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Lateralization for dynamic facial expressions in human superior temporal sulcus

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ABSTRACT

Most face processing studies in humans show stronger activation in the right compared to the left hemisphere. Evidence is largely based on studies with static stimuli focusing on the fusiform face area (FFA). Hence, the pattern of lateralization for dynamic faces is less clear. Furthermore, it is unclear whether this property is common to human and non-human primates due to predisposing processing strategies in the right hemisphere or that alternatively left sided specialization for language in humans could be the driving force behind this phenomenon.
We aimed to address both issues by studying lateralization for dynamic facial expressions in monkeys and humans. Therefore, we conducted an event-related fMRI experiment in three macaques and twenty right handed humans. We presented human and monkey dynamic facial expressions (chewing and fear) as well as scrambled versions to both species. We studied lateralization in independently defined face-responsive and face-selective regions by calculating a weighted lateralization index (LIwm) using a bootstrapping method. In order to examine if lateralization in humans is related to language, we performed a separate fMRI experiment in ten human volunteers including a 'speech' expression (one syllable non-word) and its scrambled version.
Both within face-responsive and selective regions, we found consistent lateralization for dynamic faces (chewing and fear) versus scrambled versions in the right human posterior superior temporal sulcus (pSTS), but not in FFA nor in ventral temporal cortex. Conversely, in monkeys no consistent pattern of lateralization for dynamic facial expressions was observed. Finally, LIwms based on the contrast between different types of dynamic facial expressions (relative to scrambled versions) revealed left-sided lateralization in human pSTS for speech-related expressions compared to chewing and emotional expressions.
To conclude, we found consistent laterality effects in human posterior STS but not in visual cortex of monkeys. Based on our results, it is tempting to speculate that lateralization for dynamic face processing in humans may be driven by left-hemispheric language specialization which may not have been present yet in the common ancestor of human and macaque monkeys.

Introduction

It is generally assumed that faces are processed asymmetrically in the human brain yet it remains unclear whether lateralization for faces is dependent on stimulus type, regionally selective and human-specific. It needs to be noted that lateralization for faces is a debated question in comparative neuroscience. Some argue that hemispheric specialization for facial expressions emerged in parallel with left-hemispheric specialization in verbal communication and is indeed a human property (Overman and Doty, 1982; Corballis et al., 2000), whereas others propose that lateralization was already present earlier in primate ancestors because of predisposing properties of the right hemisphere (Hamilton and Vermeire, 1988; Vallortigara et al., 1999; Zangenehpour and Chaudhuri, 2005). Split-field (Ellis and Shepherd, 1975; Broman, 1978; Reynolds and Jeeves, 1978) and brain lesion

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studies (Sergent and Signoret, 1992; De Renzi et al., 1994; Wilkinson et al., 2009; Busigny et al., 2010) have been the major source of evidence for a privileged role of the right hemisphere in face processing in humans, whereas similar studies in monkeys have yielded conflicting results (Overman and Doty, 1982; Hamilton and Vermeire, 1988; Vermeire and Hamilton, 1998). In chimpanzees results are not conclusive either with a left visual field superiority in processing chimeric faces of humans only and of human and chimpanzee faces (Morris and Hopkins, 1993; Dahl et al., 2013) whereas no such lateralization could be found in a match-to-sample task (Plotnik et al., 2003).

Most of the imaging studies that reported laterality effects for face processing used static faces and focused on the FFA (Dien, 2009). Laterality effects for dynamic faces have not yet been explicitly addressed, despite important differences in neural processing between dynamic and static faces. For instance, STS responds much stronger to dynamic than to static faces and even includes areas that respond selectively to dynamic faces (Pitcher et al., 2011) (see also de Gelder and Van den Stock (2010) for an overview of functional imaging studies using dynamic facial expressions). Furthermore, although stronger activations have been reported in right compared to left human STS, rigorous statistical methods have not been used to investigate lateralization for dynamic faces (e.g. Foley et al. (2012)). Also, recent comparative studies suggested that the specialization of the STS for dynamic facial expressions is stronger in humans than monkeys (Zhu et al., 2013; Polosecki et al., 2013). If the human or hominoid brain developed specialization for dynamic faces and lateralization occurs at the same level, this may imply that lateralization for dynamic faces is also a human-unique property.

The cognitive demands that are associated with behavioral testing hamper comparisons of species that differ importantly in cognitive abilities. Neuroimaging studies on the other hand provide a means of studying lateralized effects directly without a specific task. So far, however, comparative brain imaging studies have not explicitly addressed lateralization of dynamic face processing (Tsao et al., 2003; Pinsk et al., 2009; Polosecki et al., 2013). If language development and specialization in verbal communication are the driving forces behind lateralization for dynamic face processing in humans, one would expect the largest effects in homotopical areas relative to the classical language areas, such as Wernicke's area. Also one would predict that facial gestures that map upon lexical representations, such as speech, would be coded differently compared to non-verbal expressions.

In the present fMRI study we aimed to address three questions. Is lateralization for dynamic faces present in the human brain, and if so where? Is lateralization for dynamic faces a unique property of the human brain? Does lateralization depend on the type of facial gesture, linguistic or emotional? During event-related fMRI, we presented dynamic facial expressions (both chewing and fearful faces), as well as their spatiotemporally mosaic scrambled versions, to humans and macaques. In a separate experiment, we also presented dynamic faces producing speech to humans, in the absence of auditory stimuli. We studied lateralization not only in regions that were responsive to dynamic faces but also in face-selective regions defined by an independent localizer experiment. Lateralization was determined by calculating laterality indices (LIs) using a bootstrapping method within the LI toolbox for SPM8 (Wilke and Schmithorst, 2006; Wilke and Lidzba, 2007). This method yields a robust mean LI-value, with a minimum and a maximum LI between −1 and 1 indicating right or left hemispheric specialization respectively, while limiting the influence by statistical outliers.

Methods

Subjects

Twenty healthy volunteers (12 female, 22–34 years old) and three healthy male rhesus monkeys (*Macaca mulatta*; 5–7 kg, 4–5 years old) participated in Experiment 1 with dynamic human and monkey facial expressions (chewing and fear). Ten human subjects (6 male, 23–36 years old; 8 of which also participated in the first experiment) participated in Experiment 2 with only human dynamic faces but with speech expressions added. A localizer scan to determine face-selective areas was obtained from the latter 10 subjects and the 3 monkeys. For one of the monkeys, the data from the localizer experiment was discarded because of technical problems. The experiments were approved by the ethical committee of the University of Leuven and all human participants gave written informed consent. All human subjects were right-handed as assessed through the Edinburgh Handedness Inventory (mean for 20 subjects of Experiment 1 was 0.92; mean for 10 subjects of Experiment 2 was 0.97). All subjects had normal or corrected-to-normal visual acuity.

Stimuli

Human and monkey dynamic faces

Movie clips acquired from six professional human male actors and six male monkeys were used for each type of expression in the dynamic face experiments. The chewing and fearful expressions used in Experiment 1 have been described elsewhere (Zhu et al., 2013). The speech stimuli (Experiment 2) consisted of the neutral pronunciation of a one-syllable non-word, but only the visual component of the speech stimuli was used in the experiment. Construction of the stimuli was exactly as described in Zhu et al. (2013): All stimuli were frontal view color movie clips with external face contours removed and mean luminance equalized. Expressions were gaze-averted but with heads fixed. Mirror-reversed versions of each movie clip were also created to control for eye-gaze direction, head orientation and movement asymmetries. Spatiotemporally scrambled control stimuli were generated in which the facial shape information and the dynamic expressions were removed while the low-level motion information from the original clips was retained. Scrambled stimuli were created by applying a temporally scrambled flow field of each movie clip to the mosaic-scrambled start image of the original sequence. The mosaic scrambling was accomplished by dividing the image into a 32 × 32 grid and shuffling the positions of the grid elements. The flow field of the original movie clips was calculated using an optic flow estimation algorithm developed by Papenberg et al. (2006), then temporally scrambled by spatially dividing the flow field into an 8 × 8 grid and shuffling the frames differently for each grid across temporal blocks with five frames for each block. Fig. 1A gives an illustration of each stimulus type.

Localizer experiment

Six object categories, each containing 20 static achromatic images, were presented to both humans and monkeys during scanning. These categories included human and monkey faces, headless human bodies and two categories of inanimate manmade objects with different mean aspect ratios (objects H and objects M) (see Popivanov et al. (2012) for further description and illustration of all stimuli). Mosaic-scrambles were created by spatially scrambling one category of inanimate manmade objects (i.e. objects M). The scrambling was accomplished by dividing the image into a 38 × 38 grid and shuffling the positions of the grid within a rectangular area bordering the original object. The mean luminance was equated across stimuli. All stimuli were embedded in a random-noise background having the same luminance as the images. The noise background filled the entire screen.

Experimental design

Human and monkey dynamic faces

An event-related design was used in Experiments 1 and 2 (Fig. 1B). Every movie clip was presented once for 2 s, followed by a 2.5 s to 3.5 s inter-stimulus interval displaying only the grid. Twelve null-trials with only the grid presented for 4.5 s to 5.5 s were randomly