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Electrophysiological correlates of improved short-term memory for emotional faces

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ABSTRACT

Long-term memory (LTM) is enhanced for emotional information, but the influence of stimulus emotionality on short-term memory (STM) is less clear. We examined the electrophysiological correlates of improved visual STM for emotional face identity, focusing on the P1, N170, P3b and N250r event-related potential (ERP) components. These correlates are taken to indicate which memory processing stages and cognitive processes contribute to the improved STM for emotional face identity. In the encoding phase, one or three angry, happy or neutral faces were presented for 2 s, resulting in a memory load of one or three. The subsequent 1-s retention phase was followed by a 2-s retrieval phase, in which participants indicated whether a probe face had been present or not during encoding. Memory performance was superior for angry and happy faces over neutral faces at load three. None of the ERP components during encoding were affected by facial expression. During retrieval, the early P3b was decreased for emotional compared to neutral faces, which presumably reflects greater resource allocation to the maintenance of the emotional faces. Furthermore, the N250r during retrieval was increased for emotional compared to neutral faces, reflecting an enhanced repetition effect for emotional faces. These findings suggest that enhanced visual STM for emotional faces arises from improved maintenance and from improved detection of face repetition at retrieval.

1. Introduction

In long-term memory (LTM), emotional stimuli are better encoded, consolidated, and retrieved than neutral stimuli, which results in an emotion enhancement effect on LTM (Hamann, 2001; Kensinger, 2004, 2007; LaBar & Cabeza, 2006; Phelps, 2004). The effect of stimulus emotionality on short-term memory (STM), however, is less well established. Recent research has shown better STM for the identity of angry faces compared to happy or neutral faces (Jackson, Wu, Linden, & Raymond, in press). Functional magnetic resonance imaging (fMRI) revealed that the behavioural benefit for angry faces is supported by enhanced activation in the right superior temporal sulcus region, ventrolateral prefrontal cortex and basal ganglia (Jackson, Wolf, Johnston, Raymond, & Linden, 2008). Because of its temporal resolution, fMRI only provides limited information about the phase of the memory process at which the effect of facial expression on STM occurs.

Event-related potentials (ERPs) are a more useful measure for determining which stages of processing are influenced by a certain experimental manipulation (Linden, 2007; Luck, 2005) and ERP research on face processing and STM has yielded a number of components that index the different stages of face evaluation, encoding, and retrieval. In the current study, we measured ERPs during a task requiring STM for the identity of emotional faces (Jackson et al., 2008, in press). Examination of the electrophysiological markers may reveal during which memory phase (i.e. encoding, maintenance and/or retrieval) the emotion enhancement effect on STM occurs and may indicate the cognitive processes (such as structural face encoding, resource allocation, etc.) involved. Because of the methodological problems of such reverse inferences (Henson, 2006) it is important to use neural signatures that are robustly and specifically associated with certain cognitive processes.

In a previous study (Morgan, Klein, Boehm, Shapiro, & Linden, 2008), the effect of memory load on the ERP was investigated using the same STM task as the above-mentioned studies, but with neutral faces only. The ERP waveform during the encoding and retrieval phases contained the P1, N170, P3b, and N250r components, with the latter three components being modulated by the number of faces that had to be remembered. In the current study, using the STM task with angry, happy, and neutral faces, we

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investigated whether the P1, N170, P3b and N250r are modulated by facial expression, to see if any of those components are an electrophysiological correlate of improved STM for emotional faces. We selected the P1 because it is a marker of the integrity of early visual processing and its amplitude has been associated with later STM retrieval success (Haenschel et al., 2007). The other components were selected because of their prominent and well-studied role in face perception (N170), memory (P3b) and face repetition (N250r).

The N170 is a negative component over inferior occipito-temporal electrodes that is thought to originate from posterior-lateral occipito-temporal cortex (Schweinberger, Pickering, Jentzsch, Burton, & Kaufmann, 2002). The N170 presumably reflects the structural encoding of face stimuli prior to face recognition and is usually unaffected by facial expression (e.g. Eimer & Holmes, 2002). Nevertheless, in some studies the N170, and even the earlier P1, have been found to be modulated by facial expression (e.g. Batty & Taylor, 2003; Sprengelmeyer & Jentzsch, 2006). However, because those modulations were not expression-specific, it has been suggested that they reflect non-specific configural and attention effects rather than emotion effects (Vuilleumier & Pourtois, 2007). In the current study it is therefore hypothesized that the P1 and N170 will not be electrophysiological correlates of the emotion enhancement effect on STM.

The P3b component is a positive deflection that occurs from about 300 ms after stimulus onset and is maximal at posterior electrodes. In general, the P3b is thought to reflect processing capacity or resource allocation (Kok, 2001; Polich, 2007). The P3b is normally increased for emotional compared to neutral stimuli (see Olofsson, Nordin, Sequeira, & Polich, 2008; Schupp, Flaish, Stockburger, & Junghöfer, 2006) and has shown an amplitude increase in response to fearful compared to neutral, and to threatening compared to friendly and neutral faces (Eimer & Holmes, 2002; ; Schupp, Öhman, et al., 2004). The enhanced P3b for emotional stimuli is taken to reflect the capture of attention by stimuli that are emotionally significant (Kok, 2001; Langeslag, Franken, & Van Strien, 2008; Schupp, Cuthbert, et al., 2004; Schupp et al., 2006).

During retrieval from STM, the P3b typically decreases with increasing memory load (Busch & Herrmann, 2003; Kok, 2001; Morgan et al., 2008), implying that fewer resources are allocated to the probe stimuli as more resources are allocated to maintenance processes (Kok, 2001). Interestingly, in a study in which spatial STM for non-emotional stimuli was tested following the induction of different emotional states, the P3b elicited by the probe stimulus was smaller during a negative than during a neutral state, indicating that the negative state diverted resources away from the probe (Li, Li, & Luo, 2006). Likewise, a smaller P3b occurred in response to acoustic startle probes that were preceded by emotional versus neutral sounds or pictures, and this P3b suppression was interpreted as the allocation of resources to processing the emotional stimulus preceding the probe at the expense of processing the probe stimulus itself (Keil et al., 2007; see also Schupp, Cuthbert, et al., 2004). Thus, although the P3b is typically larger for emotional than neutral stimuli, it appears to be decreased for stimuli that have to compete for processing resources with preceding or ongoing emotional information. From the existing literature then, two contrasting hypotheses can be formulated for the current study. On the one hand, the P3b during encoding and/or retrieval could be larger for emotional compared to neutral faces. This would indicate that emotional faces are allocated increased processing resources, which could explain the emotion enhancement effect on STM. Alternatively, because an emotional probe face is preceded by the maintenance in STM of one or more emotional encoding faces, the P3b during retrieval may actually be decreased for emotional compared to neutral faces. In this scenario, more processing resources would be deployed for the maintenance of the emotional compared to neutral faces, which could account for the emotion enhancement effect as well.

In previous STM studies, the P3b consisted of an early and a late subcomponent, occurring between 300 and 400 ms and between 400 and 700 ms after stimulus onset respectively. In the context of STM retrieval, the early P3b might reflect stimulus evaluation whereas the late P3b may reflect memory search operations (Bledowski et al., 2006; Morgan et al., 2008). The P3b elicited by emotional stimuli has also been found to consist of two parts (e.g. Amrhein, Mühlberger, Pauli, & Wiedemann, 2004), where the early P3b has been taken to reflect resource allocation due to task-relevance or emotional salience and the late P3b (or slow wave) is associated with LTM formation and top-down control of emotional processing (Olofsson et al., 2008). Because the current study does not concern LTM or top-down control, it is expected that any emotional modulation of the P3b would occur in its early, and not in its late part.

The N250r or early repetition effect (ERE) is a relative negativity over inferior temporo-parietal electrodes and relative positivity over fronto-central electrodes for repeated compared to new faces around 300 ms after stimulus onset (see Schweinberger & Burton, 2003). The N250r only occurs for face repetitions across a short time period and is not observed for longer delays (Schweinberger, Pickering, Burton, & Kaufmann, 2002), suggesting that it is related to STM processes (see also Morgan et al., 2008). Because the N250r is larger for repeated familiar than unfamiliar faces, it is thought to reflect the activation of face recognition units (FRUs) (Herzmann, Schweinberger, Sommer, & Jentzsch, 2004; Schweinberger & Burton, 2003; Schweinberger, Pfütze, & Sommer, 1995). These FRUs match the products of the structural encoding process with stored structural codes that describe familiar faces, and this matching processes is supposed to be abstract and independent of image-specific details such as facial expressions (Bruce & Young, 1986; see also Haxby, Hoffman, & Gobbini, 2000). The N250r appears to originate from the fusiform gyrus (Schweinberger, Pickering, Jentzsch, et al., 2002), where the fusiform face area (FFA) that is concerned with face identification (Haxby et al., 2000) is located. Indeed, a series of studies has suggested that the FFA codes face identity irrespective of facial expression, whereas the superior temporal sulcus processes facial expressions (Haxby et al., 2000; Schwaninger, Wallraven, Cunningham, & Chiller-Glaus, 2006; Schweinberger & Burton, 2003; Vuilleumier & Pourtois, 2007).

However, previous findings challenge the notion that FRUs are ignorant of changeable aspects of faces. The N250r was, for example, larger when a probe face was preceded by the same, as opposed to a different picture of the same individual (Schweinberger, Pickering, Jentzsch, et al., 2002). Moreover, accumulating behavioural and neuroimaging evidence suggests that the processing of face identity and expression are not entirely separable (Calder & Young, 2005; Vuilleumier & Pourtois, 2007). That is, even though face identity appears to be processed independently of task-irrelevant facial expression, expression judgements are slowed by task-irrelevant variations in face identity (Schweinberger, Burton, & Kelly, 1999; Schweinberger & Soukup, 1998). Furthermore, familiar angry faces have been found to be recognized more slowly than familiar happy faces (Kaufmann & Schweinberger, 2004), and faces with a positive expression were judged as being more familiar and faces with a negative expression as less familiar compared to neutral faces (Baudouin, Gilibert, Sansone, & Tiberghien, 2000; Lander & Metcalfe, 2007). Also, FFA activity has been found to be affected by facial expression. Greater FFA activity has been reported for fearful versus neutral faces during a perceptual face matching task (Vuilleumier, Armony, Driver, & Dolan, 2001). In the fMRI study using the same STM task as the current study, the FFA was more activated by angry than by happy and neutral faces (Jackson et al., 2008). To our knowledge, it has not been investigated before