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Asymmetry in facial expression of emotions by chimpanzees

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Abstract

Asymmetries in human facial expressions have long been documented and traditionally interpreted as evidence of brain laterality in emotional behavior. Recent findings in nonhuman primates suggest that this hemispheric specialization for emotional behavior may have precursors in primate evolution. In this study, we present the first data collected on our closest living relative, the chimpanzee. Objective measures (hemimouth length and area) and subjective measures (human judgements of chimeric stimuli) indicate that chimpanzees' facial expressions are asymmetric, with a greater involvement of the left side of the face in the production of emotional responses. No effect of expression type (positive versus negative) on facial asymmetry was found. Thus, chimpanzees, like humans and some other nonhuman primates, show a right hemisphere specialization for facial expression of emotions.

Keywords: Brain asymmetry; Emotions; Facial expressions; Chimeric stimuli; Chimpanzees

1. Introduction

The neuropsychological basis of emotional behavior has been investigated for more than three decades in human subjects, with specific attention focused on the issue of brain lateralization in the control and mediation of emotions (for a review, see [11]). Emotion has been understood a biologically based state involving several components: perception, experience, physiological arousal, goal-directed activities and expression [37]. The human literature has typically explored the different processing modes (perception, expression, experience and physiological arousal) as well as different channels at the communication level (facial, prosodic, lexical, gestural and postural) (for a componential theoretical approach to emotional behavior, see [2]). As a result of these studies, two distinct conceptual models of emotion and laterality have emerged. One model proposes that the right hemisphere is dominant or specialized for the processing of all emotions [8,5]. In contrast, the valence theory proposes that there is differential hemispheric involvement as a function of emotional valence, or pleasantness–unpleasantness, and approach–withdrawal [10,11]. In this model, the right hemisphere is more active during negative/withdrawal emotion in human adults, whereas the left hemisphere is more dominant for positive/approach emotions.

With the aim to explore the phylogeny of brain asymmetries in emotional behavior, as well as the phylogeny of other functional asymmetries, attention has shifted very recently to studies in nonhuman primates and other species [6]. As with other reports on neuroanatomical and functional asymmetries in nonhuman primates (for comprehensive reviews, see [6,23]), evidence emerging from research on emotional behavior supports a human-like pattern of lateralization of emotion in nonhuman primates. Specifically, physiological studies and behavioral studies have found a greater involvement of the right hemisphere in emotional activity, at least in the case of negative emotions (for review, see [29]).

In the human literature, the facial channel, at a communicative level, is one of the behavioral components of emotion that has been most extensively investigated in relation to brain asymmetries both in terms of production (for a review and metanalysis, see [5]) and perception of emotions [1,30,42,43]. This is not surprising, since the relationship between facial expressions and emotions has been reported for centuries, particularly in the writings of Charles Darwin [15]. Regarding nonhuman primates, although a few studies have measured asymmetries in perception of faces and perception of emotional expressions [17,18,32,33,48,49], only

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two studies have explored facial asymmetries in the production of emotions in monkeys [19,24]. To our knowledge, no study has been conducted on brain asymmetries in the production of facial expressions in great apes.

Hauser [19] tested facial asymmetries in the production of four different facial expressions, including the fear grimace, copulation grimace, open mouth threat and ear flap, in 4–19 rhesus monkeys (the number of different expressions per individual is not specified in this study). Hauser [19] reported that the left side of the face began to move first during the production of the fear grimace and the open mouth threat and it maintained the expression longer than the right in the case of the copulation grimace. Moreover, the left side of the face was reported to be more expressive than the right side in the fear grimace (as reflected in the number of skin folds and height of the corner of the mouth). In addition, Hauser [19] created chimerics (composites made of each half of the face paired with its mirror-reversed duplicate) of three images representing the fear grimace expression of three different individuals and asked 43 human subjects to rate which chimeric expression looked more like the original expression. The left–left chimerics were reported to be more expressive than the right–right chimerics by 41 of the 43 human subjects. Whether that was the case for all three images is something that was not reported in this study.

Hook-Costigan and Rogers [24] found in marmosets slightly different results compared to those reported by Hauser [19]. Three facial expressions were experimentally elicited in 8–11 marmosets, depending on the expression (ten different faces in each individual). Two expressions had an accompanying vocalization and were referred to as the tisk (characterized as fearful) and the twitter expression (defined as a social contact call). The third expression was simply referred to as the silent fear expression. For each call, the experimenters recorded areas left and right of midline of the mouth to quantify asymmetry in the intensity of the expression. They also recorded the distance from the midline to the side of the mouth as an indicator of asymmetry. For the area measure, a left side asymmetry was found for the fear and tsik expression while a right side asymmetry was found for the twitter expression. For the distance to midline measure, a left side bias was found for the fear and tsik expression but no effect was found for the twitter expression.

No single study has explored facial asymmetries in the production of facial expressions in great apes despite the fact that apes, and chimpanzees in particular, would be ideal subjects for these studies, not only due to their close genetic relatedness to humans, but also because they are highly social individuals with a rich repertoire of facial expressions that have been described in detail elsewhere [9,16,35,44–47]. The aim of this study was to address the issue of brain lateralization in the production of emotions by chimpanzees by examining facial asymmetries in spontaneously produced emotional expressions. We hypothesized that the left side of chimpanzees' faces and hence the right hemisphere will be more involved in the production of emotional facial expressions, at least for the negative ones, based on previous findings in humans and monkeys.

2. Experiment 1: objective measures

2.1. Methods

2.1.1. Subjects and setting

Observations were made on a sample of 36 chimpanzees (*Pan troglodytes*) from the Yerkes Regional Primate Research Center (YRPRC) (Atlanta, USA) and the Madrid Zoo-Aquarium (Madrid, Spain). Facial expressions were recorded on 10 adults (older than 16 years of age), 8 females and 2 males; 15 subadults (between 7 and 16), 9 females and 6 males; and 11 juveniles (younger than 7), 5 females and 6 males. Twenty seven subjects were housed at the YRPRC Field Station in two different groups with 11 belonging to one group and 16 to the other. Both compounds have an outdoor area approximately 550 m^2 and five indoor rooms each about 12.6 m^2. The outdoor area is surrounded by grate walls 6 m tall with an observation tower in one of the corners from where the chimpanzees were videotaped. At the YRPRC, all observations were recorded in the outdoor portion of their home cage. Nine chimpanzees at the Madrid zoo also served as subjects. Their enclosure consists of an outdoor area 200 m^2 and four indoor rooms each 10 m^2. All walls are made of concrete and 3 m-tall glass screens, through which chimpanzees' behavior could be recorded, surround the open area and two of the four indoor rooms.

2.1.2. Procedure

The chimpanzees at the Madrid zoo were studied over two 9 month periods (i.e. October 1996 to June 1997, and October 1997 to June 1998). Observations were made three times a week, 2 h each time on average, once in the morning and twice in the afternoon. Observations of the two groups at the Yerkes Field Station took place during July–September 1998, five times a week, three times in the morning and twice in the afternoon, 2 h a day (1 h each group). This resulted in about 600 h of observation in total.

At both locations, chimpanzees were observed ad libitum (there was no limitation on what, who or when to observe) and all social interactions that spontaneously took place were recorded with a video camera (Sony SVHS) by one of the authors. That same lone observer, with a 4 year experience with chimpanzees, then reviewed the videotapes and categorized all present facial expressions according to morphological and functional criteria based on Parr et al. [35] description of the chimpanzee repertoire of facial emotions. Parr et al. [35] based their descriptions on other classic ethograms for the study of chimpanzees behavior (for example, [16,44–47]). Five categories of facial expressions (*pant-hooting, play face, silent pout, silent bared-teeth display* and *staring bared-teeth scream face*) and a neutral nonemotional category were recorded in nine