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Report

Humans and Macaques Employ Similar Face-Processing Strategies

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Summary

Primates developed the ability to recognize and individuate their conspecifics by the face. Despite numerous electrophysiological studies in monkeys [1–3], little is known about the face-processing strategies that monkeys employ. In contrast, face perception in humans has been the subject of many studies [4–6] providing evidence for specific face processing that evolves with perceptual expertise [7]. Importantly, humans process faces holistically, here defined as the processing of faces as wholes, rather than as collections of independent features (part-based processing) [8]. The question remains to what extent humans and monkeys share these face-processing mechanisms. By using the same experimental design and stimuli for both monkey and human behavioral experiments, we show that face processing is influenced by the species affiliation of the observed face stimulus (human versus macaque face). Furthermore, stimulus manipulations that selectively reduced holistic and part-based information systematically altered eye-scanning patterns for human and macaque observers similarly. These results demonstrate the similar nature of face perception in humans and monkeys and pin down effects of expert face-processing versus novice face-processing strategies. These findings therefore directly contribute to one of the central discussions in the behavioral and neurosciences about how faces are perceived in primates.

Results

Human Face Perception

Twelve adult humans performed a nonreinforced, passive viewing task (see Figure 1 and Experimental Procedures) in which eye movements were recorded. Face stimuli of neutral facial expressions of rhesus macaques and humans were used in an original (upright) presentation and two image manipulations (inverted and blurred) (Figure 1). These manipulations were chosen to selectively disrupt face-processing strategies based on prior human perceptual studies [4, 9]. Holistic face processing develops as our perceptual expertise with faces grows and is characterized by fast and parallel processing of faces, whereas part-based processing is a much slower and more serial process requiring attention to details in the face. More specifically, holistic processing is disrupted by inversion (i.e., turning a face upside down will lead to part-based processing), whereas part-based processing is disrupted by blurring (i.e., reducing high spatial frequency information will leave the holistic percept intact). Additionally, rhesus macaque faces are a stimulus class for which humans have not developed perceptual expertise and therefore should not elicit holistic processing in general [7]. Finally, prior studies have shown that for humans, the eyes play a crucial role in face processing [10–12]. In eye-tracking studies, upright faces elicited less lower face and less random part scanning than did inverted faces [13]. We can therefore take preference for the eye region as an indicator of holistic processing and expect eye-movement patterns to be modulated by the different conditions depending on the face-processing strategy afforded by the stimulus.

Participants were asked to look at the images as naturally as possible for a total of 12 s of trial duration. We analyzed the viewing time during image presentation and determined the saliency for the variables species and facial parts (eyes, nose, and mouth) as well as for all three manipulation conditions (upright, inverted, blurred). Here, we report statistics involving viewing times (statistical comparisons of number of fixations are fully compatible with viewing times) that showed significant main effects and interactions for our experimental variables. All post-hoc tests were corrected for multiple comparisons.

To examine effects of perceptual expertise, viewing times to macaque and human faces were compared. In upright faces, the viewing time was longer for eyes than for nose and mouth when human participants watched human faces (eyes versus nose: $F(1,22) = 8.44$, $p < 0.01$; eyes versus mouth: $F(1,22) = 19.53$, $p < 0.001$) compared to when they watched macaque faces (eyes versus nose: $F(1,22) = 9.37$, $p < 0.01$, while nose > eyes; nose versus mouth: $F(1,22) = 19.53$, $p < 0.001$, while nose > mouth) (Figure 2). This indicates a preference for eyes over nose and mouth of human faces, and a higher saliency for human eyes than macaque eyes, respectively. This result is further supported by directly comparing eyes of human and monkey faces, revealing that eyes were looked at significantly longer in human than in macaque faces ($F(1,22) = 11.45$, $p < 0.01$).

In contrast to upright faces, face inversion led to a drastic loss of eye preference in human faces. Comparisons between facial parts confirm that both human (eyes versus nose: $F(1,22) = 0.10$, $p = 0.75$; eyes versus mouth: $F(1,22) = 1.12$, $p = 0.30$; nose versus mouth: $F(1,22) = 1.18$, $p = 0.29$) and macaque (eyes versus nose: $F(1,22) = 1.91$, $p = 0.18$; eyes versus mouth: $F(1,22) = 0.28$, $p = 0.60$; nose versus mouth: $F(1,22) = 0.54$, $p = 0.47$) faces were treated equally because of inversion.

Finally, when reducing part-based information processing by blurring the faces, an upright-like pattern of response was observed: eyes were visited more often than nose ($F(1,22) = 7.50$, $p < 0.01$) and mouth ($F(1,22) = 28.35$, $p < 0.001$) in human, but not in macaque (eyes versus nose: $F(1,22) = 0.26$, $p = 0.62$; eyes versus mouth: $F(1,22) = 2.07$, $p = 0.16$) faces, also supported by direct comparisons of eye regions across species ($F(1,22) = 17.69$, $p < 0.001$).

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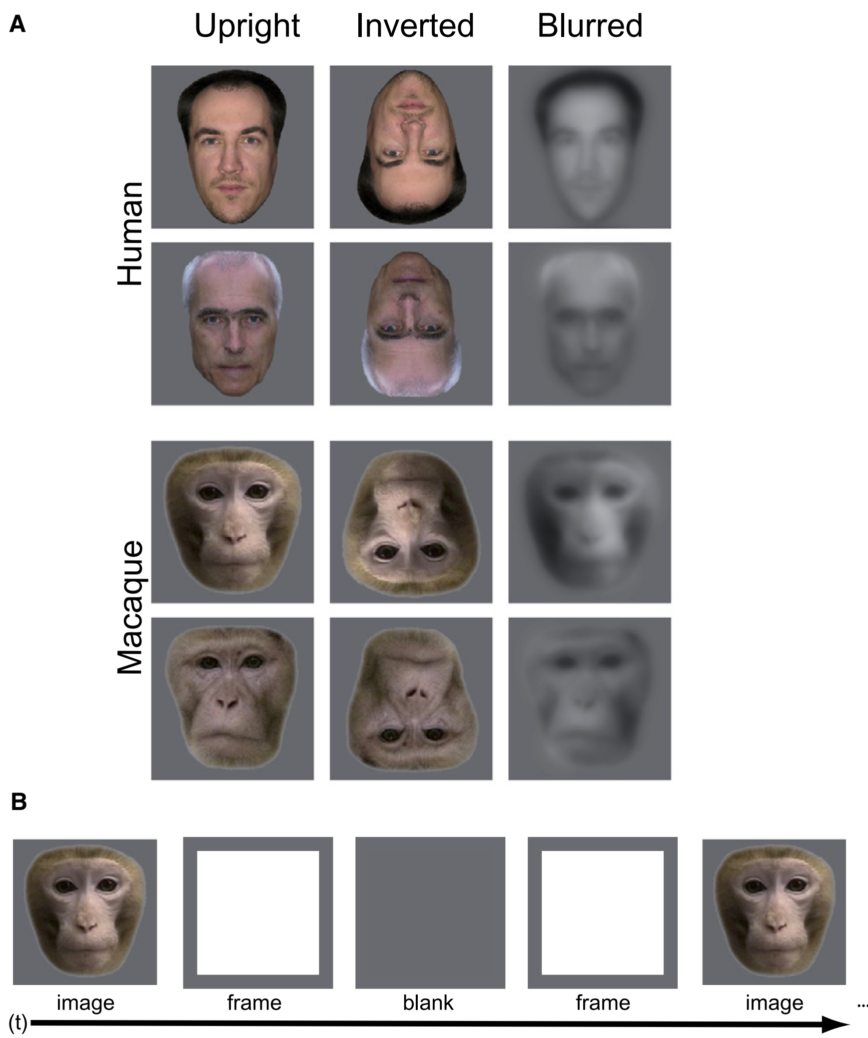

Figure 1. Example Stimuli and Experimental Design

(A) Examples of face images. For human and macaque faces the original faces (upright) were manipulated by inversion (inverted) and blurring (blurred).

(B) Participants elicited an image or blank square, alternately, by directing gaze toward the monitor, and terminated a stimulus by looking away. After 12 s of cumulative stimulus display time, a new image was displayed.

The current experiment not only supports the findings that eyes are more salient than nose and mouth regions, it also illustrates a systematic modulation of the eye preference resulting from inversion and blurring manipulations. Moreover, humans show a qualitatively different processing during the presentation of conspecific and nonconspecific faces, indicating an effect of perceptual expertise on eye-scanning strategies.

Macaque Face Perception

Three adult male rhesus macaques (*Macaca mulatta*) performed the identical passive viewing task by using the same stimuli as in the human experiment. We analyzed the total viewing time during image presentation and determined the saliency for two experimental variables (species, facial parts) as well as for all three manipulation conditions (upright, inverted, blurred). Again, corrected post-hoc tests were applied to the significant effects.

First, to determine the impact of perceptual expertise, viewing times to macaque and human faces were compared. In upright faces, the viewing time was longer for eyes than for nose and mouth when the macaques watched macaque faces (eyes versus nose: $F(1,70) = 19.50$, $p < 0.001$; eyes versus mouth: $F(1,70) = 26.19$, $p < 0.001$) (Figure 2). However, human faces did *not* elicit a preference for eyes over nose and mouth (eyes versus nose: $F(1,70) = 1.00$, $p = 0.32$; eyes versus mouth: $F(1,70) = 0.07$, $p = 0.80$) as macaque faces did, suggesting a qualitative difference with respect to species. Direct comparisons of viewing time of the eye region for macaque and human stimuli determined that the saliency of eyes differed across species ($F(1,70) = 9.60$, $p < 0.01$).

In contrast, inverting the faces, and thus reducing holistic processing, led to a drastic loss of eye preference in macaque faces (eyes versus nose: $F(1,74) = 4.11$, $p < 0.05$, while nose > eyes; eyes versus mouth: $F(1,74) = 1.82$, $p = 0.18$) as well as in human faces (eyes versus nose: $F(1,74) = 1.07$, $p = 0.31$, eyes versus mouth: $F(1,74) = 0.67$, $p = 0.41$). Thus, human and macaque faces were treated equally when inverted.

Blurring faces, however, and thus reducing access to part-based information, elicited a nearly identical pattern of responses as upright faces: eyes were visited longer than the nose (eyes versus nose: $F(1,74) = 4.38$, $p < 0.05$) and mouth (eyes versus mouth: $F(1,74) = 19.74$, $p < 0.001$) regions in macaque faces. However, this pattern was not observed for blurred human faces (eyes versus nose: $F(1,74) = 0.07$, $p = 0.78$; eyes versus mouth: $F(1,74) = 1.55$, $p = 0.21$). Overall, the eyes were more salient in macaque than in human faces ($F(1,74) = 6.38$, $p < 0.05$).

A few studies have shown that macaques perceive conspecific individuals differently than nonconspecifics. A dishabituation study [14] that used looking time demonstrated with whole-bodied images that macaques perceive their conspecifics on a different categorical level (subordinate level entry point) than nonconspecifics (basic level). Along this line, it has been shown recently that, like humans, rhesus macaques individuate conspecific faces but not nonface category exemplars or nonconspecific faces [15]. Thus, there is indication of a qualitatively different perceptual processing during the presentation of conspecific and nonconspecific faces. Although previous research has provided qualitative evidence for species-specific processing, our results show, for the first time, a clear dissociation in the behavioral characteristics in the macaque's scan pattern when observing macaque and human faces. Even though the macaque's visual system is tuned to the same facial features for both macaque and human faces [16], it employs a different oculomotor strategy to inspect macaque and human faces.