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Dissimilar processing of emotional facial expressions in human and monkey temporal cortex

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Emotional facial expressions play an important role in social communication across primates. Despite major progress made in our understanding of categorical information processing such as for objects and faces, little is known, however, about how the primate brain evolved to process emotional cues. In this study, we used functional magnetic resonance imaging (fMRI) to compare the processing of emotional facial expressions between monkeys and humans. We used a $2 \times 2 \times 2$ factorial design with species (human and monkey), expression (fear and chewing) and configuration (intact versus scrambled) as factors. At the whole brain level, neural responses to conspecific emotional expressions were anatomically confined to the superior temporal sulcus (STS) in humans. Within the human STS, we found functional subdivisions with a face-selective right posterior STS area that also responded to emotional expressions of other species and a more anterior area in the right middle STS that responded specifically to human emotions. Hence, we argue that the latter region does not show a mere emotion-dependent modulation of activity but is primarily driven by human emotional facial expressions. Conversely, in monkeys, emotional responses appeared in earlier visual cortex and outside face-selective regions in inferior temporal cortex that responded also to multiple visual categories. Within monkey IT, we also found areas that were more responsive to conspecific than to non-conspecific emotional expressions but these responses were not as specific as in human middle STS. Overall, our results indicate that human STS may have developed unique properties to deal with social cues such as emotional expressions.

Introduction

Research on emotional facial expressions in non-human primates has often attracted scientists because it opens an evolutionary window on emotions and social perception in humans (de Gelder, 2010; de Waal, 2011; Parr and Heintz, 2009; Parr et al., 2005, 2008). Since the advent of functional neuroimaging, facial expressions have been the favorite stimulus class for studying emotion processing in the human brain and insights from animal research have strongly influenced the interpretation of findings in humans. However, in contrast with the large literature of comparative studies on the processing of categorical information (Bell et al., 2009; Pinsk et al., 2009; Rajimehr et al., 2009; Tsao et al., 2003, 2008a), a direct comparison of processing emotional expressions between species has not been reported yet and it remains largely speculative how the primate brain evolved to deal with emotional cues (Ghazanfar and Santos, 2004). During evolution the repertoire of facial displays evolved in parallel with species-specific social interactions (Burrows et al., 2009; Parr et al., 2005). Hence, although many aspects of processing emotional expressions may be conserved across primate species, the differences between humans and monkeys may primarily be reflected in neural pathways involved in social cognitive processes such as attributing meaning to other's mental states (Brothers, 1989; Joffe and Dunbar, 1997; Parr et al., 2005).

Neural correlates of emotional facial expressions have been reported in humans and monkeys separately. However, the limited number of studies in monkeys hampers a comparison based on the existing neuroimaging literature. Emotion effects in monkeys include activation of face selective ventral prefrontal areas (Tsao et al., 2008b), amygdala (Hoffman et al., 2007), and modulatory effects in non-face-selective inferotemporal cortex (Hadj-Bouziane et al., 2008). In humans, orbitofrontal cortex and amygdala also respond to emotional expressions and are thought to be involved in more basic species-independent emotion operations such as control processes and decoding valence or saliency (Dolan, 2002; Rolls, 2004).

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Similar to the effects in monkey IT, emotion-dependent activity changes in human ventral temporal occipital face areas are generally interpreted as modulatory effects, as supported by lesion studies of the amygdala (Vuilleumier et al., 2004). In addition, human neuroimaging studies repeatedly documented emotion effects in the superior temporal sulcus (STS). The human STS is not only implicated in processing visual information, including variable facial information such as gaze or expressions (Graham and LaBar, 2012), but also in modality-independent higher order social cognitive functions (Allison et al., 2000; Hein and Knight, 2008; Kujala et al., 2009). Given its proposed role as an interface between perception and more complex social cognitive processes, we considered the STS as a candidate region for human-specific facial emotion effects.

To compare directly the processing of facial emotion cues between species, we used event-related fMRI in monkeys (Vanduffel et al., 2001) and humans with an identical 2×2×2 factorial design with *dynamic facial expression* (fear and chewing), *species* (human and monkey) and *configuration* (intact versus mosaic scrambled) as factors (Fig. 1). To stay as close as possible to naturalistic conditions, we used dynamic faces. We chose fear as emotional condition because this is the most widely-studied expression in neuroimaging studies of each species separately. Videos of chewing faces served as neutral controls and videos of scrambled faces were used to control for the low-level effects such as motion (Puce et al., 1998). Because the interpretation of emotional expressions is largely species-specific (Hebb, 1946), we took advantage of our factorial design to study which areas responded preferentially to conspecific emotional expressions by contrasting them with heterospecific expressions in both species. Furthermore, to relate our findings anatomically to face-*selective* regions, an independent localizer experiment was also conducted in both species.

Methods

Subjects

Three healthy male rhesus monkeys (M18, M19 and M20; 5–7 kg, 4–5 years old) and twenty-three normal human volunteers (11 male, 24–34 years old, all right-handed and had normal or corrected-to-normal visual acuity) were scanned for the dynamic facial expression experiment. Two of the three monkeys and seven human volunteers (3 male, all right-handed, 23–32 years old) were scanned in the separate localizer experiment. All human participants gave written informed consent in accordance with the Declaration of Helsinki. The ethical committee of the University of Leuven Medical School approved the experiments.

Stimuli

Twenty-four movie clips, acquired from six unfamiliar professional male human actors and six male monkeys, were used for each type of expressions (twelve for each species) in the dynamic facial expression experiment. All dynamic facial expression stimuli were frontal view color movie clips, with the external face contour removed and the mean luminance (9 cd/m^2) equalized (Fig. 1A). The expressions were all gaze-averted but with heads fixed. We chose averted gaze, because unlike similar grimaces in humans, the direct-gaze, teeth-baring expressions of rhesus macaques signal submission towards the observer (de Waal and Luttrell, 1985; Maestripieri and Wallen, 1997). To control for the eye-gaze direction, head orientation and movement asymmetries, the mirror-reversed version of each movie clip was also created. The spatiotemporally scrambled control stimuli were generated from each

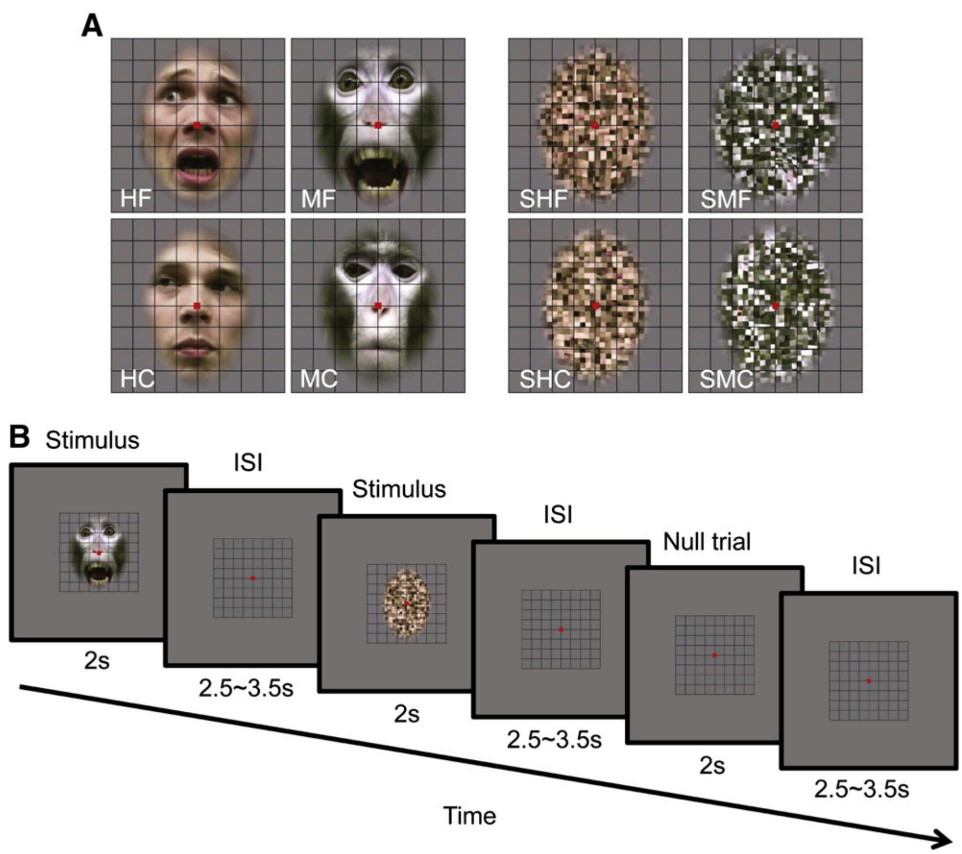

Fig. 1. Stimuli and experimental paradigm. (A) Upper row left panels: intact human *fearful* (HF) and monkey *fearful* (MF) expressions; upper row right: scrambled versions of HF (SHF) and MF (SMF). Lower row left panels: intact human *chewing* (HC) and monkey *chewing* (MC); lower row right panels: scrambled versions of HC (SHC) and MC (SMC). Examples of dynamic displays are provided in supplementary videos 1 to 8. (B) Event-related experimental design. Trials consisted of 2 s stimulus presentation followed by a variable interstimulus interval (ISI) between 2.5 and 3.5 s.