

Vervet monkeys and humans show brain asymmetries for processing conspecific vocalizations, but with opposite patterns of laterality

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A robust finding in the human neurosciences is the observation of a left hemisphere specialization for processing spoken language. Previous studies suggest that this auditory specialization and brain asymmetry derive from a primate ancestor. Most of these studies focus on the genus *Macaca* and all demonstrate a left hemisphere bias. Due to the narrow taxonomic scope, however, we lack a sense of the distribution of this asymmetry among primates. Further, although the left hemisphere bias appears mediated by conspecific calls, other possibilities exist including familiarity, emotional relevance and more general acoustic properties of the signal. To broaden the taxonomic scope and test the specificity of the apparent hemisphere bias, we conducted an experiment on vervets (*Cercopithecus aethiops*)—a different genus of old world monkeys and implemented the relevant acoustic controls. Using the same head orienting procedure tested with macaques, results show a strong left ear/right hemisphere bias for conspecific vocalizations (both familiar and unfamiliar), but no asymmetry for other primate vocalizations or non-biological sounds. These results suggest that although auditory asymmetries for processing species-specific vocalizations are a common feature of the primate brain, the direction of this asymmetry may be relatively plastic. This finding raises significant questions for how ontogenetic and evolutionary forces have impacted on primate brain evolution.

Keywords: brain evolution; primate; communication; vocalizations; functional asymmetry

1. INTRODUCTION

Twenty years ago, textbooks in the neurosciences claimed that human brains are uniquely asymmetric, both anatomically and functionally. This claim is no longer correct (Toga & Thompson 2003). A large number of studies have now reported both anatomical and functional asymmetries in almost every taxonomic group of vertebrates (Rogers & Andrews 2002). However, there are significant uncertainties with respect to questions of evolutionary ancestry: some cognitive and perceptual asymmetries in humans have not been fully explored in other species and even in cases where they have, we have little understanding of the direction of such asymmetries, whether they are free to vary or constrained in development or evolution. A case in point is the robust finding that humans show a left hemisphere bias for processing spoken language and the suggestion that this bias originates from a non-human primate ancestor dating back at least as far as the genus *Macaca*. Studies using behavioural and neurophysiological approaches suggest a left hemisphere bias for the perception of conspecific vocalizations and a right hemisphere bias for the production of both vocalizations and facial expressions (Zoloth *et al.* 1979;

Heffner & Heffner 1986; Hauser 1993; Hauser & Andersson 1994; Ghazanfar & Hauser 2001; Ghazanfar *et al.* 2001; Hauser & Akre 2001; Poremba *et al.* 2004). Although these studies have been used to support the hypothesis that processing of species-specific vocalizations in humans and non-human primates is homologous in terms of brain asymmetries (Efron 1990; Corballis 1991; Belin *et al.* 2000), there are two open questions. First, to what extent do the findings in macaques generalize to other primate species? Second, to what extent is the observed hemispheric asymmetry specific to conspecific calls? Concerning taxonomic scope, it is possible that other species lack a hemispheric bias for auditory processing, show an asymmetry as do macaques, or show an asymmetry but in the opposite direction from that of macaques. Only a broader comparative dataset will address this gap. Concerning species-specificity, although prior studies have contrasted conspecific with hetero-specific calls and sometimes added on a contrast with non-biological sounds, the range of signals within each of these categories has typically been small. For example, Hauser & Andersson's (1994) study of rhesus macaques contrasted a wide number of calls from the rhesus repertoire against the alarm call of the ruddy turnstone, a bird that lives sympatrically with rhesus at the test site. This is a contrast between familiar conspecific vocalizations and a familiar heterospecific call. Although rhesus show robust differences in their pattern of responses to these two acoustic categories,

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we do not yet know what drives this difference. For example, perhaps the right ear/left hemisphere bias to rhesus calls is mediated by some general acoustic property that characterizes other primate vocalizations, including both familiar (e.g. humans) and unfamiliar primates (e.g. chimpanzees). What is necessary, therefore, is to broaden the range of stimuli presented, testing for the effects of familiarity within and between species, as well as between biological and non-biological sounds.

In the following experiments, we build on prior research by broadening the taxonomic scope to include a different genus of Old World monkey—vervet (*Cercopithecus aethiops*)—and by presenting a broader range of stimulus conditions than in prior studies. We use a previously established, spontaneous (non-training) head orienting technique. This technique, first implemented with macaques under field conditions (Hauser & Andersson 1994), was used to explore perceptual asymmetries. In brief, an experimenter plays back sounds from a hidden speaker placed 180 degrees behind a subject, noting the direction of the orienting response to the sound. Orienting to the sound source with one ear leading causes an input bias to the contralateral hemisphere. Consistent evidence of perceptual asymmetries has been reported for macaques (Hauser & Andersson 1994), harpy eagles (Palleroni & Hauser 2003) and sea lions (Boye *et al.* 2005) using this technique. Furthermore, neurophysiological studies in macaques have supported the evidence of a hemispheric asymmetry, including the left-side bias for conspecific calls (Heffner & Heffner 1984; Poremba *et al.* 2004).

Given our general aim of broadening both the taxonomic scope of this research as well as the range of stimuli presented, we were specifically interested in testing between three competing alternative hypotheses.

Hypothesis 1. Orienting asymmetries in vervet monkeys are driven by the degree to which a sound is commonly heard in the environment. The captive vervets we test commonly hear calls from their own colony room, as well as sounds from humans that interact with them; the latter include experimenters running studies and the animal care staff that clean their cages, feed them and run routine veterinary check-ups. In contrast, the calls of other vervet monkeys that they have never encountered are unfamiliar, but from the same species. If familiarity, defined by frequency of exposure, drives the asymmetry, then vervets should show the same orienting asymmetry to calls from their colony as they do to human sounds, but different from foreign vervet monkey calls.

Hypothesis 2. Orienting asymmetries in vervet monkeys are driven by all primate sounds. Independently of whether the sounds are familiar or not, all primate sounds share some degree of acoustic overlap due to general properties of their vocal tract and the mechanisms of sound production. This similarity drives the orienting asymmetries. If similarity in acoustic morphology, as just defined, drives the asymmetry, then only non-biological sounds with different acoustic characteristics, should be processed in a different way.

Hypothesis 3. Orienting asymmetries in vervet monkeys are driven by conspecific calls. Independently of whether the call is from a familiar or unfamiliar vervet monkey or produced in the context of fear or affiliation, vervets show an asymmetry to conspecific calls that is different from their processing of all other sounds.

This is certainly not a comprehensive set of possibilities. For example, it is also possible that the orienting bias is driven by the emotional content of a signal and that aspects of the signal's morphology are relevant independently of the source of origin. For example, as Marler (Marler 1955, 1961; Green & Marler 1979) argued many years ago for birds and as Owren & Rendall (1997) have more recently argued for primates, different species may converge on the same call morphology while communicating about similar social or ecological problems. On this view, for example, the alarm calls of a macaque or human or tamarin monkey might drive the orienting bias in the same way as a vervet alarm call. Similarly, and as tested here, calls used for the function of maintaining contact may converge in call structure because of their overlapping context; in the experiments below, we present the contact calls of vervets, rhesus and tamarins. We also attempt to rule out this hypothesis by presenting different vervet calls, each with a different call structure and function, covering a range of emotive information.

2. MATERIAL AND METHODS

We selected vervet monkeys as our test subject because, like macaques, we know a considerable amount about their vocal repertoire (Cheney & Seyfarth 1990). In terms of auditory processing, we also know that they distinguish between conspecific and heterospecific signals, and in the absence of training, recognize the functional significance of some heterospecific signals.

To test for selective orienting asymmetries to conspecific vocalizations, it was necessary to tease apart two dimensions: familiarity and acoustic similarity. To achieve this goal, we therefore developed a stimulus set that included both familiar and unfamiliar sounds, from conspecifics, heterospecifics and non-biological sources. More specifically, we presented subjects with (i) vervet vocalizations from familiar individuals; (ii) vervet vocalizations from unfamiliar individuals; (iii) heterospecific vocalizations from other unfamiliar primates (rhesus macaques, *Macaca mulatta*; cotton-top tamarins, *Saguinus oedipus*); (iv) heterospecific vocalizations from a familiar primate (humans) and (v) non-biological sounds. Table 1 provides a description of the stimuli presented.

We tested five adult captive vervet monkeys (one male, four females); all were born in captivity and were socially housed with six other individuals in a large colony room. Each subject was tested alone in a soundproof chamber equipped with a hidden speaker placed 180° behind the subject, a microphone in front of the subject and a video camera to record their response (figure 1a).

We initiated a playback when the subject's head and body were oriented 180° away from the speaker, in a sitting position; the camera was lined up with both the speaker and subject. Order of stimulus presentation was randomized within session; the experimenter running the session was blind to order and could not hear the playbacks, thereby enabling a method for online blind coding. Mean stimulus duration was comparable across categories and all stimuli were normalized for amplitude. As in previous research on macaques and raptors (Hauser & Andersson 1994; Ghazanfar *et al.* 2001; Palleroni & Hauser 2003), we defined a response as a distinctive head turn in the direction of the speaker, focusing specifically on which ear faced the speaker first within 3 s after stimulus playback. Video records were subsequently digitally acquired and scored blind

Table 1. Auditory stimuli used to test for orienting asymmetry in vervet monkeys.

| signal type | function | familiar/unfamiliar |
|----------------------------------|-------------------------------------|---------------------|
| <i>conspecific calls</i> | | |
| vervet vocalizations | | |
| Harvard colony | | |
| grunts | contact, dominance, group move | familiar |
| chutter | intergroup aggression | familiar |
| screams | submission | familiar |
| B. Kenya, Uganda | | |
| grunts | contact, dominance, group move | unfamiliar |
| chutter | intergroup aggression | unfamiliar |
| screams | submission | unfamiliar |
| <i>heterospecific calls</i> | | |
| rhesus vocalization | | |
| coos | contact, affiliative, group move | unfamiliar |
| cotton-top tamarins vocalization | | |
| combination long call | contact, affiliative | unfamiliar |
| human vocalization | | |
| Darwin | none, but stated in a neutral voice | familiar |
| <i>non-biological sounds</i> | | |
| non-biological sounds | | |
| proing | none | unfamiliar |
| telephone ring | none | unfamiliar |
| gong | none | unfamiliar |
| pure tone | none | unfamiliar |
| wind | none | unfamiliar |
| toaster-jump | none | unfamiliar |
| glass | none | unfamiliar |
| thunder | none | unfamiliar |
| cork up | none | unfamiliar |
| bugle | none | unfamiliar |
| wosch | none | unfamiliar |
| danube piece | none | unfamiliar |

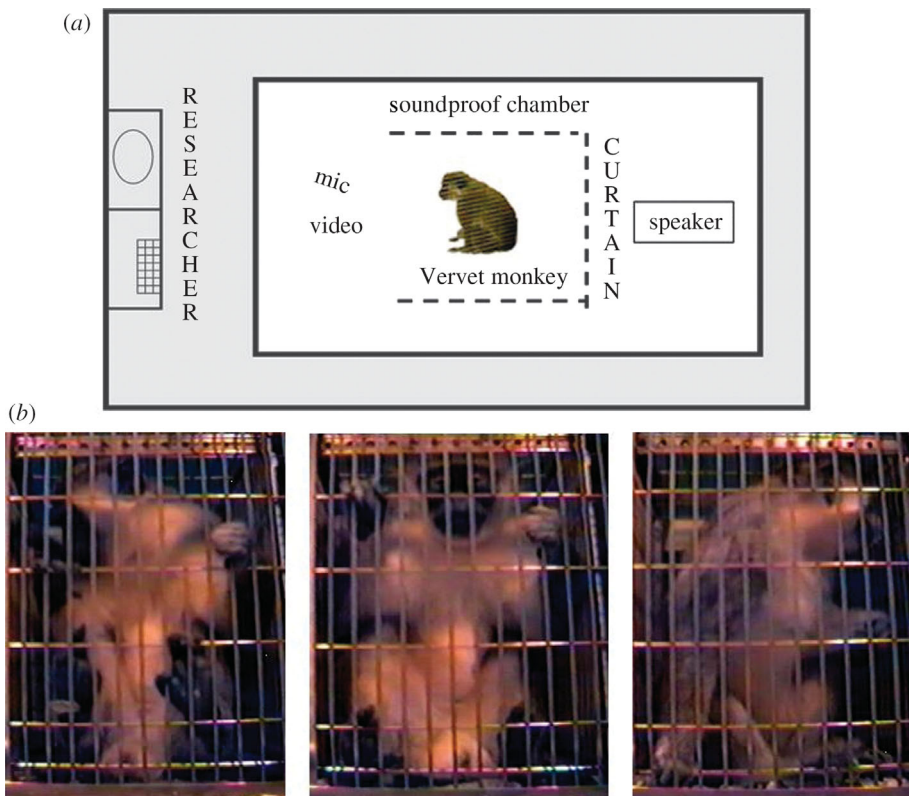


Figure 1. (a) Schematic of the auditory playback testing room. Subjects were acoustically isolated inside the sound-chamber while the experimenter controlled the playback and video/auditory recording from a computer panel outside the chamber. (b) Vervet monkey responses to the playbacks: (ii) 'no response', (i) 'right ear orient', (iii) 'left ear orient'.

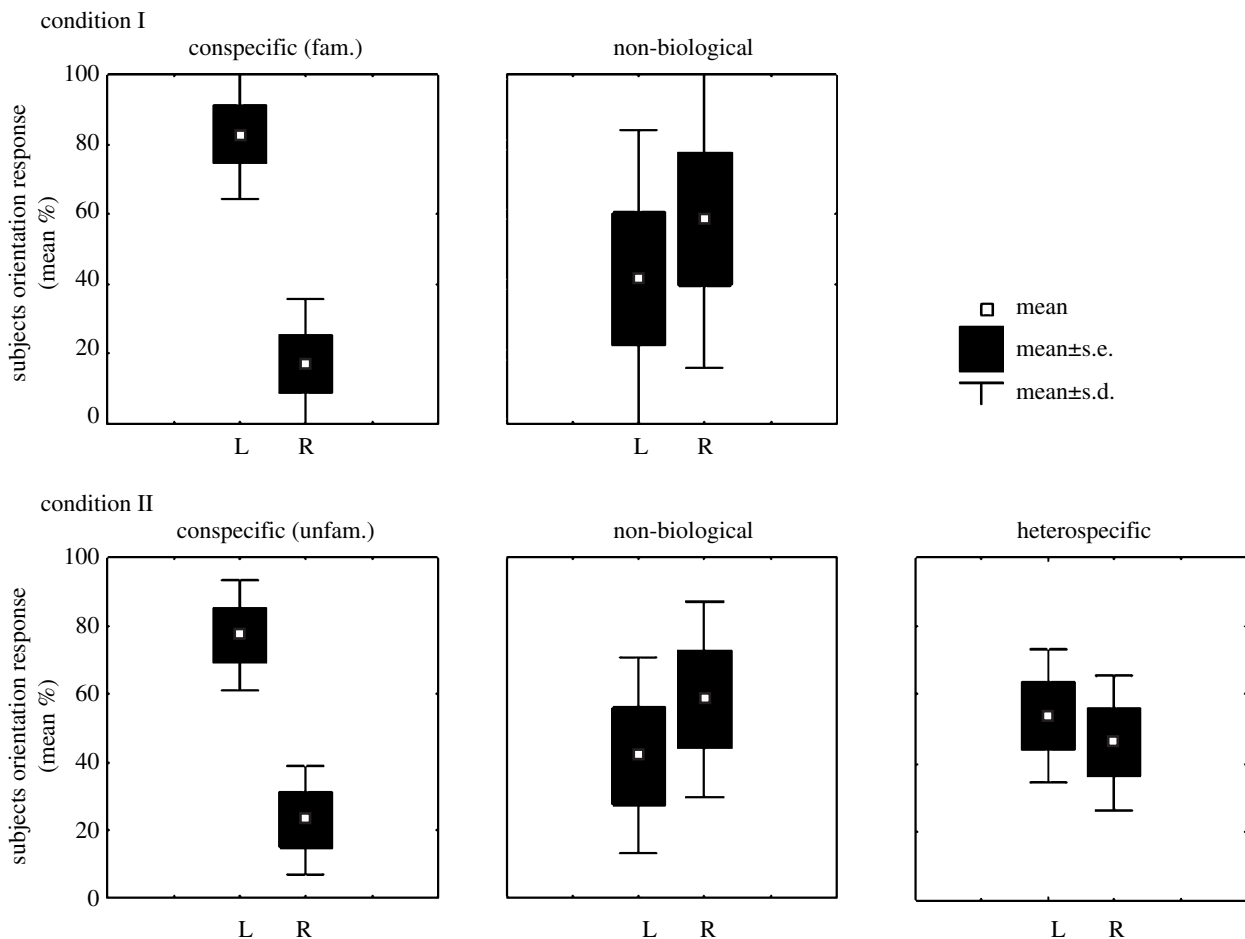


Figure 2. Box and whisker plots representing the group results for head orienting responses (%mean, mean \pm s.e., mean \pm s.d.) in condition I—familiar conspecific vocalizations versus non-biological sounds and condition II—unfamiliar conspecific vocalizations versus non-biological sounds versus heterospecific vocalizations. ‘L’ indicates left ear orienting responses and ‘R’ indicates right ear orienting responses.

by two independent observers; inter-observer reliability was 80.6%. For each trial, we scored one of four responses: ‘no response’, ‘left ear orient’, ‘right ear orient’ or ‘ambiguous’ (ambiguous included disagreement between observers; figure 1b). We discarded all ambiguous responses from the final analyses. There was no vocal response from the subjects to any of the stimuli.

Due to constraints on testing, we ran two separate conditions (I and II) separated by a six month period; one of the subjects could not be tested during condition II. In condition I, we contrasted familiar vervet vocalizations against non-biological sounds. In condition II, we contrasted the sounds of unfamiliar vervets, familiar humans, unfamiliar primates (rhesus, tamarin), and non-biological sounds. The data from conditions I and II were analysed separately. Each subject’s set of responses was reduced to a single datum point (percent score) and all analyses were conducted on the percent scores. The group analyses were performed using a *t*-test for dependent samples when comparing response rates and one-sample *t*-test (reference constant value = 50%) when evaluating head-orientation biases.

3. RESULTS

In condition I, subjects responded to *ca* 57% (mean = 57.09; s.d. = 16.45) of the trials presenting ‘familiar’ vervet vocalizations and to 33% (mean = 33.64; s.d. = 22.56) of the non-biological stimuli. However, there was no statistically significant difference between these response rates

($N=5$, $t=1.886$, d.f. = 4, $p=0.132$). For familiar vervet vocalizations, subjects showed a significant orienting asymmetry, turning with the left ear leading approximately 83% of the trials (mean = 82.83; s.d. = 18.66; $N=5$, $t=3.93$, d.f. = 4, $p<0.05$; figure 2—condition I). All subjects showed this left head-turn orienting asymmetry for vervet vocalizations (figure 3—condition I). In contrast, there was no asymmetry for non-biological sounds (mean = 41.43; s.d. = 42.38; $N=5$, $t=-0.45$, d.f. = 4, $p=0.67$; figure 2—condition I).

Acoustically, a wide variety of features distinguish biological from non-biological signals. To directly test whether the observed difference in response rates, along with the orienting asymmetry, were due to a bias in favour of conspecific vocalizations, we ran a second condition testing two hypotheses. First, if familiarity drives the orienting bias, then vervets should show similar responses to familiar heterospecifics such as humans, and a different pattern to unfamiliar conspecifics. Second, if vervets exhibit an orienting asymmetry that is mediated by the acoustic signature of their species-specific vocal repertoire, then they should respond in the same way to vocalizations from both familiar and unfamiliar vervets.

In condition II, responses to unfamiliar vervet vocalizations, as well as to non-biological sounds and heterospecific vocalizations were compared. Subjects responded to approximately 55% (mean = 55.35; s.d. = 20.66) of the conspecific vocalizations (unfamiliar vervet vocalizations),

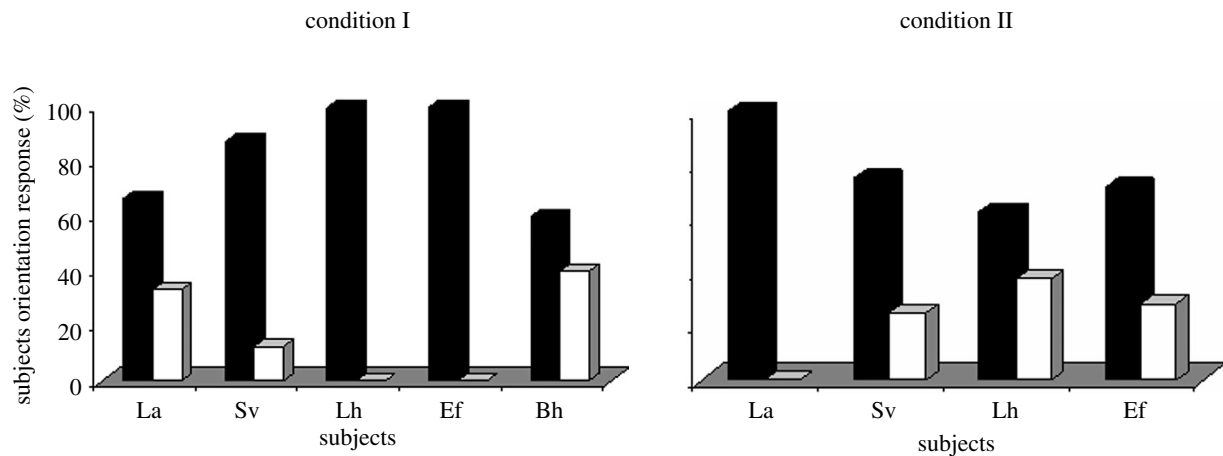


Figure 3. Histograms representing the individual results for head orienting responses to 'familiar conspecifics' (condition I) and 'unfamiliar conspecifics' (condition II). Left ear orienting responses are indicated by the black bars, while right ear orienting responses are indicated by the white bars.

to 36% (mean = 35.56; s.d. = 18.59) of the non-biological stimuli and to 45% (mean = 44.88; s.d. = 17.34) of the heterospecific vocalizations. Again, there were no statistically significant differences in response rates between these stimulus categories (conspecific versus non-biological ($N=4$, $t=2.56$, d.f. = 3, $p=0.08$); conspecific versus heterospecific ($N=4$, $t=0.86$, d.f. = 3, $p=0.45$). In parallel with condition I, a significant left ear orienting asymmetry for unfamiliar vervet vocalizations was revealed, with subjects turning left in approximately 77% of the trials (mean = 77.23; s.d. = 16.06; $N=4$, $t=3.39$, d.f. = 3, $p<0.05$; figure 2-condition II). Furthermore, all individuals showed this pattern (figure 3-condition II). There was no difference in the degree of the orienting bias to familiar as opposed to unfamiliar vervet vocalizations ($N=4$, $t=0.72$, d.f. = 3, $p=0.53$). In contrast, there was no evidence of an orienting bias for either non-biological sounds (mean = 41.67; s.d. = 28.87; $N=4$, $t=-0.58$, d.f. = 3, $p=0.60$) or heterospecific vocalizations (mean = 53.87; s.d. = 19.76; $N=4$, $t=-0.39$, d.f. = 3, $p=0.72$; figure 2-condition II).

4. DISCUSSION

The experiments presented in this paper yield two significant findings. First, we show a strong left ear/right hemisphere bias for processing conspecific vocalizations (independent of familiarity) but no asymmetry for other primate vocalizations or non-biological sounds. This is the first clear evidence of an asymmetry that is selectively triggered by the species-typical signature of a non-human primate's vocal repertoire. Second, and in contrast to previous findings with macaques and humans, the direction of this asymmetry is to the right, rather than to the left hemisphere. The difference in the direction of this orienting bias suggests that over primate evolution, hemispheric asymmetries have been favoured as part of their neural design, but the direction of this asymmetry may be relatively unconstrained, open to differences that may arise in development.

Considering the results from previous studies, showing a left hemisphere bias for auditory processing of species-specific vocalizations in rhesus monkeys and Japanese macaques, the difference in the direction of asymmetry reported here is quite surprising. In particular, these species are all quite closely related, and share many common socioecological characteristics: macaques (rhesus and

Japanese) and vervet monkeys are members of the Cercopithecidae family, with similar life histories, social organizations and mating systems. Although data on other primates will help flesh out the taxonomic distribution of this orienting bias, these data provide the first step in a phylogenetic analysis aimed at understanding how ontogenetic, physiological, ecological and evolutionary factors interact to shape the brain's design. For example, it is possible that all primate brains are destined to show functional asymmetries in auditory processing, but due to species-specific characteristics of brain development, some show a left hemisphere bias whereas others show a right hemisphere bias. Studies of rhesus monkeys reveal that prior to 1 year, infants show no asymmetries in processing their species-specific vocalizations (Hauser & Andersson 1994). We now need to understand whether this failure to find an early behavioural asymmetry is reflected in their neurophysiology, and to understand how experience generates the adult pattern of processing and response, comparing different developmental stages as well as different environmental contexts across species. To understand this neuropsychological mechanism, future studies should take into consideration this apparent plasticity in order to explore what determines the direction of such asymmetries in development and/or evolution.

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