsychologie et Cognition, Université de Montréal, Montréal, Québec, Canada
[d]Centre for Cognitive Science, University of Padova, Padova, Italy

Abstract

The goal of the present investigation was to discover whether visual working memory maintenance for faces is modulated by facial expression using event-related potentials (ERPs). Each trial consisted of two sequential arrays, a memory array and a test array, each including either two or four faces with neutral or fearful expressions. The faces were displayed to the left and to the right of a central fixation cross. Two central arrows cued participants to encode one face or two faces displayed on one side of the memory array. The sustained posterior contralateral negativity (SPCN) component of the ERP time-locked to the onset of the memory array was used as an index of visual working memory maintenance. Visual working memory performance was quantified using indexes of memory capacity (Cowan's *K* and *K*-iterative), a standard index of sensitivity (*d'*), and reaction times (RTs). Relative to neutral faces, superior memory and longer change-detection RTs to fearful face identities were observed when two faces were displayed on the cued side of the memory array. Fearful faces elicited an enhanced SPCN relative to neutral faces, especially when only one face was displayed on the cued side of the memory array. These findings suggest increased maintenance in visual working memory of faces with a fearful expression relative to faces with a neutral expression and that the representational format in which fearful faces are stored in memory may be characterized by enhanced resolution relative to that subtended in the maintenance of neutral faces.

Descriptors: Visual working memory, Emotion, Facial expression, Event-related potential

Emotion exerts a modulatory role on several functional subroutines of the human cognitive architecture, and emotional effects on attention, long term-memory, learning, and motivation are now considered well established and highly replicable phenomena in the experimental literature (e.g., Dalgleish & Power, 1999; Ekman & Davidson, 1994; Martin & Clore, 2001; Storbeck & Clore, 2007).

Among the stimuli that convey emotions most promptly, faces probably occupy a place of first order. Faces in general, and emotional facial expressions in particular, are of paramount importance for individuals, being one of the most immediate sources of social and emotional information encountered since birth. Faces are known to capture attention more readily than other meaningful objects (Mack & Rock, 1998; Ro, Russell, & Lavie, 2001; Vuilleumier, 2000; Vuilleumier & Sagiv, 2001). Humans appear to have an innate tendency to deploy attention to faces, even a few days after birth (Valenza, Simion, Macchi Cassia, & Umiltà, 1996). Furthermore, 5-month-old babies seem to have no difficulty in categorizing faces based on emotional expression (Schwartz, Izard, & Ansul, 1985).

It has been claimed that faces with a negative expression tend to attract attention more promptly than faces with different (e.g., positive and neutral) expressions. In diverse visual search designs, reaction time (RT) to target schematic negative faces was shorter than RT to happy or neutral faces (e.g., Eastwood, Smilek, & Merikle, 2001; Fox et al., 2000; Öhman, Lundqvist, & Esteves, 2001; Suslow, Junghanns, & Arolt, 2001). Attentional biases toward negative faces were also described in studies using a dot probe detection task, in which one irrelevant neutral face and one irrelevant negative face (briefly presented on the left or right of fixation) were followed by a peripheral to-be-detected dot. Though irrelevant, negative faces speeded up dot detection when the dot and the negative face were displayed on the same side of fixation (Bradley, Mogg, & Millar, 2000; Mogg, & Bradley, 1999), compatibly with the idea that negative faces bias the distribution of attention automatically.

The special status of faces associated with negative emotions is corroborated by several studies using the event-related poten-

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Address correspondence to: Paola Sessa, Department of Developmental Psychology, University of Padova, Via Venezia 8, 5131 Padova, Italy. E-mail: paola.sessa@unipd.it

tial (ERP) approach. ERP studies have shown that negative facial expressions can modulate amplitude and/or latency of a family of ERP components, including the P1 and N1 complex (e.g., Ashley, Vuilleumier, & Swick, 2004; Batty & Taylor, 2003; Pizzagalli, Regard, & Lehmann, 1999; Pizzagalli et al., 2002; Pourtois, Dan, Grandjean, Sander, & Vuilleumier, 2005; Sato, Kochiyama, Yoshikawa, & Matsumura, 2001; Schupp et al., 2004), the N170 (e.g., Campanella, Quinet, Bruyer, Crommelinck, & Guerit, 2002; see, however, Eimer & Holmes, 2002, and Eimer, Holmes, & McGlone, 2003, for opposing views), and later components such as the P3 (e.g., Carretie, & Iglesias, 1995; Langeslag, Morgan, Jackson, Linden, & Van Strien, 2009).

With a specific focus on the attention demands associated with processing of emotional face expressions, Eimer and Kiss (2007) have shown that fearful faces tend to capture attention involuntarily compared to faces with a neutral expression. These authors asked participants to monitor a stimulus at fixation for a luminance change. While engaged in this task, participants were also exposed to task-irrelevant lateralized faces with different expressions. An electrophysiological indicator of the allocation of visual spatial attention (i.e., the N2pc; Brisson & Jolicœur, 2007a, b; Eimer, 1996; Luck & Hillyard, 1994; Woodman & Luck, 2003), time-locked to the presentation of the faces, was monitored in this study. Eimer and Kiss found that an N2pc was elicited only by fearful faces, in trials both with or without a target luminance change, and argued that task-irrelevant fearful faces biased the allocation of spatial attention. Following up on this study, the same authors showed that fearful faces were likely to be encoded unconsciously, because an N2pc elicited by fearful faces was found when these stimuli were heavily masked and plausibly processed subliminally (Kiss & Eimer, 2008; see also de Gelder, Pourtois, van Raamsdonk, Vroomen, & Weiskrantz, 2001, and de Gelder, Vroomen, Pourtois, & Weiskrantz, 1999, for ERPs results from patients affected by blindsight and Pasley, Mayes, & Schultz, 2004, Vuilleumier et al., 2002, Whalen et al., 1998, and Williams, Morris, McGlone, Abbott, & Mattingley, 2004, for fMRI results consistent with the results of Kiss & Eimer, 2008).

In contrast with the many investigations on the perceptual/attentional processing of negative facial expressions (some of which were briefly reviewed in the foregoing section), the interaction of negative facial expression and visual working memory (VWM) processing has been systematically investigated in only few recent studies (e.g., Bankó, Gál, & Vidnyánszky, 2009; Jackson, Wu, Linden, & Raymond, 2009; Langeslag et al., 2009). In particular, Jackson et al. (2009) and Langeslag et al. (see also Jackson, Wolf, Johnston, Raymond, & Linden, 2008, for related fMRI results) demonstrated enhanced VWM performance (assessed by means of indices of sensitivity) for emotional faces relative to neutral faces. These authors presented participants with study arrays of a variable number of to-be-remembered faces (ranging from one to four in Jackson et al.'s 2009 study and from one to three in Langeslag et al.'s study), all of which were either angry, happy, or neutral. After a 1-s retention interval, recognition was assessed by presenting a single test face whose expression was emotionally consistent with the faces composing the previously displayed array. Participants were instructed to report whether the single face matched one of the faces in the previous study array based on face identity. In both studies, better recognition performance was found for emotional faces when more than one face had to be encoded. More specifically, Jackson et al. (2009) found better recognition performance for just angry faces, whereas Langeslag et al. found better face recognition performance that extended to both angry and happy faces. Despite this slight inconsistency, both studies provided evidence compatible with the idea that significantly more information about face identity associated with an emotional expression can be stored in VWM compared to the information required to store face identities associated with a neutral expression. Langeslag et al. examined a number of ERP components (i.e., P1, N170, P3b, and N250r) time-locked to both the faces array and the single probe face. Interestingly, none of these ERP components was modulated by emotion during the encoding and maintenance of the study arrays. Emotion effects were instead manifest in the ERP time-locked to the probe face, mainly in the form of a decrement of the P3b amplitude elicited by emotional faces relative to neutral faces. The authors explained this pattern of results by proposing that more resources ought to be allocated for VWM maintenance of emotional faces following their exposure in the initial study array, leaving less memory resources available for the accurate evaluation of the probe face, as reflected in the decreased P3b amplitude time-locked to the probe face.

Moving from the Langeslag et al. (2009) findings, the scope of the present investigation was to provide a fine-grained analysis of the allocation of VWM resources when subjects maintained neutral versus fearful faces while concurrently evaluating the possibility that the finding of a better memory for negative faces could relate in some way to the quantity and/or quality of the information required for storing these particular stimuli in VWM relative to neutral faces. To this aim, we propose a method allowing a direct quantification of the differential VWM maintenance of neutral and negative faces (i.e., fearful faces) under conditions similar to those implemented in Langeslag et al. We monitored an electrophysiological marker of processing occurring during VWM maintenance, namely, the sustained posterior contralateral negativity (SPCN) component of the ERP (Brisson & Jolicœur, 2007a, b; Dell'Acqua, Sessa, Jolicœur, & Robitaille, 2006; Jolicœur, Sessa, Dell'Acqua, & Robitaille, 2006a, b). There is indeed growing evidence linking the SPCN to brain activity specifically related to the maintenance of representations in VWM (Klaver, Talsma, Wijers, Heinze, & Mulder, 1999; McCollough, Machizawa, & Vogel, 2007; Robitaille, Grimault, & Jolicœur, 2009; Vogel & Machizawa, 2004) and suggesting that the SPCN amplitude correlates positively with VWM informational load (e.g., Jolicœur, Brisson, & Robitaille, 2008; Perron et al., 2009; Robitaille et al., 2009; Vogel & Machizawa, 2004). Importantly, the amplitude of the SPCN component has been shown to increase as the number of objects to be held in VWM is increased (i.e., the SPCN amplitude appears to be sensitive to the set size of the to-be-encoded objects), up to the level of VWM saturation (three or four simple objects), at which point the SPCN component usually tends to level off and reach an asymptote (Vogel & Machizawa, 2004). The amplitude of the SPCN component has also been shown to be affected by the complexity of objects (Luria, Sessa, Gotler, Jolicœur, & Dell'Acqua, 2010), that is, the SPCN amplitude has been found to be larger for complex objects (i.e., random polygons) than for simple objects (i.e., colored squares), with the SPCN tendency to level off when VWM is saturated by a maximum of two complex objects.

Taken together, these results suggest strongly that the SPCN amplitude is sensitive to the overall quantity of information encoded in VWM from an attended visual scene. The enhancement of processing of negative faces at early stages would have as a consequence that negative faces would be stored in VWM as higher resolution representations relative to neutral faces, and this in turn would be reflected, all else (e.g., set size) being equal, in larger SPCN amplitudes elicited by fearful than neutral faces (see Bays & Husain, 2008, for analogous considerations). Higher resolution representations of negative faces would enable a more accurate identification of these faces than neutral faces, as suggested by the studies briefly overviewed in a foregoing paragraph.

In the present investigation, we used a variant of a standard change detection task typically used in studies on VWM maintenance to elicit the SPCN (e.g., Eimer & Mazza, 2005; Luck & Vogel, 1997; Vogel & Machizawa, 2004). The paradigm is illustrated in Figure 1a,b. Each trial consisted of two sequential visual arrays of faces, a memory array and a test array, and the faces had either a neutral or a fearful expression. The participants were cued to encode in VWM the faces displayed in just one visual hemifield (either left or right). The SPCN component of the ERP time-locked to the onset of the memory array of faces was measured. The SPCN is typically elicited 300 ms after stimulus onset at posterior electrode sites, and it consists of a sustained activity throughout the interval of memory retention. Our prediction was straightforward. If faces with a negative expression are encoded and maintained as higher resolution representations in VWM than faces with a neutral expression, an SPCN of larger amplitude should be observed in response to memory arrays containing fearful faces compared to memory arrays containing neutral faces. Although the amplitude of the SPCN component has also been shown to be affected by the complexity of objects (Luria et al., 2010), it is important to note that the same faces were presented with two different emotional expressions in the present work. Given that the same features were contained in a given face and that two expressions of the same face could only be distinguished on the basis of slight differences in spatial arrangement and subtle changes in the shape of the features (i.e., mainly the shape of the mouth and the inclination of the eyebrows), one assumption underlying the present investigation was that the results would be minimally affected by differences in the complexity of the stimuli. In other words, we assumed that a fearful face was not more visually complex than a neutral face.

A secondary goal of the present investigation was to test whether the benefit observed for angry face identities in previous studies in terms of behavioral indices of sensitivity (Jackson et al., 2009; Langeslag et al., 2009) could be extended to other threat-

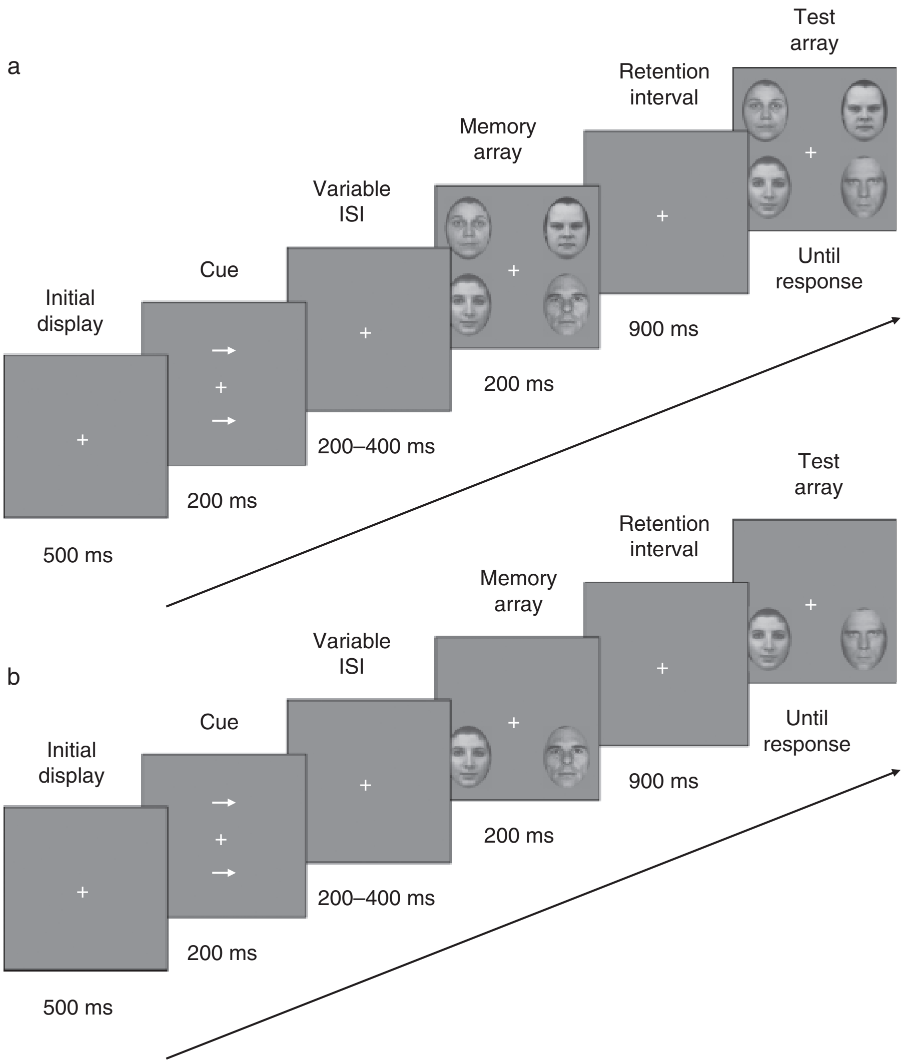

Figure 1. Example of a change detection task trial for the right hemifield when either two faces (a) or one face (b) had to be memorized. ISI: interstimulus interval. The relative distance between faces is approximately to scale.

related expression, namely, fear. Indeed, angry and fearful faces communicate different aspects of threat, with anger communicating immediate menace, and fear signaling potential risk in the environment (e.g., Lipp, Price, & Tellengen, 2009), and existing evidence strongly suggests that the perception of fear and anger is mediated by dissociable neural circuitries (Adolphs, Tranel, Damasio, & Damasio, 1994; Fitzgerald, Angstadt, Jelsone, Nathan, & Phan, 2006; Whalen et al., 2001). In addition, the present investigation gave us the opportunity to test a tenet of the model proposed by Kiss and Eimer (2008), that emotional expressions are processed automatically. To provide such a test, participants in the present study were instructed to monitor the faces in the sequential arrays to detect a change in face identity, being explicitly informed at the beginning of the experiment that the emotional expression of the faces was irrelevant for carrying out the experimental task. Importantly, all faces at both memory and test arrays of one trial were either neutral or fearful; therefore, the crucial, task-relevant information that participant had to encode in VWM for the successful completion of the change detection task was face identity.

Method

Participants

The participants were 28 undergraduate students (18 women and 10 men, aged 18–28 years, mean age: 22 years) at the University of Padova, who participated for course credit after giving their written informed consent. All participants reported normal or corrected-to-normal vision, normal color vision, and no history of neurological disorders.

Data from 10 participants were discarded from the analyses because of an excessive rate (higher than 30% of trials) of EEG artifacts.

Stimuli

The stimuli were grayscale digital photographs of upright faces of 12 individuals (7 females and 5 males) with a neutral (12 photographs) and a fearful (12 photographs) expression selected from Ekman and Friesen's (1976) and Lundqvist, Flykt, and Öhman's (1998) databases. These 24 photographs were scaled using image-processing software so that each face fit in a 3.3° × 4.5° (width × height) rectangle from a viewing distance of approximately 70 cm. The memory and test arrays were composed of two or four faces with either neutral or fearful expressions that were located at the corners of an imaginary rectangle centered around fixation. The horizontal and vertical distances between the center of two faces were respectively 7° and 5.7° and the distance between the center of the face and the fixation cross was 4.9°. When the memory and test arrays were composed of two faces, they were horizontally aligned and occupied either the upper or the lower two quadrants of the visual field, preserving the symmetry of the visual display.

Procedure

Figure 1a,b illustrates the sequence of events on each trial. A fixation cross at the center of the computer monitor remained on the screen throughout the trial. Participants were instructed to initiate the trial by pressing the spacebar of the computer keyboard. After trial initiation, 500 ms elapsed before the presentation of two arrow cues, one above and one below the fixation cross, both pointing to the same direction (i.e., both left or both right). The two arrow cues were displayed for 200 ms and were followed, after a variable stimulus onset asynchrony (SOA) of 400–600 ms (interstimulus interval [ISI], of 200–400 ms), by the memory array of faces, which was displayed for 200 ms. The memory array was composed of two or four faces with either neutral or fearful expressions. Following the memory array, a blank interval of 900 ms preceded the onset of the test array, which was exposed until the response. Each memory and test array contained faces with the same emotional expression (all neutral or all fearful), and trials with neutral faces and fearful faces were presented in separate blocks. The variable was blocked because it has been shown that aversive information has the ability to affect the processing of following stimuli (e.g., Li, Li, & Luo, 2006). That is, trials with fearful faces could affect the processing of successive trials with neutral faces (blocking conditions assured us of measuring a "pure" SPCN elicited by neutral faces that would not be affected by negative emotion conveyed by the fearful faces).

Participants were instructed to maintain fixation throughout the trial and to memorize only the faces in the memory array displayed on the side indicated by the arrow cues (i.e., either one or two faces; indeed, in a previous study it was demonstrated that people can store approximately two faces, or less, in VWM; Jackson & Raymond, 2008), and were explicitly informed that the faces displayed on the opposite side were of no importance for the response they had to make at the end of the trial. The numerousity of the to-be-memorized faces (set size) was manipulated within blocks. The task was to compare the cued side of the memory array and test array in order to indicate whether the identity of one of the faces had changed. On 50% of the trials, the memory array and the test array were identical. On the other 50% of trials, one face on the arrow-cued side of the memory array was replaced with a different face in the test array. When a change occurred, one face was replaced with a different face of a same-gender individual with the same expression. Half of the participants pressed the "F" key to indicate that a face had changed between the memory array and the test array and the "J" key to indicate that the memory array and the test array were identical. The other half of the participants responded using the opposite mapping. The response had to be made without speed pressure and participants were explicitly informed that speed of response would not be considered to assess their performance. Following the response, a variable intertrial interval of 1210–1300 ms elapsed before the presentation of the fixation cross indicating the beginning of the next trial.

The experiment began with a practice phase, during which the 24 faces, printed on an A4 sheet of paper, were shown to participants for 1 min. After this initial familiarization with the faces, participants performed 2 practice blocks of 12 trials each, 1 practice block with neutral faces and 1 with fearful faces, in counterbalanced order across participants. In the experimental phase, participants performed 12 experimental blocks of 64 trials each (i.e., 768 total trials), 6 blocks with neutral faces and 6 with fearful faces, that were organized always in the following order so as to minimize possible effects due to the repeated exposure to a given emotional expression: neutral (2 blocks), fearful (2 blocks), fearful (2 blocks), neutral (2 blocks), neutral (2 blocks), and fearful (2 blocks).

Behavioral Data Analysis

VWM performance was quantified using a standard index of sensitivity (*d'*; Green & Swets, 1974). These values were submitted to an analysis of variance (ANOVA) that considered set size (one face vs. two faces, displayed on the cued side of the screen) and expression (neutral vs. fearful) as within-subject factors. This was a critical control to identify how sensitive the participants were to changes between the memory and test arrays independent of possible response biases. We also estimated for each participant the number of faces encoded in VWM in each condition, using the formula developed by Cowan (2001): $K = S \times (H - FA)$, where K is the memory capacity, S is the size of the array (one face or two faces), H is the observed hit rate, and FA is the false alarm rate. Moreover, we also computed K-iterative (K_{it}) to reduce the likelihood of underestimating/overestimating individual capacity (see Jackson et al., 2009, for details).

The reaction time (RT) data were also submitted to an ANOVA that considered set size and expression as within-subject factors.

Alpha level for all the behavioral analyses was set to .05.

EEG Data Acquisition and Analysis

EEG activity was recorded continuously using a head cap with tin electrodes from the FP1, FP2, Fz, F3, F4, F7, F8, C3, C4, Cz, P3, P4, Pz, O1, O2, T7, T8, P7, P8, and right earlobe sites (see Pivick et al., 1993), referenced to the left earlobe. Horizontal EOG (HEOG) was recorded bipolarly from electrodes positioned lateral to the outer canthi of both eyes. Vertical EOG (VEOG) was recorded bipolarly from two electrodes, one above and one below the left eye. EEG, HEOG, and VEOG signals were amplified, filtered using a bandpass of 0.01–80 Hz, and digitized at a sampling rate of 250 Hz. Impedance at each electrode was maintained below 5 kΩ. The EEG was re-referenced off-line to the average of the left and right earlobes.

To eliminate high-frequency noise, the data were filtered using a high cutoff filter at 30 Hz and medium slope of 24 dB/oct. The EEG was segmented into 1200-ms epochs starting 100 ms prior to the onset of the memory array. The epochs were baseline corrected based on the mean activity during the 100-ms prestimulus period, for each electrode site. Trials associated with a HEOG exceeding ± 60 μV and eyeblinks or any other artifact exceeding ± 80 μV were discarded from analyses, which accounted for the exclusion of an average of 25% of trials (ranging from 22% of the trials when one neutral face was displayed to 28% of the trials when two fearful faces were displayed). Only trials associated with a correct response were included in the calculation of the ERPs. Following artifacts rejection, separate average waveforms for each condition were computed, and difference ERPs were constructed by subtracting the average activity recorded at posterior electrodes (i.e., O1/P7 and O2/P8) ipsilateral to the arrow-cued side of the memory array from the average activity recorded at symmetrical electrodes contralateral to the arrow-cued side of the memory array. Following previous studies, the SPCN was quantified as the mean amplitude of this difference ERP in a time window of 350–1050 ms relative to the onset of the memory array (Luria et al., 2010; McCollough et al., 2007; Vogel & Machizawa, 2004) for each experimental condition. The mean SPCN amplitudes were submitted to an ANOVA that considered set size (one face vs. two faces) and expression (neutral vs. fearful) as within-subject factors. We also conducted paired t tests to isolate the effects of set size and expression on any main effects and interactions. Alpha level was set to .05.

Results

Behavior

A summary of the behavioral results is reported in Figure 2. We submitted to ANOVAs d' values considering set size (one face vs. two faces) and expression (neutral vs. fearful) as within-subjects factors. Mean d' values for neutral faces were 3.45 and 2.12 for one and two neutral faces, respectively, and 3.44 and 2.38 for one and two fearful faces, respectively. Participants were more accurate in detecting a change when one face was displayed than when two faces were displayed in the cued visual hemifield, $F(1,17) = 212.30$, $p < .001$, $\eta_p^2 = .926$. Further, a main effect of expression occurred, $F(1,17) = 5.50$, $p < .05$, $\eta_p^2 = .244$. This main effect was modulated by a significant Set Size × Expression interaction, $F(1,17) = 5.84$, $p < .05$, $\eta_p^2 = .256$, indicating that memory benefit for fearful faces occurred only when two faces had to be encoded in VWM. This observation was substantiated by paired t tests (one fearful vs. one neutral face: $t < 1$; two fearful vs. two neutral faces: $t[17] = 8.22$, $p < .001$). These results dovetail nicely with previous studies discussed in the Introduction (Jackson et al., 2009; Langeslag et al., 2009)

We also computed K values to estimate the number of faces available in VWM for each participant in each condition. The average computed capacity for neutral faces was 0.80 and 0.88 for one and two faces (mean K for neutral faces was equal to 0.84), respectively, and 0.81 and 0.98 for one and two fearful faces, respectively (mean K for fearful faces was equal to 0.90). The greatest estimated K within the sample of participants was 1.39 when two fearful faces were displayed, indicating that participants found it difficult to encode both faces when two faces were displayed on the cued side of the screen. K values were significantly greater when two faces were displayed than when one face was displayed, $F(1,17) = 21.36$, $p < .001$, $\eta_p^2 = .557$. More important, K values were significantly greater for fearful faces than for neutral faces, $F(1,17) = 12.27$, $p < .005$, $\eta_p^2 = .419$. In line with the ANOVA on d' values, the interaction between set size and expression was significant, $F(1,17) = 13.38$, $p < .005$, $\eta_p^2 = .440$, indicating that memory benefit for fearful faces was restricted to the condition in which two faces had to be encoded in VWM, as demonstrated by paired t tests (one neutral vs. one fearful face: $t < 1$; two neutral vs. two fearful faces: $t[17] = -5.17$, $p < .001$).

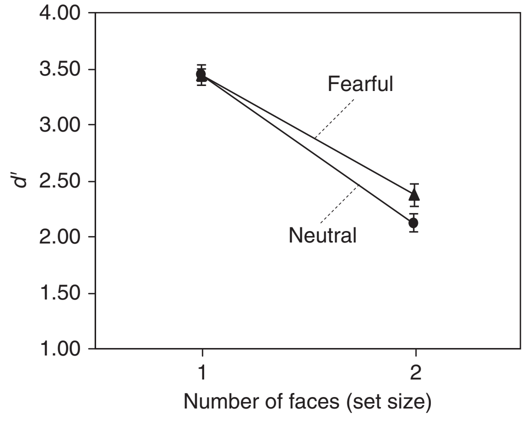

Figure 2. Discrimination index (d') plotted as a function of set size (one face vs. two faces) and as a function of facial expression (neutral vs. fearful).

As expected, K_{it} computed for each participant and each experimental condition was significantly greater for fearful faces ($K_{it} = .99$) than for neutral faces ($K_{it} = .88$), $t(17) = 5.17$, $p < .001$, $\eta_p^2 = .612$. These results dovetail nicely with Jackson et al.'s (2009) and Langeslag et al.'s (2009) findings of an angry face benefit for faces in VWM and demonstrated for the first time that this benefit can be extended to other threat-related expression, namely, fear.

We also submitted to an ANOVA mean RT data for correct responses. The ANOVA revealed a main effect of expression, $F(1,17) = 25.52$, $p < .001$, $\eta_p^2 = .600$, indicating that participants were slower in detecting a change in the cued visual hemifield when fearful faces were displayed ($M = 1043$, $SE = 59$) than when neutral faces were displayed ($M = 910$, $SE = 43$). These apparently contrasting results with a VWM benefit for fearful faces are discussed in the Discussion. The main effect of set size was marginally significant ($p = .09$) indicating that participants tended to respond faster when two faces were presented ($M = 953$, $SE = 48$) relative to when one face was presented ($M = 1000$, $SE = 55$).

Event-Related Potentials: SPCN

The contralateral and ipsilateral waves to the to-be-memorized faces recorded at electrode sites O1-P7/O2-P8 and time-locked to the onset of the memory array are displayed in Figure 3. The contralateral minus ipsilateral waves are shown in Figure 4. The figure shows four SPCN waves, one for each combination of the two main independent variables (number of faces and expression). Figure 5 displays posterior views of isovoltage contour maps of the scalp distribution of contralateral minus ipsilateral activity in a 350–1050-ms interval for each experimental condition (neutral vs. fearful faces and one vs. two faces). As expected, these maps revealed a focus of activity over posterior parietal and occipital areas.

Memorizing two faces elicited a larger SPCN than memorizing one face (two faces: $M = -.94$, $SE = .11$; one face: $M = -.65$, $SE = .13$). Most important, memorizing fearful faces elicited a larger SPCN than memorizing neutral faces (neutral faces: $M = -.70$, $SE = .10$; fearful faces: $M = -.90$, $SE = .12$). These observations were substantiated by an ANOVA carried out on the mean amplitude of the SPCN in the time window 350–1050 ms after memory array onset that considered the same variables as those considered in the behavioral analyses. The ANOVA revealed a significant effect of set size, $F(1,17) = 4.49$, $p < .05$, $\eta_p^2 = .209$. Importantly, the SPCN amplitude was significantly larger in response to fearful faces than neutral faces, as confirmed by a significant effect of expression, $F(1,17) = 4.54$, $p < .05$, $\eta_p^2 = .211$. The interaction between set size and facial expression was not significant, $F(1,17) = 1.37$, $p > .05$, $\eta_p^2 = .075$. These results, taken together, demonstrate increased maintenance for fearful faces than neutral faces. Further, they are in line with the pattern of P3b modulations observed by Langeslag et al. (2009). Although the interaction between set size and facial expression was not significant, visual inspection of the SPCN waveforms (see Figure 4) suggested to us that the effect of facial expression was mainly driven by the one-face condition. This informal observation was substantiated by planned t tests of simple effects, one neutral versus one fearful face: $t(17) = 2.31$, $p < .05$; two neutral versus two fearful faces: $t < 1$. The effect of set size was mainly driven by the neutral faces condition, one neutral face versus two neutral faces: $t(17) = 2.62$, $p < .05$; one fearful face versus two fearful faces: $t < 1$. Consid-

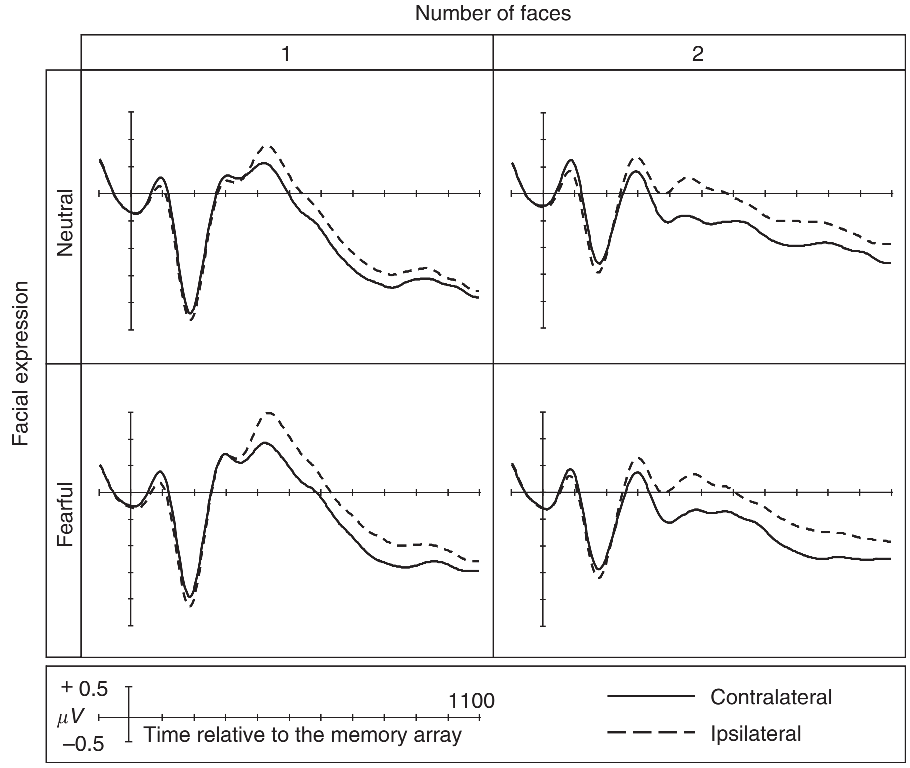

Figure 3. Contralateral and ipsilateral waveforms based on pooled activity recorded at O1/P7-O2/P8 sites, time-locked to the onset of the memory array, plotted as a function of set size (one face vs. two faces) and as a function of facial expression (neutral vs. fearful). Note that negative is plotted down. Waveforms were filtered with a high cutoff filter of 5 Hz (slope 24 dB/oct) for visual inspection only.

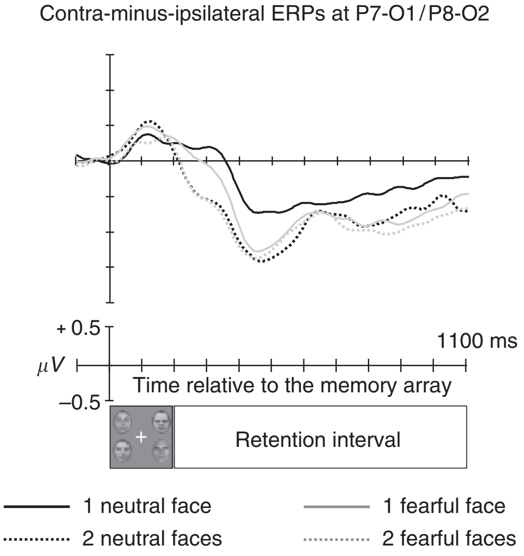

Figure 4. SPCN (contralateral minus ipsilateral), recorded at the O1/P7-O2/P8 sites, time-locked to the onset of the memory array, plotted as a function of set size (one face vs. two faces) and as a function of facial expression (neutral vs. fearful). Waveforms were filtered with a high cutoff filter of 5 Hz (slope 24 dB/oct) for visual inspection only.

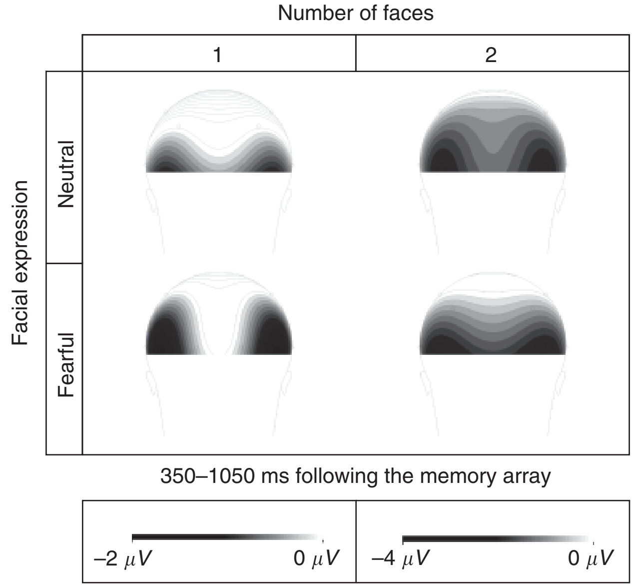

Figure 5. Posterior views of isovoltage contour maps for each experimental condition (one vs. two faces and neutral vs. fearful faces) generated from contralateral minus ipsilateral activity recorded during a 350–1050-ms interval following the onset of the memory array.

ering the *K* values reported above together with previous findings that the asymptote of the SPSN amplitude is reached when only one or two complex objects (i.e., random polygons) have to be memorized (Luria et al., 2010), the present ERP results suggest that one face was sufficient to saturate the available storage capacity of VWM (Jackson & Raymond, 2008).

Discussion

The goal of the present study was to provide a relative quantification of the processing resources involved in the VWM maintenance of negative and neutral faces while focusing on the notorious memory advantage for and/or better identification of negative faces compared to neutral faces. The electrophysiological results of the current investigation provide the first evidence that brain responses related to VWM maintenance of fearful and neutral faces are different. When neutral faces were presented, the amplitude of the SPCN was larger for two faces than for one face. These results demonstrate that the SPCN can reflect VWM maintenance for faces in a way similar to that observed for other types of visual stimuli, such as geometric shapes, colored disks, or alphanumeric characters (e.g., Brisson & Jolicœur, 2007a, b; Dell'Acqua et al., 2006; Jolicœur et al., 2008; McCollough et al., 2007; Vogel & Machizawa, 2004; Vogel, McCollough, & Machizawa, 2005). Critically, the SPCN was larger for fearful faces than for neutral faces. Although interactive effects of expression and set size were not significant, further analyses indicated that the effect of facial expression on the SPCN amplitude was mainly driven by the one-face condition. Interactive effects of expression and set size were also manifest behaviorally (see Figure 2) in the form of better identification of fearful faces relative to neutral faces when two faces (and not just one face) were memorized. An account of the apparent discrepancy between behavioral and electrophysiological results is offered later.

We momentarily restrict the discussion to the possible sources of the larger SPCN for fearful faces relative to neutral faces. Neurons with memory-related sustained responses have been found in several brain regions, including the prefrontal cortex, the cingulate and limbic areas, other subcortical structures, and parietal and temporal association areas (e.g., Chafee & Goldman-Rakic, 1998; Chelazzi, Duncan, Miller, & Desimone, 1998; for a review, see Constantinidis & Procyk, 2004). Related work using fMRI also points to the pivotal role of the parietal and occipital cortices in VWM maintenance (e.g., Grimault et al., 2009; Robitaille et al., 2009; Todd & Marois, 2004). Importantly, the voltage scalp topography of the SPCN reveals a focus of activity over posterior parietal and occipital areas (see Figure 5), which is consistent with memory-related activity taking place in these cortical regions (Brisson & Jolicœur, 2007b; Jolicœur et al., 2008; McCollough et al., 2007; Robitaille et al., 2009), a localization that is compatible with the hypothesis that SPCN activity is a direct reflection of processing required for VWM maintenance. In light of this extensive evidence on the localization and functional significance of the SPCN activity, the current observation of larger SPCN amplitudes for fearful faces than neutral faces demonstrates for the first time increased maintenance of fearful faces in VWM.

Why should representations of fearful faces be better maintained in VWM? A particularly appealing model is that based on behavioral and psychophysiological evidence compatible with the notion of prioritized perceptual/attentional processing of negative faces relative to positive or neutral faces, starting at early stages of visual processing. According to this model, more efficient and automatic processing of negative emotions at early stages (e.g., Kiss & Eimer, 2008) translates into a more detailed VWM representation of negative faces compared to neutral faces. Evidence corroborating this perspective originates from studies showing that long-term memory for visual details is superior for stimuli associated with negative emotions than for stimuli associated with neutral/positive emotions (Kensinger, 2007; Kensinger, Garoff-Eaton, & Schacter, 2006, 2007a, b). On this view, negative faces would be stored in VWM as higher resolution representations (Bays & Husain, 2008) relative to positive/neutral faces, and this would be compatible with the more ample SPCN described in response to fearful faces versus neutral faces. Previous research has shown that the processing of invariant facial attributes (such as the identity or the gender of a face) and the processing of changeable facial attributes (such as facial expression) take place on specialized, to some extent independent processing subroutines (Calder & Young, 2005; Haxby, Hoffman, & Gobbini, 2000). However, our findings, in line with Langeslag et al. (2009), provide evidence against two completely separate routes of processing of facial identity and facial expression. In contrast, our results suggest that the SPCN activity monitored in the present investigation reflects the active interplay of distinct neural circuitries involved in the processing of facial identity and in the processing of facial expression, likely resulting in the generation of high-resolution VWM representations of negative faces. The idea of higher resolution VWM representations for negative faces provides a straightforward basis for an account of the more accurate identification of negative faces relative to neutral faces.

Even though the SPCN amplitude was sensitive to emotional expression (mainly when one face had to be maintained in VWM), a more accurate identification of fearful faces was documented in the present context only when two faces had to be memorized (and not just one). Overall, this pattern of behavioral results replicates Jackson et al.'s (2009) and Langeslag et al.'s (2009) findings of an angry face benefit in a VWM task only when more than one face had to be memorized. The present results help to generalize prior findings concerning angry faces in particular to faces characterized by negative expressions of a different nature, namely, fear. It is worth noting that dissociations between neural activity related to the processing of emotional faces under different set size conditions and behavioral data was also reported by Langeslag et al. (2009) who have found reduced P3b amplitudes for angry probe faces relative to neutral probe faces independent of the set size condition, whereas the interaction between emotion and set size condition was evident behaviorally.

This observed dissociation between ERPs and behavior raises a number of considerations. First, brain responses may be more sensitive to subtle processing differences than behavioral measures, as shown by experiments where changes in the neural activity were not accompanied by behavioral effects (e.g., Heil, Rolke, & Pecchinenda, 2004; Luck, Vogel, & Shapiro, 1996). Owing to their higher sensitivity, it has been proposed that neural measures of brain activation may convey information on possible modulations affecting the processing underlying a particular cognitive task even when such modulations do not translate into overt behavioral manifestations (see Wilkinson & Halligan, 2004). Second, the lack of a behavioral advantage in terms of a more accurate identification of one fearful face than one neutral face could be due to a ceiling effect insisting on the range of behavioral variables monitored in the present context, as suggested by the high reported mean d' (3.44 and 3.45 for one fearful and one neutral face, respectively) and Cowan's K (.81 and .80 for one fearful and one neutral face, respectively). To note, similar high levels of indices of sensitivity for one face were previously reported also by Jackson et al. (2009) and Langeslag et al. (2009), where the behavioral advantage for angry faces appeared to emerge only when more than one face had to be encoded in VWM. To avoid ceiling effects, future research could address this issue by intentionally lowering the overall level of accuracy by using briefer presentation times of or increasing the overall similarity between the to-be-encoded faces.

On the other hand, the main effect of facial expression on the SPCN amplitude was mainly driven by the one-face condition, although the negative face benefit was manifest behaviorally only when two faces had to be encoded in VWM. One possible account for this finding is related to the available capacity of VWM and/or other limitations at the encoding stage due to the brief duration of the memory array (see, e.g., Eng, Chen, & Jiang, 2005; Jackson & Raymond, 2008). For instance, a recent study using a dual-target identification task during rapid serial visual presentation has shown that emotional arousing stimuli facilitate processing, particularly when resources are limited (Ihssen & Keil, 2008). It seems plausible that, under capacity and/or temporal constraints, participants selected only some low-level features rather than the whole face configurations, and this was more likely the case in which two faces were displayed. Although this, per se, cannot explain the fearful faces behavioral advantage for two fearful faces compared to two neutral faces, a plausible corollary of this hypothesis is that fearful faces contain features that are more relevant for the subsequent identification when compared to features of neutral faces. In fact, research addressing this issue has yielded mixed results. Jackson et al. (2009, Experiment 4) used a perceptual face-matching task and asked participants to judge whether pairs of angry, happy, or neutral faces matched or did not match. No advantage for angry faces relative to faces of different emotional categories was found in this study. Furthermore, using a memory task similar to those described in the Introduction, these authors (2009, Experiment 5) showed that the effect of superior memory for angry faces vanishes when faces are inverted, a result that apparently is not in line with the proposal that the processing and/or storage of simple visual features underlies the memory benefit found in the present empirical context. In contrast with these findings, another recent study using a visual search task of different facial expressions (i.e., anger, fear, sadness, happiness) provided evidence consistent with the view that inversion does not affect the perception of facial expression, that is, the threat superiority effect (faster detection of angry and fearful faces among neutral faces than vice versa) was similar for upright and inverted faces, suggesting that, at least in some instances, threat superiority can be conveyed by low-level features rather than holistic face processing (Lipp et al., 2009). To disentangle the presently unsettled role of low- versus high-level features processing in the maintenance of face stimuli, future studies may adopt a family of expedients, such as titration of the exposure duration of the stimuli in order to equate the information stored in VWM across different set sizes (i.e., the longer the exposure durations the more the stimuli displayed) and/or selection of participants on the basis of their overall VWM capacity (i.e., high capacity individuals would eventually show enhanced SPCN amplitude for two fearful faces than two neutral faces).

Finally, participants were slower in detecting a change in the cued visual hemifield when fearful faces were displayed relative to when neutral faces were displayed. At first sight, this pattern of RT data appears in contrast with findings of faster detection of schematic negative (sad or angry) faces than positive/neutral faces (e.g., Eastwood et al., 2001; Fox et al., 2000; Öhman et al., 2001; Suslow et al., 2001). However, it is relevant to note that in the current investigation only accuracy was emphasized when instructing participants. Also, different from these previous studies, facial identity, and not facial expression, was the only task-relevant dimension. Under conditions similar to those implemented in the present investigation, Langeslag et al. (2009) reported that participants were equally fast in responding to angry, happy, and neutral faces. However, in that study, participants were explicitly required to respond as fast and accurately as possible. Further, perception of fear and anger appears to be mediated by dissociable neural circuitries and often elicits different neurophysiological and behavioral responses (e.g., Adolphs et al., 1994; Fitzgerald et al., 2006; Springer, Rosas, McGetrick, & Dawn, 2007; Whalen et al., 2001). For instance, Whalen et al. (2001) suggested that, because angry expressions represent viewer-directed threat, the exposure to angry faces may induce a response potentiation via output signals at the level of the basolateral complex within the ventral amygdala (and this could eventually translate in faster RTs to these faces). Vice versa, fearful faces communicate potential risk in the environment and may require additional processing to disambiguate the source of threat (i.e., information processing potentiation) until the basolateral complex has received adequate information to create a response plan. This overall process would have as a consequence a delayed response to fearful faces relative to angry faces.

To conclude, our findings provide the first ERP evidence of increased maintenance in VWM of faces with a fearful expression relative to faces with a neutral expression. In particular, faces with a fearful expression elicited an enhanced SPCN relative to faces with a neutral expression, suggesting that fearful faces are maintained in memory as high-resolution representations.

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