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Face processing limitation to own species in primates: A comparative study in brown capuchins, Tonkean macaques and humans

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Abstract

Most primates live in social groups which survival and stability depend on individuals' abilities to create strong social relationships with other group members. The existence of those groups requires to identify individuals and to assign to each of them a social status. Individual recognition can be achieved through vocalizations but also through faces. In humans, an efficient system for the processing of own species faces exists. This specialization is achieved through experience with faces of conspecifics during development and leads to the loss of ability to process faces from other primate species. We hypothesize that a similar mechanism exists in social primates. We investigated face processing in one Old World species (genus Macaca) and in one New World species (genus Cebus). Our results show the same advantage for own species face recognition for all tested subjects. This work suggests in all species tested the existence of a common trait inherited from the primate ancestor: an efficient system to identify individual faces of own species only.

Keywords: Brown capuchin monkey; Evolution; Face recognition; Tonkean macaque

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1. Introduction

There are several lines of evidence that the face processing system presents similarities between different species. First, faces represent a highly attractive stimulus for infant primates, including humans (*Homo sapiens*) (Goren et al., 1975), pigtailed macaques (*Macaca nemestrina*) (Lutz et al., 1998), gibbons (*Hylobates agilis*) (Myowa-Yamakoshi and Tomonaga, 2001) and chimpanzees (*Pan troglodytes*) (Kuwahata et al., 2004). Three-week-old lambs (*Ovis ovis*) spend more time sniffing a picture of sheep than a picture displaying other stimuli (Porter and Bouissou, 1999). Second, in most primate species, faces are a way to communicate emotions via the production of mimics (van Hoof, 1967; Parr, 2003; Niedenthal et al., 2000). Third, neurons responding specifically to faces compared to other stimuli have been found in non-human primates (Perrett et al., 1992) and in sheep (Kendrick et al., 2001). In human a face specific electrophysiological response, named the N170, is elicited by faces (Bentin et al., 1996; de Haan et al., 2002). Such similarities suggest the existence of similar mechanisms in primates (Campbell et al., 1997). One putative mechanism is the specialization to own species that lead to difficulties processing well faces from other species. It has been observed both in humans (Pascalis et al., 2002; Dufour et al., 2004) and in rhesus macaques (*Macaca mulatta*) (Pascalis and Bachevalier, 1998). In the present study we aim to test whether this advantage extent to two other non-human primate species, Tonkean macaques (*Macaca tonkeana*) and brown capuchin monkeys (*Cebus apella*). If so, our results will provide convincing evidence to a common origin of the face recognition system in primates.

We shall first review the similarities between the face processing system in human and non-human primates. Even if the morphological variability between human faces is limited, human adults are very efficient at recognizing faces; they are able to discriminate hundreds of them (Bahrick et al., 1975). It has been suggested that we differentiate individuals' faces on the basis of relational information, such as the particular distance between the eyes, or between lips and chin (Leder and Bruce, 2000). The ability to process these parameters is called configural processing and contrasts with feature processing (Diamond and Carey, 1986; Maurer et al., 2002). Yin (1969) has shown that faces are recognized more accurately and faster when presented

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in their canonical orientation than when presented upside-down. A widely accepted claim is that the cause of the inversion effect is a disruption of configural processing leading to the use of a less efficient feature processing (Diamond and Carey, 1986; Leder and Bruce, 2000; Maurer et al., 2002). The human face processing system does not however extend toward faces of other primate species that share the same face configuration (Dufour et al., 2004; Pascalis et al., 2002).

Conspecifics' face identification is present in non-human primates and can be studied using pictures (Pascalis et al., 1999, for a review). For example, Dasser (1987) showed that long-tailed macaques could associate the picture of a member of their group to the real individual. Individual's faces discrimination based on pictures has been demonstrated in chimpanzees (Parr et al., 1998), Japanese macaques (*Macaca fuscata*) (Tomonaga, 1994) and rhesus macaques (Wright and Roberts, 1996; Pascalis and Bachevalier, 1998; Parr et al., 1999) among other species. It is important to highlight that those abilities are not restricted to primates but can be observed in other species, such as sheep. Sheep can categorise their species based on faces (Kendrick et al., 1995). They can also discriminate sheep of their own breed from sheep of other breed, and between two individuals from their own breed as measured with a two-way discrimination task (Kendrick et al., 1996).

Similarities in the face processing system include also the inversion effect. Face recognition is sensitive to inversion in sheep (Kendrick et al., 1996) but its presence is still debated for non-human primates. In chimpanzees, Tomonaga et al. (1993) did not observe an inversion effect for chimpanzees or humans familiar faces but they tested only one subject with a limited number of stimuli. More recently, Parr et al. (1998) demonstrated an inversion effect in five chimpanzees, for human and chimpanzee faces but not for capuchin faces or cars. In longtailed macaques, Bruce (1982) did not observe an effect of inversion using a concurrent discrimination task. Overman and Doty (1982), using a matching-to-sample task, found an inversion effect in pigtailed macaques for both human and macaque faces. An inversion effect was also demonstrated in a squirrel monkey (*Saimiri sciureus*) by Phelps and Roberts (1994) for human faces (but not for monkey faces). The discrepancy observed in the non-human primate literature might be due to several factors such as the experimental paradigms that are different. However, since face recognition in sheep is sensitive to inversion, the possibility of the existence of inversion effect in monkeys cannot be rejected.

Nelson (2001) has suggested that the systems underlying human face processing may be sculpted by experience with different kinds of faces present in the visual environment. The face processing system is indeed developing until teenage hood (Carey and Diamond, 1994; Campbell et al., 1999). The early system is able to cope with different type of faces, for example, Pascalis et al. (2002) showed that 6-month-old humans discriminated between both human and monkey faces, but that 9-month-olds and adults discriminated only between human faces. Moreover, adults find easier to differentiate between faces from their own ethnical group (Meissner and Brigham, 2001). This *other-race* effect has been attributed to the relatively common experience of having greater exposure to faces of ones own-race compared to other races during development (Valentine, 1991; Sangrigoli and de Schonen, 2004). Three-month-olds but not newborns, prefer own-race faces (Kelly et al., 2005). Similarly, greater exposure to human faces compared to non-human primate faces, could explain the species-specific recognition observed in human adults (Nelson, 2003).

In sheep, experience with other species during infancy also influences the development of the face processing system. Kendrick et al. (1998) showed that male sheep reared by goats (*Capra aegagrus hircus*) and male goats reared by sheep preferred to socialize with females from their maternal species compared with their genetic species. In non-human primates, visual preference for maternal species has also been shown for chimpanzees reared by humans (Tanaka, 2003) and for Japanese monkeys reared by rhesus macaques (Fujita, 1990, albeit not true for rhesus macaques). Pascalis et al. (2005) demonstrated that exposure to Barbary macaques faces (*Macaca sylvanus*) – between 6 and 9 months of age – facilitates the discrimination of monkey faces in human infants, an ability that is otherwise lost around 9 months of age. The adults' human limitation to process own-species faces has been observed in rhesus macaques (Pascalis and Bachevalier, 1998) and sheep (Kendrick et al., 1996). However, there are also evidences that non-human primates can discriminate between faces of other species. This is the case for chimpanzees as measured with a sequential matching-to-sample task (Parr et al., 1998) and for rhesus macaques tested with a similar paradigm (Parr et al., 1999, see also Wright and Roberts, 1996). Other studies nonetheless demonstrated a limitation to process own-species faces: Humphrey (1974) with a habituation dishabituation task in rhesus monkeys and Kim et al. (1999), using a visual paired comparison task in young pigtailed macaques. The existence of a limitation to own species in other non-human primates remains to be explored. It is indeed important to test whether the face recognition system could extend to the processing of phylogenetically close species faces, with the assumption that faces from the same genera would probably share greater morphological proximity than faces from a different genera.

Our aim was to study inter-individual discrimination of faces of different species in a wider range of primates with the technique used by Pascalis and Bachevalier (1998). We investigated face recognition in humans, brown capuchins and Tonkean macaques. Each species tested had none or limited experience with other primate species. In order to test the common origin of the face system, we tested the face processing ability of one macaque species that radiated a few million years before the anthropoid branch, but also of brown capuchin monkeys who diverged earlier than macaques from the ancestral lineage. Moreover, we explored if the recognition ability extended to phylogenetically close species i.e. same-genus species, or was restricted to the recognition of their own species. Therefore, the subjects were tested with faces of more or less close species. We used the visual paired comparison (VPC) task which indexes the relative interest in a pair of visual stimuli consisting of one novel item and one familiar item viewed during a prior familiarization period (Pascalis and de Haan, 2003). Recognition is