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Retention of identity versus expression of emotional faces differs in the recruitment of limbic areas

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ABSTRACT

Faces are multidimensional stimuli that convey information for complex social and emotional functions. Separate neural systems have been implicated in the recognition of facial identity (mainly extrastriate visual cortex) and emotional expression (limbic areas and the superior temporal sulcus). Working-memory (WM) studies with faces have shown different but partly overlapping activation patterns in comparison to spatial WM in parietal and prefrontal areas. However, little is known about the neural representations of the different facial dimensions during WM. In the present study 22 subjects performed a face-identity or face-emotion WM task at different load levels during functional magnetic resonance imaging. We found a fronto-parietal-visual WM-network for both tasks during maintenance, including fusiform gyrus. Limbic areas in the amygdala and parahippocampal gyrus demonstrated a stronger activation for the identity than the emotion condition. One explanation for this finding is that the repetitive presentation of faces with different identities but the same emotional expression during the identity-task is responsible for the stronger increase in BOLD signal in the amygdala. These results raise the question how different emotional expressions are coded in WM. Our findings suggest that emotional expressions are re-coded in an abstract representation that is supported at the neural level by the canonical fronto-parietal WM network.

1. Introduction

Functional imaging studies of visual working memory have focused on the maintenance and manipulation of visual objects, features and spatial information (Linden, 2007; Wager & Smith, 2003). Important areas involved in visual working memory processes are the prefrontal cortex, intraparietal sulcus and higher visual areas. Each of these regions is supposed to subserve a special function in this network. It has been suggested that some areas in the prefrontal cortex are specialised regarding the material type (object, spatial, verbal) (Jennings, Van der Veen, & Meltzer, 2006; McIntosh, Grady, Haxby, Ungerleider, & Horwitz, 1996; Ventre-Dominey et al., 2005), while others suggest that differences are mainly based on processes such as maintenance, manipulation, or inhibition, which are necessary to perform the WM task (Petrides, 2005; Petrides, Alivisatos, & Frey, 2002) or by an interaction between material type and processes (Mohr, Goebel, & Linden, 2006).

Faces are multidimensional stimuli and convey many important features simultaneously. They represent a special category in the field of visual objects, probably based on their importance for the recognition of relevant others (identity) and for nonverbal communication (emotional expression). The identity of a person can be recognised by his/her individual physiognomy, which is based on the spatial composition of facial features (nose, eyes, mouth, etc.). Emotional expression is then derived from subtle changes in the spatial composition of facial features (Bruce & Young, 1986). Neuroimaging has elucidated the brain structures involved in the processing of faces (Haxby et al., 2001; Kanwisher, Stanley, & Harris, 1999) and their emotional expression (Gur, Schroeder, et al., 2002; Phillips et al., 2001; Vuilleumier & Pourtois, 2007). These studies converge to suggest that structures involved in the recognition of the identity of faces (structural and static properties of faces) are mainly located in the extrastriate visual cortex (Adolphs, 2002; Haxby, Hoffman, & Gobbini, 2000). More changeable configurational features of faces (emotional expression) are processed in the superior temporal lobe (Adolphs, 2002; Haxby, Hoffman, et al., 2000; Haxby, Petit, Ungerleider, & Courtney, 2000b). Further support for the role of the superior temporal cortex comes from animal studies with single cell recordings (Hasselmo, Rolls, &

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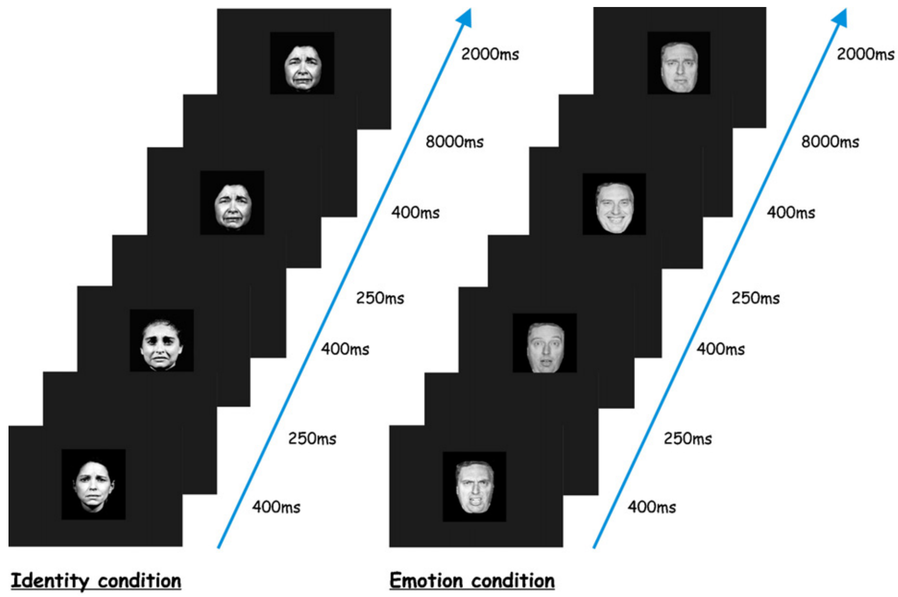

Fig. 1. Experimental design for load 3. Left: identity condition with 3 females displaying the same emotion. Right: emotion condition with the same male displaying 3 different emotions.

Baylis, 1989; Jellema & Perrett, 2003) Many functional neuroimaging studies have investigated the impact of emotional expression of human faces on brain activity (Gläscher, Tuscher, Weiller, & Buchel, 2004; Gur, Schroeder, et al., 2002; Hariri, Tessitore, Mattay, Fera, & Weinberger, 2002; Pegna, Khateb, Lazeyras, & Seghier, 2005; Phillips et al., 2001). The amygdala is the structure mostly associated with the recognition of emotional expressions (Gur, Schroeder, et al., 2002; Hariri et al., 2002; Morris et al., 1998; Wright, Martis, Shin, Fischer, & Rauch, 2002; Yang et al., 2002), although the debate is ongoing as to whether the amygdala primarily is active to negative facial expressions as fear and sadness or relevant in recognizing all human emotional expressions. Breiter et al. (1996) found that the repeated presentation of faces with emotional expressions causes a reduction of amygdala activity, but Gläscher et al. (2004) found increased amygdala activity for the repeated presentation of fearful faces of different subjects compared to conditions where either identity was constant or emotion was varied.

In working memory, faces show partly overlapping activation patterns in comparison to spatial WM (Haxby, Petit, et al., 2000; Sala, Rama, & Courtney, 2003) with a dorso-ventral gradient for spatial versus facial stimuli (Haxby, Hoffman, et al., 2000; Haxby, Petit, et al., 2000).

Two recently published studies investigated WM of emotional faces. LoPresti et al. (2008) explicitly instructed subjects to match a sample and a test face either for identity or for the emotional expression. In the identity condition, sample and test faces expressed a different emotion, whereas in the emotion condition sample and test faces differed in identity. The authors focused on three structures more active in the delay for faces versus a control stimulus, the left orbitofrontal cortex (OFC), the left amygdala and the left hippocampus. Only the OFC had significantly higher activity for the emotion task during the presentation of the sample face and significantly higher activity for negative faces during the presentation of the test face. The absence of differences between the two conditions during delay came as a surprise. However, it is important to notice that the authors only measured working memory at a load of one, which may have led to a marginal activation of emotion- or identity specific networks. Jackson, Wolf, Johnston, Raymond, and Linden (2008) used a design wherein emotional expression was varied at four load levels. Subjects were only asked to match the faces for identity, so the emotional aspect was studied implicitly. Another important difference was the short delay of only 1 s, which did not allow for a separation of the processes of encoding, maintenance and retrieval. This study revealed higher activity for negative emotion (angry faces) in the right hemispheric inferior frontal gyrus, superior temporal gyrus and globus pallidus internus for all conditions.

Load-dependent changes are an inherent characteristic of the brain's working memory networks (Linden, 2007). We therefore regarded the manipulation of the number of faces to be maintained in either the identity or emotion task as crucial. In the present study we focused on neural processes during the maintenance phase for identity or emotional expression of faces at different load levels. Because of its dual role in emotion processing and memory, we hypothesized that the amygdala and connected limbic areas would play an important role in the maintenance of emotional faces.

2. Methods

2.1. Participants

Twenty-two right-handed volunteers (13 females/9 males) (mean age = 27.3, *SD* = 4.3) with normal or corrected to normal vision participated in the experiment. The subject's physical health was verified in an interview before the study, and those who had a history of neurological diseases, psychiatric diseases, or drug or alcohol abuse were excluded. No subject was taking medication affecting cerebral blood flow at the time of the study. All participants gave informed consent and experimental procedures were approved by the local ethics committee and in accordance with the Declaration of Helsinki 1975.

2.2. Stimuli and experimental procedure

In each trial of the paradigm, participants had to memorize one, two, or three sequentially presented black-and-white exemplars human faces taken from the samples of Ekman (Ekman, Friesen, & Ellsworth, 1972) and Gur, McGrath, et al. (2002) in a forced choice paradigm. Faces displayed the following emotions: anger, disgust, fear, happiness, sadness, surprise or a neutral expression. Trials consisted either of the same subject expressing different emotional expressions (emotion condition) or different subjects with the same emotional expression (identity condition), leaving some ambiguity in the case of only one presented stimuli. Faces were cropped with an individually formed shape in order to avoid that peripheral face features allow easy identification of faces. The term emotion was explicitly not named in the instruction to avoid verbalization of emotional expressions. Stimuli were matched for gender, but not for emotional expressions, due to the fact that there are more negative facial emotional expressions and a limited number of faces. Sample stimuli were presented for 500 ms each. In case of presentation of two or three faces, stimuli were separated by 250 ms blank screens. After a 8 s delay, one