Visual Field Information in the Face Perception of Chimpanzees *(Pan troglodytes)*

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ABSTRACT: Evidence for a visual field advantage (VFA) in the face perception of chimpanzees was investigated using a modification of a free-vision task. Four of six chimpanzee subjects previously trained on a computer joystick match-to-sample paradigm were able to distinguish between images of neutral face chimeras consisting of two left sides (LL) or right sides (RR) of the face. While an individual's ability to make this distinction would be unlikely to determine their suitability for the VFA tests, it was important to establish that distinctive information was available in test images. Data were then recorded on their choice of the LL vs. RR chimera as a match to the true, neutral image; a bias for one of these options would indicate an hemispatial visual field advantage. Results suggest that chimpanzees, unlike humans, do not exhibit a left visual field advantage. These results have important implications for studies on laterality and asymmetry in facial signals and their perception in primates.

KEYWORDS: laterality; asymmetry; face recognition

A study was conducted on the response of chimpanzees (*Pan troglodytes)* to normal and chimeric photographs of other chimpanzee faces. Morris and Hopkins found evidence of a left visual field advantage in the response of chimpanzees to images of human faces;[1] we sought to confirm their findings

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and examined potential chimpanzee preference for a certain side of the face using conspecific images—a hemispace visual field advantage (VFA).

Recent studies of human and nonhuman primate face recognition and emotion have frequently used facial images to identify cognitive biases and brain laterality. Levy *et al.*, for example, used chimeras—compound images formed by matching half of an image with the reverse of the same half image—to test the hypotheses that humans exhibit a left hemispace VFA and that this bias correlates with handedness.[2] A left VFA would suggest that the left half of the visual field (and the right side of the subject in view) is the source of the majority of the visual information used. Fernández-Carriba *et al.* found that chimpanzee facial expressions exhibited a greater left hemimouth size, hence right-hemispheric dominance in the production of expression.[3] We tested the hypothesis that there was a similar lateral bias in chimpanzee perception of images of neutral (i.e., nonexpressive) chimpanzee faces.

Using a Canon XL-1 digital camera, we recorded video of freely interacting chimpanzees in June and July, 2002, in two social groups (n = 18 and 19 individuals) at the Yerkes Regional Primate Research Center field station in Lawrenceville, GA (details in Ref. 4). We used 2–3 images of each of the 37 chimpanzees chosen from video frames for clarity, lighting, subject orientation (i.e., facing the camera), and neutral expressions. All video was captured and clipped using Adobe Premiere 6.0. Suitable frames from the video were formatted using Adobe Photoshop 6.0. We cropped each image to ca. 5.1 × 5.1 cm and formed chimeras by pairing one half of each image with its mirror image (FIG. 1).

Using a computerized matching-to-sample (MTS) paradigm, we tested each of six chimpanzees previously trained to operate a computer joystick with the MTS program. Two experiments were performed. Recognition testing sought to determine whether the chimpanzees could distinguish between

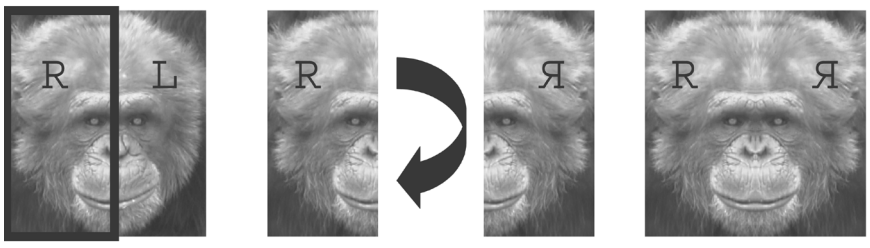

FIGURE 1. Chimeras formed from digital photographs by pairing one half of a facial image with the mirror image of that same half.

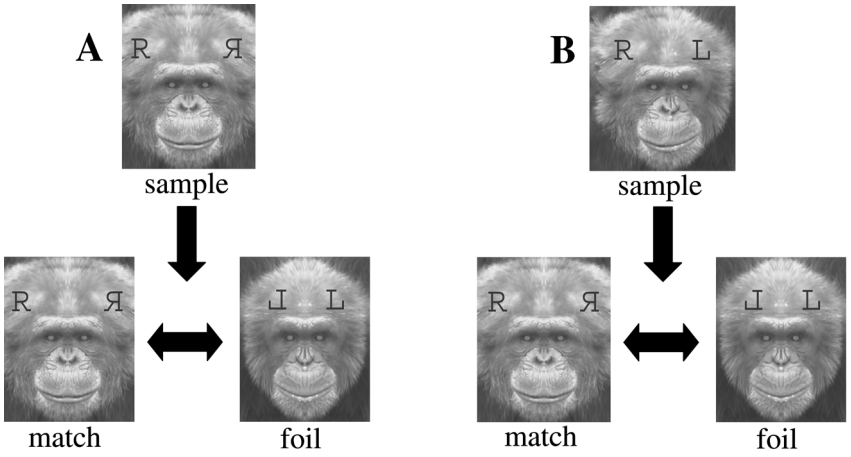

FIGURE 2. Recognition testing (**A**) required the subject to distinguish the image matching the sample from the foil. Successful matches were rewarded. Chimera testing (**B**) offered two alternatives (still "match" and "foil" by convention for the subject to pair with the sample). Selection of either alternative was rewarded.

LL and RR chimeras by requiring them to choose between LL and RR chimeric images as a match to an identical LL or RR chimera (FIG. 2A). Five of six chimpanzees responded to 12 repeats (the 6th responded to 9) of 20 trials; correct responses were rewarded. Chimera testing examined the chimpanzee's preference for either the LL or RR chimera following presentation of the unaltered image from which the chimera had been fashioned (FIG. 2B). Here, each chimpanzee responded to 6 sets of 30 trials consisting of a random arrangement of 10 LL-RR trials and 20 filler trials. In the filler trials, the subject was required to distinguish between matching and nonmatching chimpanzee faces (identity), a task (based on Parr *et al.*[5]) at which these subjects had previously proved themselves (de Waal, unpublished data). Thus the chimpanzees had to attend to the task in order to receive the maximal number of rewards. All data were analyzed using a heterogeneity G-test,[6] which compared observed and predicted values for individual, pooled, and total data.

Each of the six chimpanzees tested scored significantly better than 50% chance on the recognition test, indicating that there was sufficient visual information available to make this distinction ($Gh = 31.9$, $df = 5$, $P < 0.001$; $Gp = 115.2$, $df = 1$, $P < 0.001$; FIG. 3). This was the first time these chimpanzees had been presented with chimeric faces, and the high success is indicative of their strong understanding of the MTS paradigm. None of the six chimpan-

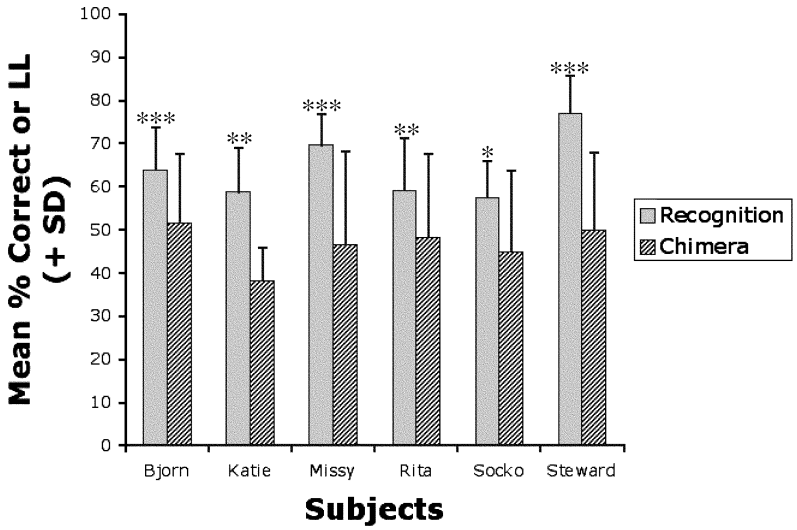

FIGURE 3. Mean percent correct (recognition testing) or percent of LL chimera choices (chimera testing). $*P < 0.05$; $**P < 0.01$; $***P < 0.001$.

zees showed an apparent hemispace VFA, choosing LL and RR chimeras with roughly equal frequency ($Gh = 2.70$, $df = 5$, $P = 0.75$; $Gp = 1.60$, $df = 1$, $P = 0.21$) in the chimera testing (FIG. 3).

Our tests show that chimpanzees can make the fine distinction between left and right sides of the same face. Using conspecific faces, they do not support the hypothesis of a visual field advantage (VFA) in face perception. Our results do not mean that chimpanzees (or other nonhuman primates) lack a hemispace visual bias. We plan additional trials using abstract images, but suggest that the application and modification of Levy's free-vision task for assessing VFAs be used cautiously.

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REFERENCES

1. MORRIS, R.D. & W.D. HOPKINS. 1993. Perception of human chimeric faces by chimpanzees: evidence for a right hemisphere advantage. Brain Cogn. **21:** 111–122.
2. LEVY, J., W. HELLER, M.T. BANICH & L.A. BURTON. 1983. Asymmetry of perception in free viewing of chimeric faces. Brain Cogn. **2:** 404–419.
3. FERNÁNDEZ-CARRIBA, S., A. LOECHES & W.D. HOPKINS. 2002. Asymmetry in facial expression of emotions by chimpanzees. Neuropsychologia **40:** 1523–1533.
4. SERES, M., F. AURELI & F.B.M. DE WAAL. 2001. Successful formation of a large chimpanzee group out of two preexisting subgroups. Zoo Biol. **20:** 501–515.
5. PARR, L.A., W.D. HOPKINS & F.B.M. DE WAAL. 1998. The perception of facial expressions by chimpanzees, *Pan troglodytes*. Evol. Commun. **2:** 1–23.
6. SOKAL, R.R. & F.J. ROHLF. 1995. Biometry. W.H. Freeman & Co. New York.