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The inversion effect reveals species differences in face processing

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ABSTRACT

Face recognition is a complex skill that requires the integration of facial features across the whole face, e.g., holistic processing. It is unclear whether, and to what extent, other species process faces in a manner that is similar to humans. Previous studies on the inversion effect, a marker of holistic processing, in nonhuman primates have revealed mixed results in part because many studies have failed to include alternative image categories necessary to understand whether the effects are truly face-specific. The present study re-examined the inversion effect in rhesus monkeys and chimpanzees using comparable testing methods and a variety of high quality stimuli including faces and nonfaces. The data support an inversion effect in chimpanzees only for conspecifics' faces (expert category), suggesting face-specific holistic processing similar to humans. Rhesus monkeys showed inversion effects for conspecifics, but also for heterospecifics' faces (chimpanzees), and nonfaces images (houses), supporting important species differences in this simple test of holistic face processing.

1. Introduction

The inversion effect refers to a relative impairment in the ability to discriminate faces when they are turned upside down compared to when they are in their typical upright orientation (Valentine, 1988; Yin, 1969). Among humans, the inversion effect is augmented by stimulus categories for which people have developed expertise, like human faces. Because there is no other natural stimulus category for which we garner as much expertise from birth as faces, it has often been assumed that the inversion effect is face-specific. Several studies, however, have shown impairments in the discrimination of other highly familiar stimulus categories for which there are many individual exemplars, such as dogs, sheep, and birds, including trained categories of man-made objects, like Greebles (Diamond & Carey, 1986; Gauthier & Tarr, 1997). Although the effect of inversion is not as detrimental to the recognition of Greebles as it is for faces (Gauthier et al. 1999; McKone & Yovel, 2009; Robbins and McKone 2007), the data, nonetheless, confirm the important role of expertise in holistic processing and help to explain why the effect of inversion on faces is so robust. Throughout this paper, we use the term expertise to refer to developmental familiarity with conspecifics' faces, and the special (expert) status that these faces have in eliciting cognitive specializations in humans.

There is some disagreement on the underlying cause of the inversion effect. Some authors suggest that the inversion effect is due to impairments in the ability to extract 2nd order configural information from an inverted face. Second-order configural cues refer to the relative size and spacing of features (Diamond & Carey, 1986; Freire, Lee, & Symons, 2000; Maurer, Le Grand, & Mondloch, 2002). These claims are supported by studies that show quantitatively greater inversion effects when subjects are required to utilize the spacing of features compared to the identity of features when discriminating faces (Mondloch, Geldart, Maurer, & Le Grand, 2003). An alternative account, however, suggests that the inversion effect results as a consequence of holistic processing for upright faces and thus can be used as a marker of holistic face processing (Rossion, 2008). This holistic approach refers to a perceptual process whereby the features of a face, their relative size, placement, and spacing, are simultaneously integrated into a perceptual whole (Tanaka & Farah, 1993). The inability to extract holistic information from an inverted face qualitatively shifts the strategy towards detecting spacing differences. Moreover, in several classic tasks of holistic processing, the effects are minimized or eliminated when the stimuli are inverted. The composite face effect, for example, is a task that combines the upper and lower face parts of two different individuals. The effect is that the individual in the upper face part is easier to identify when it is offset from the lower part, disengaging holistic processing, compared to when the face parts are aligned in a face-like configuration (Young, Hellawell, & Hay, 1987). The misaligned advantage disappears when the faces are inverted because inverted faces do not engage holistic processing. Similarly, the Thatcher illusion, the grotesque appearance

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of faces after selective inversion of the eyes and the mouth in an upright face, disappears when the faces are inverted (Thompson, 1980). Finally, the other-race effect, poorer discrimination of faces from an unfamiliar race, is believed to result from the lack of holistic processing for other-race faces. Deficits in identifying own versus other-race faces disappears when the faces are inverted (Rhodes, Brake, Taylor, & Tan, 1989; Sangrigoli & de Schonen, 2004). While it is not the purpose of this paper to disentangling whether the inversion effect is a cause or consequence of holistic processing, these studies confirm the important relationship between these two face processing phenomena.

There is also considerable debate about whether the numerous face processing specializations observed in humans are shared by other species or whether they reflect true cognitive specializations. As is the case for the human literature, the inversion effect is by far the most widely tested phenomenon in comparative face recognition studies, but the results of these studies have been inconsistent and difficult to interpret for several reasons. The main source of this confusion is whether conspecifics' faces share a special status in holistic processing, eliciting stronger inversion effects than heterospecific faces or nonface stimuli, in nonhuman primates that is comparable to human reports (Parr, 2011 for a detailed review of this literature). In brief, studies of inversion effects in chimpanzees report consistent findings. Using a matching-to-sample (MTS) task, Parr, Dove and Hopkins (1998) found clear expertise effects in five chimpanzees. Subjects were significantly worse discriminating inverted compared to upright faces of expert categories only (chimpanzee and human faces), but no significant inversion effects were found for unfamiliar, heterospecific faces (capuchin monkeys) or nonface categories (automobiles or clip art). Using a similar MTS task format, Tomonaga (1999) found the inversion effect for unfamiliar human faces compared to houses in one chimpanzee. The same subject was significantly faster identifying upright human faces compared to upright chairs or hands in a visual search task (Tomonaga, 2007). A follow-up study showed that chimpanzees were faster to identify the inner features of an upright face compared to inverted distracters (Tomonaga, 2007).

In contrast to chimpanzees, data on inversion effects in monkeys are inconsistent and often fail to support a special status for conspecifics' faces, or even face-selective effects more generally. Some studies have reported evidence of the face inversion effect in monkeys (Neiworth et al. 2007-cotton-top tamarins; Overman and Doty 1982-pigtail macaques; Tomonaga 1994-Japanese macaques; Vermeire and Hamilton 1998-rhesus monkeys), while others have failed to find evidence of inversion effects specific for faces (Bruce 1982; Dittrich 1990-longtail macaques; Gothard et al. 2004; Parr, Winslow, & Hopkins, 1999; Rosenfeld and van Hoesen 1979-rhesus monkeys; Weiss et al. 2001-cotton-top tamarins). When rhesus monkeys were tested using procedures comparable to chimpanzees, Parr and colleagues (1999) reported inversion effects for conspecifics' faces, unfamiliar capuchin monkey faces, and automobiles, but not human faces (which could have been considered an expert category as the monkeys were born and raised in captivity with human caregivers), or clip art (Parr et al., 1999). Using an identical testing method in a separate group of rhesus monkeys, inversion effects were found for conspecifics' faces, human faces, and unfamiliar chimpanzee faces, but not houses or clip art (Parr, Heintz, & Pradhan, 2008). Using eye-tracking as a dependent measure in rhesus monkeys, Gothard et al. (2009) demonstrated a reduction eye-fixations when subjects viewed inverted compared to upright conspecifics, but not human faces. These authors speculated that monkeys have different perceptual strategies for processing conspecifics' faces compared to human faces. Using a similar methodology in rhesus monkeys, Dahl et al. (2009) also reported reduced fixations to the eye region of inverted conspecifics compared to human faces. In both of these studies, no control stimuli were used to assess the face-selectivity of the scan patterns, and the monkey subjects were all born and raised in captivity by humans, so the quality of the expertise manipulation was also unclear.

Because of continued debate in the literature concerning similarities and differences in the face processing strategies of humans and nonhuman primates, we present data from a new series of inversion studies in both chimpanzees and rhesus monkeys. The testing methods were directly comparable and the stimuli contained both conspecific (expert) and heterospecific (nonexpert) faces, as well as several complex nonface categories (shoes, houses and clip art). The goal was to directly compare the face-selectivity of inversion effects in two species of nonhuman primates using comparable methods. Consistent with previous studies, we hypothesized that both chimpanzees and rhesus monkeys would show inversion effects for conspecifics' faces (Dahl, Wallraven, Bülthoff, & Logothetis, 2009; Gothard, Brooks, & Peterson, 2009; Parr, Dove, & Hopkins, 1998; Parr et al., 1999; Parr et al., 2008). In contrast to the monkeys, however, we predicted that the inversion effects for chimpanzees would be shown exclusively for conspecifics' faces. We also predicted that the inversion effects shown by rhesus monkeys would extend to other categories, in addition to conspecifics' faces, including both face and nonface categories. We report all training data in an effort to alleviate concerns about unusual responses biases in operant procedures (Adachi, Chou, & Hampton, 2009; Dahl, Logothetis, & Hoffman, 2007). Finally, researchers have recently cautioned that any reports of face-specific inversion effects should account for general impairments that occur when stimuli are inverted (Crookes & McKone, 2009). To address this, we present an additional analysis using inversion scores for each stimulus category that have been adjusted by the general costs shown by each subject for inverted clip art.

2. General methods

2.1. Subjects

Six chimpanzees (4 males, 2 females) participated in these studies ranging in age from 16 to 22 years. These subjects were all raised by humans in peer groups in the Yerkes Primate Center nursery until 4 years of age when they joined established social groups consisting of a range of older individuals. All subjects had extensive experience performing computerized tasks of face recognition using MTS prior to the onset of these studies (Parr & Hecht, 2011). All subjects were socially housed and tested voluntarily in their home cage using a computerized-joystick testing system.

Six rhesus monkeys (2 males, 4 females born in 2000 and 2001) participated in these studies. Four subjects were 8 years of age when tested and 2 females were 7 years of age. They were each born into large social groups at the Yerkes National Primate Research Center's field station, Lawrenceville, GA and in 2004, they moved to the main campus to participate in experimental studies of social cognition. At this time, they were housed in same-sex pairs in the same home room, and tested daily in their home cage using a custom designed touchscreen computer system (see Parr et al., 2008). This consisted of a 15″ acoustic wave touchscreen (Elo touch) that could be inserted into the doorway of the home cage for access without obstruction from caging. Treats were delivered to a small cup located beneath the touchscreen. All subjects had extensive experience performing computerized tasks of face recognition using matching-to-sample (MTS) prior to this study (see Parr et al., 2008; Parr & Heintz, 2006). All testing was voluntary.

2.2. Stimuli

All stimuli consisted of high-quality digitized images presented on the computer using a stimulus height of 300 pixels and 150 dpi. Chimpanzee and rhesus monkey face images were acquired from colonies living at the Yerkes National Primate Research Center field