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A regional composite-face effect for species-specific recognition: Upper and lower halves play different roles in holistic processing of monkey faces

Zhe Wang[a], Paul C. Quinn[b], Haiyang Jin[a], Yu-Hao P. Sun[a,c,*], James W. Tanaka[d], Olivier Pascalis[e], Kang Lee[f,*]

[a] *Department of Psychology, Zhejiang Sci-Tech University, PR China*
[b] *Department of Psychological and Brain Sciences, University of Delaware, USA*
[c] *Department of Psychology, University of Nanjing, PR China*
[d] *Department of Psychology, University of Victoria, Canada*
[e] *Laboratoire de Psychologie et Neurocognition, Université Grenoble Alpes, France*
[f] *Dr. Eric Jackman Institute of Child Study, University of Toronto, Canada*

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ABSTRACT

Using a composite-face paradigm, we examined the holistic processing induced by Asian faces, Caucasian faces, and monkey faces with human Asian participants in two experiments. In Experiment 1, participants were asked to judge whether the upper halves of two faces successively presented were the same or different. A composite-face effect was found for Asian faces and Caucasian faces, but not for monkey faces. In Experiment 2, participants were asked to judge whether the lower halves of the two faces successively presented were the same or different. A composite-face effect was found for monkey faces as well as for Asian faces and Caucasian faces. Collectively, these results reveal that own-species (i.e., own-race and other-race) faces engage holistic processing in both upper and lower halves of the face, but other-species (i.e., monkey) faces engage holistic processing only when participants are asked to match the lower halves of the face. The findings are discussed in the context of a region-based holistic processing account for the species-specific effect in face recognition.

Face recognition is species-specific. Human observers match human (own-species) faces with higher accuracy than monkey (other-species) faces (Dufour, Coleman, Campbell, Petit, & Pascalis, 2004), and monkeys prefer a novel over familiar monkey face (own-species) but not a novel over familiar human face (other-species) in a paired-comparison task (Pascalis & Bachevalier, 1998). The species specificity of face recognition appears to develop in infancy via the phenomenon of perceptual narrowing, a process in which infant responsiveness is maintained for stimuli present in the environment and declines for stimuli absent in the environment. For example, human 6-month-olds can discriminate both human (own-species) faces and monkey (other-species) faces, but 9-month-olds can discriminate only human faces (Pascalis, de Haan, & Nelson, 2002).

An unresolved issue in the literature concerns the basis for the superior recognition of own-species faces relative to other-species faces. However, a related effect, the other-race effect (ORE), which refers to the better matching (typically in an old/new task) of own-race faces relative to other-race faces by human observers (see Anzures et al., 2013; Meissner & Brigham, 2001, for reviews), has been explained with an experience-based holistic processing account. This account maintains that the face processing system constructs a holistic representation by integrating multiple facial parts into an organized whole (Farah, Wilson, Drain, & Tanaka, 1998; Galton, 1907; Young, Hellawell, & Hay, 1987). Recognition occurs by matching a face to the holistic representation. By this account, own-race faces are better matched than other-race faces because other-race faces are less experienced and thus not processed holistically to the same extent as own-race faces.

Much evidence has accumulated to support a holistic processing account for the ORE with the use of established measures of holistic processing (Tanaka & Gordon, 2011): the parts/wholes task (Tanaka & Farah, 1993), the face composite task (Young et al., 1987), and the face inversion task (Yin, 1969). For example, studies using the part-whole task have found that Caucasian participants show a part-whole effect only for Caucasian faces, and Asian participants exhibit a larger part-whole effect for Asian than for Caucasian faces (Crookes, Favelle, & Hayward, 2013; Michel, Caldara, & Rossion, 2006; Tanaka, Kiefer, & Bukach, 2004). Also, with the composite face task (Michel, Rossion, Han, Chung, & Caldara, 2006), experiments have shown that both Caucasian and Asian participants process own-race faces more

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* Corresponding authors at: Department of Psychology, Zhejiang Sci-Tech University, PR China.
E-mail addresses: sunyuhao@zstu.edu.cn (Y.-H.P. Sun), kang.lee@utoronto.ca (K. Lee).

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holistically than other-race faces. In addition, using the inversion task, Hancock and Rhodes (2008) have found that inversion disrupts the matching of own-race faces more than that of other-race faces for both Caucasian and Asian participants. Moreover, a positive correlation was found between the magnitude of holistic processing and the ORE in face matching performance, suggesting that the degree of holistic processing is able to predict extent of the ORE (Degutis, Mercado, Wilmer, & Rosenblatt, 2013).

Can the holistic processing account be extended to explain the species-specific effect? Using the inversion paradigm in an old/new task, Dufour et al. (2004) examined own- and other-species face matching with human participants. When ‘old faces’ were studied for 750 ms, participants showed an inversion effect for both human and monkey faces; however, when ‘old faces’ were studied for only 50 ms, participants showed an inversion effect for human faces, but not monkey faces. Such a data pattern indicates that a monkey face needs more processing time than a human face to induce an inversion effect, suggesting that a monkey face is also processed in a holistic manner, but less automatically or strongly than a human face.

Spatial constraints (e.g., different regions in a face) may also play a role in the holistic processing of faces from other-races and -species. For example, Wang et al. (2015) showed that the other-race effect only emerges when participants make same/different judgments based on the upper- but not lower-half of the face, using the Face Dimensions Test designed by Tanaka, Kaiser, Bub, and Pierce (2009); see also Bukach, Le Grand, Kaiser, Bub, and Tanaka (2008). Also, studies have found that Caucasian participants show a part-whole effect for both eyes and mouth in processing own-race (Caucasian) faces (DeGutis, Cohan, Mercado, Wilmer, & Nakayama, 2012; Degutis et al., 2013) but not for eyes, only for mouth, in processing other-race (Asian) faces (Degutis et al., 2013). Furthermore, studies have found that information in the eye region is preserved more than that in the mouth region during face inversion (Barton, Keenan, & Bass, 2001; Malcolm, Leung, & Barton, 2004; Tanaka, Kaiser, Hagen, & Pierce, 2014; Xu & Tanaka, 2013). In addition, studies have indicated that individuals with autism (Wolf et al., 2008) and prosopagnosia (Caldara et al., 2005; Bukach et al., 2008; Rossion, Kaiser, Bub, & Tanaka, 2009) show ability to detect change only when asked to process the bottom parts of the face. Collectively, these studies suggest that holistic processing might be constrained in a region-based all-or-none manner (i.e., upper face vs. lower face).

The current study examined two specific questions: (1) Will human participants process other-species (i.e., monkey) faces less holistically than own-species (i.e., human) faces from both own- and other-races? and (2), If yes, which pattern will be shown in other-species monkey faces: quantitatively weaker effects in both upper and lower halves of other-species faces relative to human faces from own- and other-races, or a region-selective effect in the upper versus lower half of a monkey face?

To address these questions, we presented Asian participants with three categories of faces (i.e., Asian, Caucasian, and monkey) as stimuli and employed a composite-face task with a complete design (Richler, Tanaka, Brown, & Gauthier, 2008). Using this complete-design for the composite-face task, we conducted two experiments. In Experiment 1, we asked participants to judge whether the upper parts of a pair of faces, successively presented, were the same or not. In Experiment 2, with the same procedure, participants were asked to judge whether the lower parts of the same faces were the same or not. Faces in a pair were always from the same category (i.e., Asian faces, Caucasian faces, or monkey faces) and were constructed with either the same (or different) upper halves or the same (or different) lower halves.

We had three hypotheses: (1) Asian participants have the most experience with own-race Asian faces, less experience with other-race Caucasian faces, and even less experience with other-species monkey faces. On the assumption that the holistic processing account applies to differences in perceiving both own- and other-race faces, and own- and other-species faces, Asian participants should show smaller and smaller composite-face effects for other-race and other-species faces, respectively, relative to own-race, own-species faces. (2) If monkey face holistic processing is quantitatively weaker than human face holistic processing for both own- and other-race faces, then the data pattern noted for Hypothesis 1 should be observed in both the upper- and lower-half judgment tasks (Experiments 1 and 2). (3) If monkey face holistic processing differs from human face holistic processing for both own- and other-race faces in its region-sensitivity, then we would expect the data pattern noted for Hypothesis 1 to be observed in either the upper-face test (Experiment 1) or the lower-face test (Experiment 2), but not both.

1. Experiment 1: Upper-half composite-face task

1.1. Method

1.1.1. Participants

Forty-four Chinese college students (21 females) served as participants (Mean age = 19.7 years, *SD* = 0.93, age range: 18–22), with normal or corrected-to-normal vision. The students had no direct contact with any Caucasian individuals or monkeys. This study was carried out in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki). Informed consent was obtained for experimentation with human subjects.

1.1.2. Material

Three sets of faces were prepared. They were 16 Asian (8 males), 16 Caucasian (8 males), and 16 monkey face photos. There was no jewelry, glasses, or makeup on these faces. The faces were in frontal pose with neutral expression. The photographs were converted to gray-scale (283 pixels in width and 284 pixels in height). The visual angle of one whole face photo on the PC screen to an observer was approximately $8.5^{\circ} \times 8.5^{\circ}$. In each face set, we produced 16 upper and 16 lower halves by cutting every face photo into two halves and re-combining the upper halves with a randomly assigned lower half from another face to make 16 aligned and 16 misaligned composite faces. For the “aligned” faces, we used a black rectangle with a transparent oval to cover every photo so that any external cues (hair, ears, accessories, shape of head) were excluded. This manipulation ensured that participants would perceive these faces and make identification judgments based on face internal parts and their configuration, not hairstyles. For the “misaligned” faces, we moved the upper half face to the left by 25 pixels and the lower half to the right by 25 pixels. Each photo had a 3-pixel white middle line (Fig. 1 shows aligned and misaligned samples for an Asian, a Caucasian, and a monkey face).

1.1.3. Paradigm

Compared to the so-called “partial design” composite-face task (Gauthier & Bukach, 2007), the “complete design” measures the composite-face effect by discriminability (*d′*) as the primary indicator, which may rule out response bias in participant judgments. The complete design has good construct validity (Richler, Palmeri, & Gauthier, 2012), including correlation with face-selective neural markers (Gauthier, Curran, Curby, & Collins, 2003) and prediction of face recognition performance (DeGutis, Wilmer, Mercado, & Cohan, 2013). Fig. 2 (Richler, Cheung, & Gauthier, 2011) shows the composite face task in a complete design.

1.1.4. Procedure and design

Participants were asked to judge whether the upper halves of two faces successively presented in a trial were the “same or different”. Instructions were to press keys (“1” for “same” or “2” for “different” in the number pad of a standard keyboard) with one hand as accurately and rapidly as possible. Each trial started with a fixation cross (300 ms) in the screen center, followed by a blank screen (200 ms). Then, a

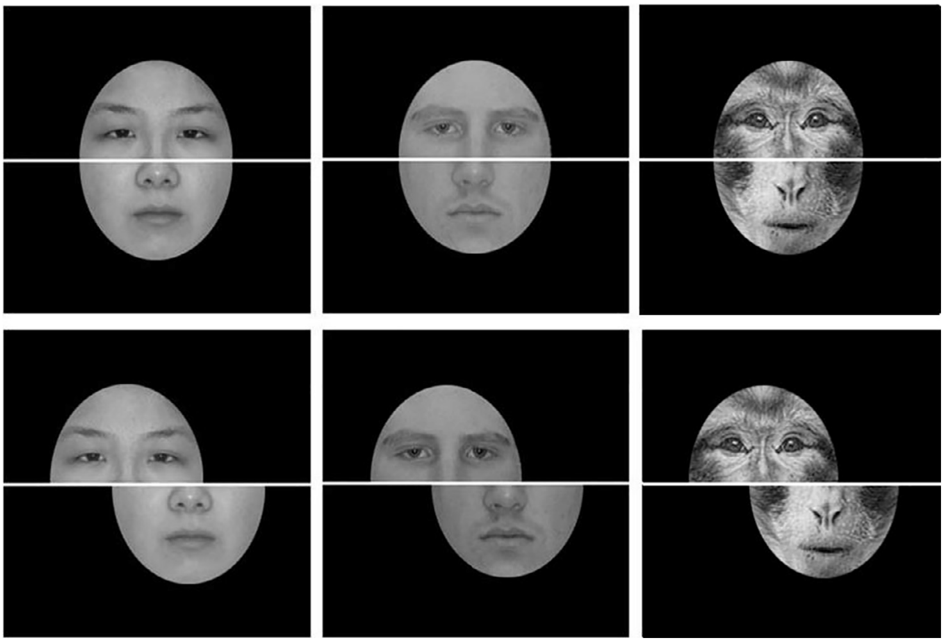

Fig. 1. Samples of aligned (Row 1) and misaligned (Row 2) Asian, Caucasian, and monkey faces.

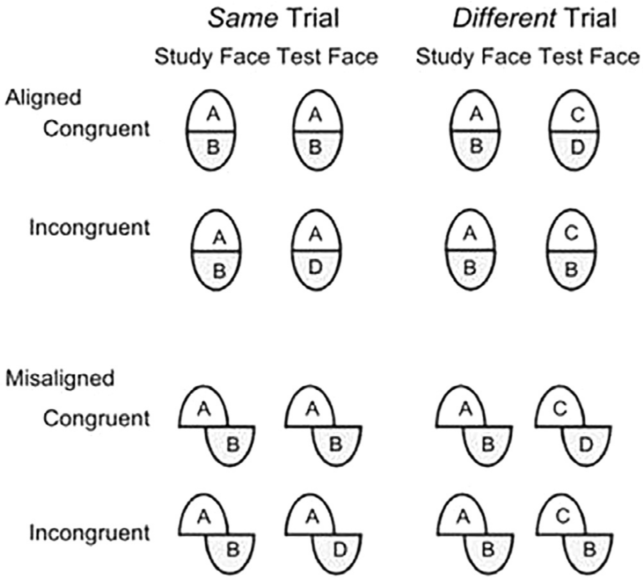

Fig. 2. Schematic diagram of the composite-face task in a complete design (Richler et al., 2011). Participants were asked to study the upper half of the first face and judge whether the second face had the same or different upper half. In "same" trials, the upper halves of the first and second faces were the same; in "different" trials, they were different. The letters A, B, C, and D refer to facial identities of each half. "Aligned" and "Misaligned" refer to the spatial relation between the upper and lower halves of a face. "Congruent" and "Incongruent" refer to the second-order logic relation: if the upper halves of the two faces are the same (or different), and the lower halves are the same (or different), they are congruent; if the upper halves of the two faces are the same (or different), but the lower halves are different (or the same), they are incongruent.

"study composite face" was displayed (800 ms), followed by a mask (500 ms). After that, a "target composite face" was presented until a response occurred. The inter-trial interval was 500 ms. Participants completed 16 practice trials before the actual experimental trials began. Feedback was provided on practice trials but not on experimental trials. The mapping of 2 keys to 2 responses was counterbalanced across participants (Fig. 3 illustrates the events occurring during the course of a trial along with their timing).

We used a within-subject design. A pair of composite faces successively presented varied based on the manipulation of two different dimensions: 1) alignment, which refers to the relative position of the upper and lower half of a face; and 2) congruency. A face pair was called "congruent" if their upper halves were the same (or different) and their lower halves were the same (or different). A face pair was called "incongruent" if their upper halves were the same (or different) and their lower halves were different (or the same). Collectively, each participant was presented with 384 trials in 3 blocks of faces (Face category: Asian, Caucasian, and Monkey block). Each block had 2 (Face alignment: aligned vs. misaligned) × 2 (Trial congruency: congruent vs. incongruent) × 2 (Trial correct response: same vs. different) × 16 individual faces = 128 trials. Order of presentation of the 3 blocks was counterbalanced across participants.

1.2. Results and discussion

d' scores were calculated as the dependent measure by using correct "same" responses as Hits, incorrect "same" responses as False Alarms, incorrect "different" responses as "Misses", and correct "different" responses as Correct Rejections. Results are shown in Fig. 4.

A 3 (Face category: Asian, Caucasian, and Monkey) × 2 (Congruency: Congruent vs. Incongruent) × 2 (Alignment: Aligned vs. Misaligned) repeated measures analysis of variance (ANOVA) was performed using d' as the dependent variable. Performance was better on congruent trials than on incongruent trials as confirmed by a significant main effect of Congruency, $F(1,43) = 81.42$, $p < 0.001$, $\eta_p^2 = 0.65$. The interaction of Face Category and Alignment was also significant, $F(2,86) = 4.29$, $p = 0.017$, $\eta_p^2 = 0.09$, indicating that the alignment effect differed for the 3 face categories. In addition, the interaction of Congruency and Alignment was significant, $F(1,43) = 19.68$, $p < 0.001$, $\eta_p^2 = 0.31$. The three-way interaction among Face Category, Congruency, and Alignment was marginally significant, $F(2,86) = 2.65$, $p = 0.076$, $\eta_p^2 = 0.06$. No other significant effect was found.

To explore the interaction between congruency and alignment in each face category, we performed a 2 (Congruency: Congruent vs. Incongruent) × 2 (Alignment: Aligned vs. Misaligned) repeated-measures ANOVAs on the data for the three categories separately. The

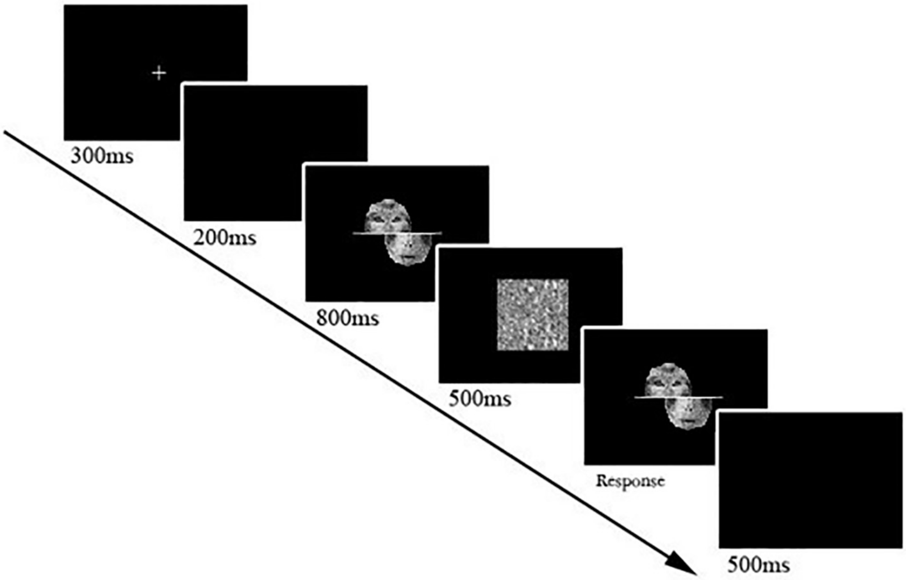

Fig. 3. Events occurring during the course of a trial and their timing in the composite-face task.

interaction was significant for Asian faces, $F(1,43) = 15.44, p < 0.001$, $\eta_p^2 = 0.26$, and Caucasian faces, $F(1,43) = 5.23, p = 0.027, \eta_p^2 = 0.11$. However, the interaction was not significant for monkey faces, $F(1,43) = 2.43, p = 0.126, \eta_p^2 = 0.054$. These results indicate that Asian participants showed a composite face effect for own-species (both own- and other-race human) faces, but not for other-species (monkey) faces when judging the upper halves. The findings suggest that the lower halves of the own-species (Asian and Caucasian) faces were integrated into holistic processing when participants processed the upper halves, but this was not the case for other-species (monkey) faces.

Additionally, to explore the size of the composite-face effect difference between own-race faces and other-race faces, we performed a paired *t*-test by using Interaction Size $[(d'_{\text{aligned/congruent}}\text{-}d'_{\text{aligned/incongruent}})\text{-}(d'_{\text{misaligned/congruent}}\text{-}d'_{\text{misaligned/incongruent}})]$ as the dependent variable (e.g., Chua, Richler, & Gauthier, 2014). Results showed that the composite-face effect for Asian faces was larger than that for Caucasian faces, $t(43) = 2.057$, $p = 0.046$, suggesting that the degree of holistic processing induced by own-race faces is stronger than that induced by other-race faces when participants are asked to attend to the upper half of the faces. Results are shown in Fig. 5.

2. Experiment 2: Lower-half composite-face task

In Experiment 1, Asian participants showed a composite-face effect for Asian and Caucasian faces, but not for monkey faces, indicating that the Asian participants processed own-species faces (i.e., Asian faces and Caucasian faces) holistically when the upper halves of the faces were judged as same or different. However, they did not do so with other-species faces (i.e., monkey faces). While this species-specific effect indicates that the lower half of the monkey faces was not integrated into holistic processing when the upper half of the face was processed, it is unclear whether the upper-half monkey face would evoke holistic processing when the lower half of the face is processed. Upper-half engagement of holistic processing is also an open question for the Asian and Caucasian faces. In Experiment 2, we examined this issue by asking participants to match the lower halves of the Asian, Caucasian, and monkey faces using the same procedure as in Experiment 1.

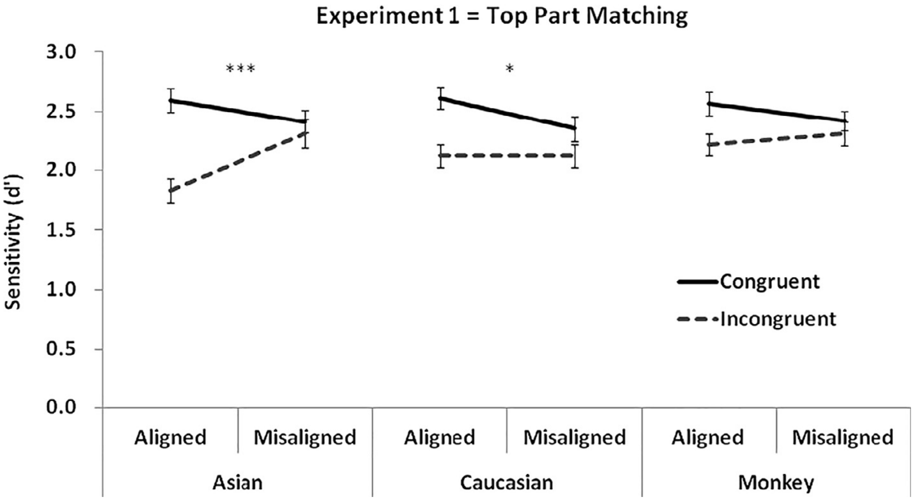

Fig. 4. Sensitivity (d') as a function of alignment, congruency, and face category in Experiment 1. Error bars are SEs. * and *** indicate significant differences ($p < 0.05$) and ($p < 0.001$), respectively.

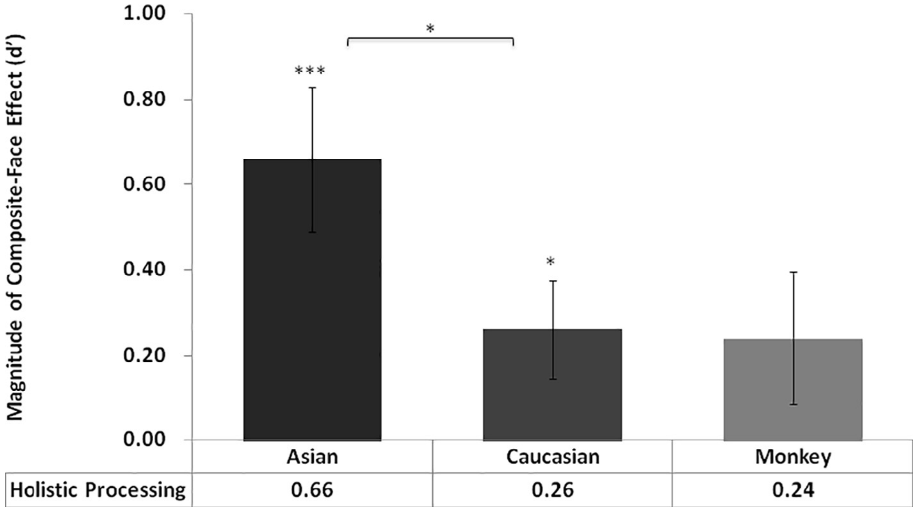

Fig. 5. Magnitude of composite-face effect calculated as the congruency effect (congruent minus incongruent) on aligned trials minus the congruency effect on misaligned trials (*d′*) in Experiment 1. Error bars are SEs. * and *** indicate significant differences ($p < 0.05$) and ($p < 0.001$), respectively.

2.1. Method

2.1.1. Participants

Forty-two Chinese college students (24 females) served as participants (Mean age = 19.4 years, *SD* = 1.32, age range: 18–25), with normal or corrected-to-normal vision. The students had no direct contact with any Caucasians or monkeys. This study was carried out in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki). Informed consent was obtained for experimentation with human subjects.

2.1.2. Material

The same face photographs used in Experiment 1 were used in Experiment 2.

2.1.3. Paradigm

Fig. 6 shows the complete design of composite face task for bottom half face matching.

2.1.4. Procedure and design

Participants were asked to judge whether the lower half of the two faces successively presented were the “same or different”. The procedure and design of Experiment 2 was identical to that of Experiment 1 except that, to prevent responses with long latencies, the second face was presented for no longer than 2000 ms or until a participant responded within 2000 ms (Mean RT = 839 ms), on each trial of Experiment 2.

2.2. Results and discussion

d′ scores were calculated as the dependent measure by using correct “same” responses as Hits and correct “different” responses as Correct Rejections. Results are shown in Fig. 7.

A 3 (Face category: Asian, Caucasian, and Monkey) × 2 (Congruency: Congruent vs. Incongruent) × 2 (Alignment: Aligned vs. Misaligned) repeated measures analysis of variance (ANOVA) was performed using *d′* as the dependent variable. The main effect of Face Category was significant, $F(2,82) = 3.27$, $p = 0.043$, $\eta_p^2 = 0.074$, indicating that *d′* differed for the lower-half judgment for Asian, Caucasian, and monkey faces. The main effect of Congruency was also significant, $F(1,41) = 32.07$, $p < 0.001$, $\eta_p^2 = 0.44$, indicating that participants performed better on congruent trials than on incongruent trials. The main effect of Alignment was not significant, $F(1,41) = 2.59$, $p = 0.116$, $\eta_p^2 = 0.059$. The interaction of Face Category and Congruency was also not significant, $F(2,82) = 2.44$, $p = 0.093$, $\eta_p^2 = 0.056$, indicating that the congruency effect did not differ for the 3 face categories. The interaction of Congruency and Alignment was significant, $F(1,41) = 16.08$, $p < 0.001$, $\eta_p^2 = 0.28$, indicating a composite-face effect for the 3 face categories. The interaction of Face Category and Alignment was not significant, $F(2,82) = 0.756$, $p = 0.473$. The three-way interaction among Face Category, Congruency, and Alignment was also not significant, $F(3,129) = 0.42$, $p = 0.18$, $\eta_p^2 = 0.836$.

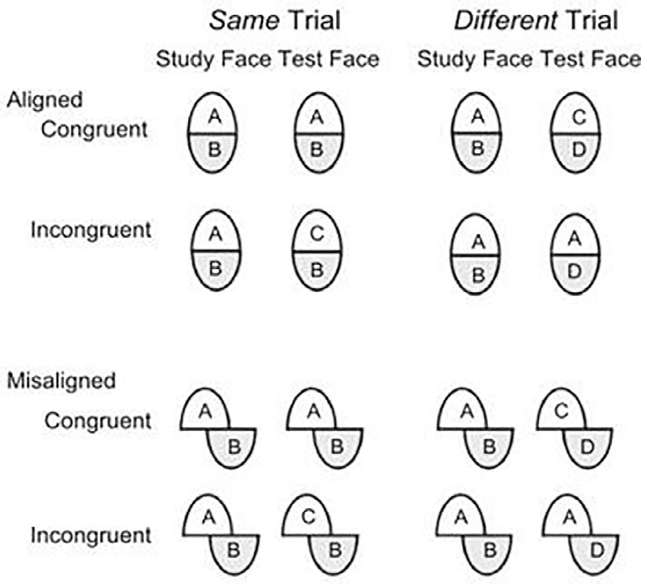

Fig. 6. Schematic diagram of the composite-face task for bottom-half face matching. Participants were asked to study the lower half of the first face and judge whether the second face had the same or different lower half. In “same” trials, the lower halves of the first and second faces were the same; in “different” trials, they were different. The letters A, B, C, and D refer to facial identities of each half. “Aligned” and “Misaligned” refer to the spatial relation between the upper and lower halves of a face. “Congruent” and “Incongruent” refer to the second-order logic relation: if the lower halves of the two faces are the same (or different), and the upper halves are the same (or different), they are congruent; if the lower halves of the two faces are the same (or different), but the upper halves are different (or the same), they are incongruent.

To further explore whether there were any differences among the three significant composite-face effects across own-race faces, other-

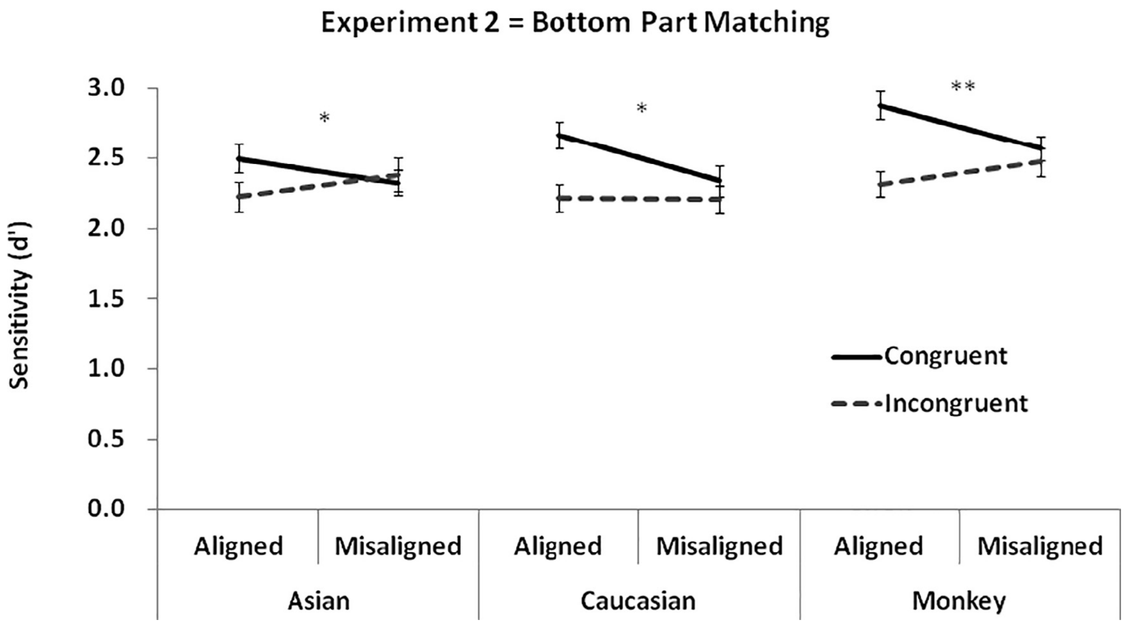

Fig. 7. Sensitivity (d') as a function of alignment, congruency, and face category in Experiment 2. Error bars are SEM. * and ** indicate significant differences ($p < 0.05$) and ($p < 0.01$), respectively.

race faces, and other-species faces, we performed a repeated measure ANOVA by using Interaction Size [($d'_{\text{aligned/congruent}}$-$d'_{\text{aligned/incongruent}}$)-($d'_{\text{misaligned/congruent}}$-$d'_{\text{misaligned/incongruent}}$)] as the dependent variable. Results showed that the Face Category effect was not significant, $F(2,82) = 0.183$, $p = 0.833$, suggesting that the degree of holistic processing induced by own-race faces, other-race faces, and other-species faces was the same when participants were asked to attend the lower-half of the faces.

3. General discussion

In the current study, we examined whether and how a holistic processing account can be extended to explain the effect of species specificity on matching of sequentially presented faces by human observers. First, we found that when participants were asked to judge the upper halves of three different categories of faces as same or different, they showed a strong composite-face effect for Asian (own-race) faces, a relatively weaker but still significant composite-face effect for Caucasian (other-race) faces, but no composite-face effect for monkey (other-species) faces. Second, we found a different data pattern when participants were asked to match the lower halves across these three categories of faces: Asian (own-race) faces, Caucasian (other-race) faces, and monkey (other-species) faces all induced the composite-face effect significantly. Specifically, the magnitude of the composite-face effect induced by monkey (other-species) faces was as strong as that induced by own-species (both Asian and Caucasian) faces. Taken together, the findings provide evidence suggesting that (1) the composite-face effect, which was previously observed to be stronger for own-race faces than for other-race faces (Michel, Rossion et al., 2006), is also found to be stronger for own-species faces than for other-species faces; and (2) a region-selective holistic processing account can explain why humans show a species-specific effect in face recognition: because the holistic processing for the other-species faces is limited to the upper half, while both halves of the face are holistically processed when participants process own-species faces.

Our data demonstrate that the species-specific effect of face recognition has region selectivity during a composite-face matching task for sequentially presented faces. The composite-face effect was not observed when human participants matched the upper-face halves of the other-species faces and was significant only in the lower-half matching task. The findings indicate that the species-specific effect in face processing is influenced by the information in the to-be-matched facial region in a monkey face. This finding is consistent with other reports of region-dependency in face perception (e.g., Bukach et al., 2008; Quinn & Tanaka, 2009; Quinn, Tanaka, Lee, Pascalis, & Slater, 2013; Tanaka et al., 2014; Wang et al., 2015). It is clear in our data pattern that this region-dependency plays a role in the differential processing of own- versus other-species faces.

Our data reveal that holistic processing by human observers can be observed during matching of both the upper and lower regions of the face when perceiving human faces, but can only be observed during matching of the upper region of the face when perceiving monkey faces. By extending the experience-based holistic processing account for own-race relative to other-race faces, own-species faces should also be better recognized than other-species faces because other-species faces are less experienced and thus not processed holistically to the same extent as own-species faces. In the current study, the amount of contact experience influenced the "range" of holistic processing in a face: participants have little contact experience with other-species (i.e., monkey) faces so that the composite-face effect was limited to the upper halves of the monkey faces, while participants have much more contact experience with own-species (i.e., human) faces so that the composite-face effect involved both the upper and lower halves of human faces. In other words, even though we did not manipulate experience directly, the presumed greater contact experience with own-species faces may be an important determinant of expanding the range of the face to be processed holistically to the whole face.

Why was the composite-face effect not observed when human participants matched the upper halves of monkey faces relative to the upper halves of human faces, but in evidence when human participants matched the lower halves of monkey and human faces? One interpretation of these results is that it is possible to focus on the eyes and ignore mouth information in monkey faces relative to human own- or other-race faces (Experiment 1 results), but difficult to look just at the mouth and ignore the human eyes (Experiment 2 results). Based on the evidence from eye-movement studies, it is possible that when participants were asked to match the upper halves of faces, the *Facespan* (the minimum spatial extent of processing from a given fixation necessary for face recognition; see Papinutto, Lao, Ramon, Caldara, & Miellet, 2017) covers almost the entire area encompassed by the internal features of human faces, but covers only the eyes and their surrounding area for monkey faces. However, when participants matched the lower halves of faces, the Facespan automatically covered the upper half of the faces for both human and monkey faces. The reason that Facespan automatically included the upper halves of faces can be explained by the notion of a biological barcode (Dakin & Watt, 2009). According to this idea, most of the information about face identity resides in the upper parts of the face along a horizontal axis, with the eyes being the most prominent. This information provides biological "barcodes" for different face identities. Thus, to perform the matching task in Experiment 2, participants could not help but automatically attend to this biological barcode information and therefore their performance reflected the influence of this information.

However, why would the ability to ignore the mouth be present only for the monkey faces, and not the human faces (as in Experiment 1)? This may occur because human face holistic processing drives integration of the mouth with the eyes. That is, attention to the eyes of a same-species face whether it belongs to our own race and to a lesser extent, a different race, compels integration of the mouth region. However, when attending to the less familiar other-species monkey face, the mouth region can be more readily ignored. Thus, perception of the eyes in the more familiar, own-species faces is more holistic and produces interference from the to-be-ignored mouth. In Experiment 2, when participants are asked to attend to the mouth, across-the-board holistic interference from the eyes is observed, irrespective of the race or species of the face. Overall, then, there may be something about the eyes of the face that automatically commands our attention, which can be again explained by the biological barcode idea.

Now, why then there are differential effects for own-race faces, other-race faces, and monkey faces? To further understand the effect of face species and related work on face race, we borrow from a theoretical construct known as the *perceptual field*, which was originally proposed by Rossion (2008, 2009) to explain the face inversion effect, and is complementary to the Facespan and barcode notions. This construct suggests that because of extensive experience with upright faces, an observer extracts diagnostic visual information across a broad area of the visual field when a face is upright, but this perceptual area is reduced when a face is inverted. The perceptual field construct has also been applied to understanding a processing difference for own- versus other-race faces in which participants were shown to be more sensitive to both configural and featural changes in the eye region but not mouth region for own- relative to other-race faces (Wang et al., 2015). This result implies that more expertise in own-race face processing resulted in an "expertise area" which has "higher perceptual resolution" in the upper half of own-race faces relative to other-race faces. Such an outcome was reflected in the current data set in a relatively weaker, although still significant composite-face effect for Caucasian (other-race) faces. Moreover, our current results in which only the upper half of the other-species faces showed the composite-face effect and engaged holistic processing suggest that the perceptual field may be even more reduced for these less experienced faces.

By the perceptual field account, the race and species findings taken together would suggest that the perceptual field covers less area of the lower half of other-race faces (relative to own-race faces) and none of the lower half of monkey faces. A possible difference in the magnitude of perceptual field reduction for other-race versus -species faces (i.e., smaller field for other-species faces) would be consistent with other-species faces being less experienced than other-race faces or the similarity between own- and other-race faces being greater than the similarity between own-race and other-species faces or both.

Investigations of the effect of real-life face experience (e.g., Pachai, Sekuler, Bennett, Schyns, & Ramon, 2017; Ramon, 2015a, 2015b; Ramon & Van Belle, 2016) provide further support for our claim that contact experience can broaden the spatial extent across which facial information is integrated. For example, Ramon (2015a) used a two alternative forced-choice delayed matching task and found that vertical inter-feature distance changes were discriminated more accurately in familiar faces than in unfamiliar faces. In addition, Pachai et al. (2017) used personally familiar and unfamiliar faces in a face discrimination task and found increased horizontal sensitivity for upright, familiar faces.

Relatedly, Zhou, Cheng, Zhang, and Wong (2012) found a smaller composite face effect in art students than in non-art control students. Art students have more face drawing experience than non-art students. On first pass, this finding seems to run counter to our argument that more contact experience enhances holistic processing for own-race and own-species faces relative to other-race and other-species faces. However, the drawing experiences of art students differ from daily contact experiences in terms of their task demands. In particular, the face drawing experiences of art students may push attention more to the individual parts of a face, whereas the daily contact experience that is associated with face identification may engage processing of both part and configural information (i.e., the relationship among parts) in faces. Moreover, Zhao, Bülthoff, and Bülthoff (2016) reported that line patterns with salient Gestalt properties can be processed as holistically as faces without any training, indicating that object-based Gestalt information can activate holistic processing. This finding, together with the data indicating that observer-based experience plays a crucial role, suggests that holistic processing can be engendered both through an expertise-driven top-down route and a Gestalt-driven bottom-up route. The present findings have their basis in presumed differences in experience, and are thus consistent with holistic processing achieved via the top-down route.

One limitation of our results is that we tested human faces versus only one non-human species: monkey faces. One could argue that it is the particular geometry of the monkey faces with large eyes and small mouths, and consequent selective attention to the eyes over the mouth that is driving the finding that monkey faces are perceived less holistically. It will therefore be important in future work to test how observers perform with additional non-human species faces, such as those of cats or dogs, to determine how broadly the current results will generalize. It would also be informative in evaluating this alternative explanation based on selective attention to use an eye-tracking procedure in conjunction with the current behavioral measure to assess the distribution of attention to the internal features. In this way, one could directly assess the relative proportion of fixations to the eyes versus the mouth, and examine the association between these fixations and performance on the composite-face task.

In summary, we examined the composite-face effect induced by own-race faces, other-races faces, and other-species faces in Asian observers. Results revealed that own-species faces induced the composite-face effect in both the upper and lower half of faces, but the other-species faces induced the composite-face effect only when participants were asked to recognize the lower half. These findings suggest that the species-specific effect in face recognition by human observers reflects reduced integration of facial information from the lower face region in other-species faces.

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