Left hemisphere dominance for processing vocalizations in adult, but not infant, rhesus monkeys: Field experiments

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ABSTRACT   In humans, the left hemisphere of the brain is dominant for processing language. To assess the evolutionary origins of this neuropsychological mechanism, playback experiments were conducted on a large population of free-ranging rhesus monkeys (*Macaca mulatta*). Playbacks provided an equal opportunity to orient the right or left ear toward the speaker. Results revealed that 61 of 80 adult rhesus favored the right ear (left hemisphere) when vocalizations from their own repertoire were heard but favored the left ear when listening to heterospecific vocalizations. In contrast, infants less than a year old showed no perceptual asymmetry for conspecific or heterospecific calls. Thus, like humans, adult rhesus monkeys also evidence left hemisphere dominance for processing species-specific vocalizations. The emergence of such asymmetry, however, may depend on both differential maturation of the two hemispheres and experience with the species-typical vocal repertoire.

Humans show significant hemispheric asymmetries for communicative expression and perception, including left hemisphere dominance for spoken and signed language and right hemisphere dominance for face perception and expression (e.g., refs. 1–5). These hemispheric biases, however, must not be interpreted to mean that the less dominant hemisphere is *quiet* during a particular cognitive task. Thus, for example, the right hemisphere appears dominant with regard to processing the prosodic features of language (5). To understand the evolutionary origins of hemispheric asymmetries for communication in humans, it is necessary to determine whether phylogenetically proximal species, such as the monkeys and apes, process vocal and facial expressions from their own repertoire in similar ways. Present understanding of this problem is limited to two sets of studies. First, based on field studies of acoustic communication in Japanese macaques (6), psychophysical (7) and neurobiological (8) experiments have demonstrated that this species, but not closely related species, shows a left hemisphere bias for processing a single call type from the repertoire; these experiments mirrored those used on humans and involved playbacks of calls through headphones, measuring reaction time differences during a call discrimination task. Second, free-ranging rhesus macaques show a right hemisphere bias for the production of facial expressions, in terms of both timing and expressiveness (9).

The present project sought to build on previous research by (*i*) testing individuals under natural conditions, (*ii*) using a large sample of individuals so that population-level asymmetries could be detected, (*iii*) recording subjects' responses to multiple call types within the repertoire so that the effects of variation in call meaning and affect (10–13) could be discerned, and (*iv*) testing young infants to determine the extent of developmental change in hemispheric function. Rhesus

monkeys were selected as test subjects because of previous research on their communicative repertoire (9–13) and because of data indicating a longer left sylvian fissure (14, 15), a crucial structure for auditory processing in humans.

Tape-recorded vocalizations were played back to adult and infant (4–12 months) rhesus monkeys living on Cayo Santiago, Puerto Rico (16). In each experiment, a speaker was concealed in dense vegetation 180° behind the target subject (Fig. 1). Subjects were tested when they were seated and eating at one of the three food dispensers, providing a consistent context for testing. Our response assay was to score whether the subject turned the right or left ear in the direction of the speaker; no response was scored when the focal subject showed no detectable change in head position. In all tests where a response was detected, the subject turned its head more than 45°, looking in the direction of the speaker. Although both ears clearly received auditory input during these tests, biasing the response toward one side causes a relative increase in the intensity of the stimulus at that ear and, consequently, in the contralateral hemisphere. Playbacks to adults were completed in a 3-week period. Playbacks to infants were conducted 2 months later and were completed in 4 weeks.

Fifty-one vocalizations were used in the experiments, including three to five exemplars from 12 call types, encompassing much of the vocal repertoire (11). The call types fell into three broad contexts: aggressive, fearful, and affiliative. The alarm call of the ruddy turnstone (*Arenaria interpres*), a seabird that lives on Cayo Santiago, both near the shoreline and away from it, was used as a control (four different exemplars). The turnstone's alarm call is frequently heard and is thus familiar to the rhesus. Moreover, natural observations indicate that rhesus monkeys orient to turnstone alarm calls, presumably because these birds often call to humans. Although human observers did not interact with the monkeys, there are at least two situations where humans evoke alarm: (*i*) once a year, when the monkeys are trapped and marked for identification and (*ii*) when infants are approached closely. As a result, turnstone alarms represent potentially useful sources of information for rhesus monkeys.

For adults, 61 individuals turned the right ear toward the speaker in response to rhesus calls, whereas 19 turned the left ear. Thus, 76.3% of the adult population tested exhibited a right ear bias ($\chi^2 = 22.0$, df = 1, $P < 0.001$). In addition, statistically significant ($P < 0.01$) right ear biases were observed for each of the three social contexts (Fig. 2A). When the turnstone's call was played, a significant ($P < 0.01$) number of individuals (13 of 15) favored the left ear rather than the right ear (Fig. 2A).

In contrast to adults, infants revealed no evidence of asymmetry. In response to conspecific calls, 20 of 37 infants (54.1%) turned their right ear toward the speaker, whereas 9 of 15 infants (60.0%) turned the right ear in response to the turnstone's call. Moreover, the lack of asymmetry was consistent for all three social contexts (Fig. 2B).

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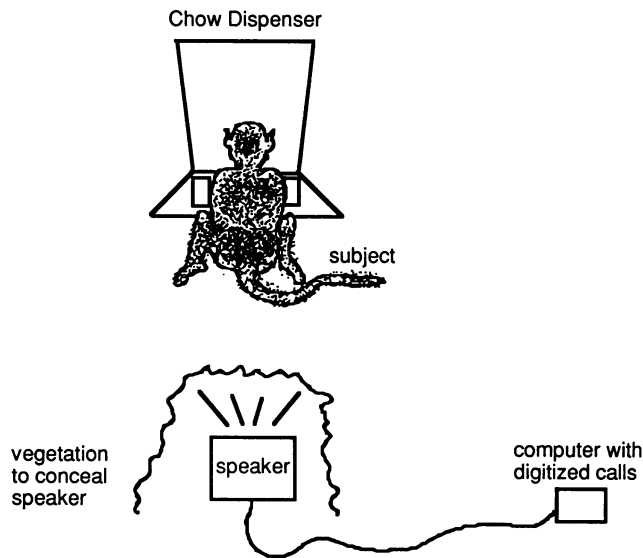Proc. Natl. Acad. Sci. USA 91 (1994)   3947

FIG. 1. Schematic illustration of the playback setup. Playback experiments were conducted in close proximity to one of the three food dispensers on the island. Each food dispenser was physically, visually, and acoustically separate, and playbacks at one dispenser could not be heard by individuals located at the other two. At each dispenser there were two playback stations, one on each side; a station was defined as an area of dense vegetation located 180° and 10–12 m from the dispenser. Prior to testing, the speaker was lined up with the center of the dispenser to ensure that the direction of broadcasting was directly at the subject's back. Playback experiments were conducted only when an individual sat and faced the food dispenser straight on. The response assay was to record whether, following playback, subjects turned the right or left ear toward the speaker. This response was unambiguous. When individuals responded, they never turned completely around but, from our perspective, could see with both eyes. Thus, we did not detect an eye-bias, only an ear-bias. Separate playbacks were conducted on a total of 169 individuals. On 10 trials with conspecific calls, and 12 control trials, the subject failed to respond (i.e., did not look toward the speaker). Tests with conspecific calls in which the subject oriented toward the speaker included 80 trials with adults (44 males, 36 females) and 37 trials with infants. Tests with the bird call included 15 trials with adults (7 males, 8 females) and 15 with infants. For conspecific playbacks, the mean distance between the subject and speaker was 9.1 ± 2.0 m (mean ± SD, n = 80); for playbacks with the ruddy turnstone's call, the mean subject-to-speaker distance was 9.2 ± 1.8 m (n = 16). For conspecific playbacks, the mean number of individuals within 5 m of the target subject was 5.5 ± 3.9 (n = 80), and for playbacks with the ruddy turnstone's call, the mean was 5.3 ± 4.3 (n = 16). Vocalizations from the rhesus monkey's repertoire were used for playbacks and were digitized onto a Macintosh Quadra 950 using the 16-bit Audio Media card and Sound Designer II software interface. Following acquisition, each vocalization was integrated into a control panel for sound playback. Field playback experiments were run from a Macintosh Powerbook 170 connected to an Anchor AN-256 speaker.

In humans, left hemisphere dominance for language is most prominent in right-handers (5). For a subset of the rhesus monkeys sampled (21 adults), data on handedness were available based on observations at the dispensers. As reported elsewhere (17), the monkeys must lift and stabilize the lids to the dispenser before gaining access to the chow; most individuals lift the lid with the left hand, hold with the right, and eat with the left. Handedness was assigned on the basis of which hand was used to eat food, since it demanded the greatest amount of manipulation. There was no statistically significant effect of handedness on the direction of head turning in response to playbacks of conspecific calls (x^2, P = 0.58). Thus, the right ear bias for processing conspecific calls cannot be entirely explained by a right-side bias for motor production.
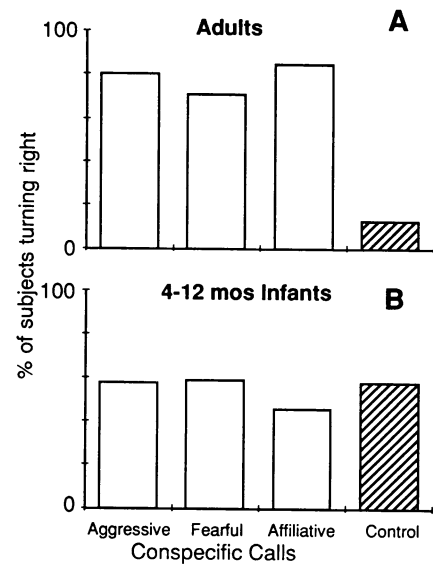

FIG. 2. Proportion of subjects orienting right (i.e., turning the right ear toward the speaker) in response to three categories of conspecific calls (open bars) and one heterospecific call (hatched bar)—the ruddy turnstone's alarm call (control). (A) Adult responses. Sample sizes for each category of call are as follows: aggressive, 11 males and 9 females; fearful, 22 males and 19 females; affiliative, 11 males and 8 females; control, 9 males and 6 females. (B) Responses of 4- to 12-month infants. Sample sizes for each category of call are as follows: aggressive, 12; fearful, 10; affiliative, 15; control, 15.

Results suggest that for adult rhesus, the left hemisphere is dominant for processing conspecific vocalizations whereas the right hemisphere is dominant for a familiar heterospecific vocalization. Comparable results have been demonstrated for songbirds (18). The asymmetry exhibited by adult rhesus is not, however, evidenced by infants.

Two factors limit our ability to directly compare the results presented in this report with those obtained for humans. First, most tests of human adults and infants involve a dichotic listening paradigm (5, 19). The directional orientation technique used here for rhesus has been used less often in human studies (20) but has nonetheless found a left hemisphere bias for language. With an orienting response, it is more difficult to separate motor from perceptual effects. Nonetheless, because handedness had no statistical effect on the direction of orientation, and because playbacks of rhesus and turnstone calls elicited different head orientations, it seems most likely that the asymmetry observed is perceptual rather than motoric. Moreover, although an orienting response also involves the visual system, we believe the observed asymmetry is primarily due to the auditory system. If the response bias were due to the visual system—seeking additional information on who called and to whom—we would have expected individuals to turn to the left, since neurobiological studies clearly implicate the right hemisphere in face processing (21). Additionally, a visual processing asymmetry cannot explain the differences in response to rhesus and turnstone calls.

Second, although humans show left hemisphere dominance for processing the linguistic properties of language, the right hemisphere appears dominant for the emotional content of language. It is difficult to divide the rhesus monkey's vocal repertoire into the equivalent of linguistic and nonlinguistic components. Regardless of their informational content, however, rhesus adults show a left hemisphere bias for processing conspecific calls. If most calls in the repertoire convey some "linguistic" information, and the orienting response is guided by such information, then the pattern of asymmetry is similar

to that demonstrated for humans. In contrast, if the calls convey only emotional information (i.e., nonlinguistic), as perhaps would be argued for facial expressions (9), then the pattern of asymmetry is opposite that described for humans. Data on rhesus infants may shed some light on this problem. Several studies of nonhuman primates indicate that adult comprehension of call meaning can take up to 2 years to acquire (22). Consequently, hemispheric asymmetries in perception may emerge only once calls within the repertoire acquire meaning, and in the present case, such abilities may not arise until the second year of life. It thus becomes all the more urgent to distinguish between the linguistic and nonlinguistic components of nonhuman primate signals (22, 23), to determine when infant comprehension of call meaning develops, and to establish whether there is differential maturation of the right and left hemispheres (24).

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