

On the Relationship Between Lateralized Brain Function and Orienting Asymmetries

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Hemispheric specializations for language perception constitute one of the classic topics in cognitive neuroscience. Evidence has accumulated to suggest that lateralized acoustic processing is not restricted to humans but is also found in numerous animal species. One of the methods used to track such lateralization is the *orienting-asymmetry paradigm*, a simple, noninvasive means to study lateralization that has been applied to a range of different species ranging from harpy eagles to humans. Here we summarize and compare the results of studies employing the orienting-asymmetry paradigm, showing that these studies yield largely inconsistent results. We critically discuss the methodology's implicit assumptions and conclude that the empirical inconsistencies produced by the orienting-asymmetry paradigm, and the lack of sufficient evidence supporting the paradigm's underlying assumptions, warrant serious caution when interpreting results obtained by the method. Nontrivial interpretations of orienting-asymmetry results will require a much better understanding of how lateralized brain functions interact with overt behaviors.

Keywords: hemispheric asymmetry, laterality, primate vocalizations, speech perception, cerebral asymmetry

In the fledgling stage of cognitive neuroscience, neuropsychological work on patients with difficulties in speech perception and production led to important early successes in localizing cognitive processes to specific areas of the brain (Broca, 1861; Wernicke, 1874). The loci of brain lesions detected by postmortem autopsies of these aphasic patients implied a central role of the left hemisphere in speech processing. Almost 150 years later, research in the field of lateralized perception and production of speech is still thriving (Friederici & Alter, 2004), with intriguing and novel contributions coming from animal research (Hopkins & Cantalupo, 2008; Weiss, Ghazanfar, Miller, & Hauser, 2002). These studies indicate that lateralization in processing acoustic stimuli is not an exclusive characteristic of humans as previously thought, but is shared with nonhuman primates and other vertebrate taxa (Rogers & Andrew, 2002).

Whereas spoken language and animal vocalizations differ fundamentally in their acoustic structure as well as in their meaning and function (Owren & Rendall, 2001; Seyfarth & Cheney, 2003),

both constitute *species-specific* acoustic signals. A comparative perspective on the functional characteristics of lateralized processing of species-specific calls might thus shed light on the evolutionary precursors of neural specializations in humans and is a promising approach to provide novel insights into the neural basis of speech perception (Ghazanfar & Hauser, 1999, 2001). It is therefore not surprising that the *orienting-asymmetry paradigm*—a novel methodology to track lateralized acoustic processing in nonhuman primates devised by Marc Hauser and colleagues (Hauser & Andersson, 1994)—has attracted a considerable amount of attention during the past decade or so. This novel assay promised to provide a simple, noninvasive means to study lateralization in different species and has been used by various research labs working with wide range of species, from monkeys and harpy eagles to dogs and humans (Basile, Boivin, et al., 2009; Basile, Lemasson, & Blois-Heulin, 2009; Böye, Güntürkün, & Vauclair, 2005; Fischer et al., 2009; Ghazanfar & Hauser, 2001; Gil-da-Costa & Hauser, 2006; Hauser, Agnetta, & Perez, 1998; Hauser & Andersson, 1994; Palleroni & Hauser, 2003; Scheumann & Zimmermann, 2008; Teufel, Hammerschmidt, & Fischer, 2007; see Table 1 for a summary). In this article, we summarize and compare the results of studies employing the orienting-asymmetry paradigm and evaluate them in light of what is currently known about brain lateralization in acoustic processing. Furthermore, we assess the methodology's implicit assumptions and briefly discuss some statistical pitfalls associated with the analysis of a binary response variable such as orienting behavior. We conclude that the unexplained empirical inconsistencies produced by the orienting-asymmetry paradigm, and the lack of sufficient evidence supporting the paradigm's

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Table 1
Summary of Studies Employing the Orientation-Asymmetry Paradigm

Reference	Species/testing conditions	Design	<i>n</i>	Stimuli & results	Interpretation given by authors
Hauser & Andersson (1994)	Rhesus macaques (adult and infant), field study	Independent*	10–41	<ul style="list-style-type: none"> Species-specific affiliative, fearful, aggressive calls: right-turning bias in adults but not infants Heterospecific alarm call of ruddy turnstone: left-turning bias in adults but not infants 	Adult but not infant rhesus macaques process conspecific calls in the left and heterospecific calls in the right hemisphere.
Hauser et al. (1998)	Rhesus macaques, field study	Independent*	7–19	<ul style="list-style-type: none"> Species-specific affiliative, alarm, mating calls: right-turning bias Temporally manipulated affiliative and alarm calls: left-turning bias or no bias Temporally manipulated mating call: right-turning bias 	Temporal cues are used to classify affiliative and alarm calls but not mating calls as conspecific.
Ghazanfar & Hauser (2001)	Rhesus macaques, field study	Independent	10–20	<ul style="list-style-type: none"> Species-specific alarm and food calls: right-turning bias Time-reversed alarm and food calls: left-turning bias 	Temporal cues are used to classify alarm and food calls as conspecific.
Palleroni & Hauser (2003)	Harpy eagles, laboratory and field study	Mixed	4 (captive, nonhunters); 3 (wild, hunters)	<ul style="list-style-type: none"> Species-specific contact call: right-turning bias Heterospecific call of a nonprey animal and nonbiological sound: right-turning bias Heterospecific call of a potential prey: Wild eagles showed a right-, captive eagles a left-turning bias 	Left-hemispheric auditory processing is determined by hunting experience.
Böye et al. (2005)	California sea lions (adult and infant), laboratory study	Paired*	6 adult; 2 infant	<ul style="list-style-type: none"> Familiar and unfamiliar species-specific calls: right-turning bias in adults but not infants (only familiar calls were used in infants) Familiar and unfamiliar heterospecific calls: no turning bias in adults and infants (only unfamiliar calls were used in infants) 	Adult but not infant California sea lions process species-specific sounds in the left hemisphere.
Gil-da-Costa & Hauser (2006)	Vervet monkeys, laboratory study	Paired*	4–5	<ul style="list-style-type: none"> Various species-specific vocalizations from familiar and unfamiliar individuals: left-turning bias Familiar and unfamiliar heterospecific vocalizations from various primate species: no turning bias Nonbiological sounds: no turning bias 	Vervet monkeys process species-specific calls in the right hemisphere, indicating that asymmetries in acoustic processing are a general principle of the primate brain but the direction of this asymmetry is plastic.
Teufel et al. (2007)	Barbary macaques, field study	Independent	19–36	<ul style="list-style-type: none"> Various species-specific and heterospecific calls: no turning bias 	Questions the validity of the orienting paradigm to track lateralized acoustic processing.

Table 1 (continued)

Reference	Species/testing conditions	Design	<i>n</i>	Stimuli & results	Interpretation given by authors
Scheumann & Zimmermann (2008)	Grey mouse lemurs, laboratory study	Paired*	20–28	<ul style="list-style-type: none"> Species-specific calls with positive valence (trill): no turning bias Species-specific calls with negative valence (whistle and tsak): ♀♀ no turning bias; ♂♂ right-turning bias Various heterospecific calls: no turning bias Nonbiological sound: no turning bias 	In the mouse lemur, there is a sex-specific left-hemispheric lateralization in acoustic processing of species-specific calls with a negative valence.
Fischer et al. (2009)	Humans (adult), laboratory and field study	Paired (lab);	22	<ul style="list-style-type: none"> Functional MRI blood oxygen level-dependent response is lateralized to the left hemisphere in response to speech stimuli 	There is no contingency between lateralized acoustic processing (as measured by functional MRI) and asymmetries in orienting behavior.
		Independent (field)	40–63	<ul style="list-style-type: none"> Species-specific speech sounds: left-turning bias in response to speech stimuli in one sample (Germany) but not the other (UK) Non-biological sounds: no turning bias 	
Basile, Lemasson, et al. (2009)	Campbell's monkeys and human girls (8–9 years old), laboratory study	Paired	7 monkeys; 13 girls	<p><i>Monkeys:</i></p> <ul style="list-style-type: none"> Species-specific call with a positive valence: no turning bias Species-specific call with a negative valence: left-turning bias Heterospecific calls with a positive valence of various primate species: no turning bias Heterospecific calls with a negative valence by red-capped mangabeys: left-turning bias in second but not first block Heterospecific calls with a negative valence by Brazza monkeys: no turning bias <p><i>Girls:</i></p> <ul style="list-style-type: none"> Species-specific vocalization with a positive valence by a familiar class mate: no turning bias Species-specific vocalization with a negative valence by a familiar class mate: right-turning bias Species-specific vocalization with a positive or negative valence by a familiar non-class mate: no turning bias 	Lateralized auditory processing in Campbell's monkeys and human girls exists only for intragroup vocalizations with a negative valence; in monkeys, this processing is lateralized to the right; in girls, it is lateralized to the left hemisphere.

(table continues)

Table 1 (continued)

Reference	Species/testing conditions	Design	<i>n</i>	Stimuli & results	Interpretation given by authors
Basile, Boivin, et al. (2009)	Domestic horses, laboratory study (stable)	Paired	12	<ul style="list-style-type: none"> Species-specific call of a familiar nongroup member: right-turning bias Species-specific call of a familiar group member: no turning bias Species-specific call of an unfamiliar nongroup member: no turning bias Nonbiological sound: no turning bias 	Lateralization of acoustic processing of species-specific signals is dependent on social factors.
Siniscalchi et al. (2008)	Domestic dogs, laboratory study (garden of owner)	Paired	14	<ul style="list-style-type: none"> Species-specific calls produced during isolation and disturbance: right-orienting bias Species-specific calls produced during play: trend toward a right-orienting bias Nonbiological sound (thunderstorm): left-orienting bias 	Dogs process species-specific vocalizations in the left hemisphere and thunderstorm (via an increased arousal state) in the right hemisphere.
Lemasson et al. (2010)	Japanese macaques, laboratory study	Paired	5–6	<ul style="list-style-type: none"> Familiar species-specific contact calls: left-turning bias Familiar chimpanzee calls: left-turning bias Other familiar primate calls and familiar nonbiological sounds: no turning bias Various unfamiliar primate calls and other unfamiliar sounds: no turning bias 	Japanese macaques process species-specific and some other familiar sounds in the right hemisphere, indicating that lateralized auditory processing is influenced by experience.
Leliveld et al. (2010)	Grey mouse lemurs, laboratory study	Paired	8–16	<ul style="list-style-type: none"> Species-specific calls with positive (trill) and negative valence (tsak) by a familiar same-sex sender: no orienting bias Species-specific calls with positive (trill) and negative valence (tsak) by an unfamiliar same-sex sender: no orienting bias Species-specific calls with positive (trill) and negative valence (tsak) by an unfamiliar opposite-sex sender: right-turning bias 	Grey mouse lemurs process species-specific calls of a sender of the opposite sex in the left hemisphere.

Note. *n* = minimum and maximum number of subjects that responded to the playback and were included in at least one analysis.

^a Direct comparisons between conditions were not conducted.

underlying assumptions, warrant serious caution when interpreting results obtained by this method.

The Orienting-Asymmetry Paradigm

The orienting-asymmetry paradigm was first employed in a study on semifree ranging rhesus macaques (*Macaca mulatta*) by Hauser and colleagues (Hauser & Andersson, 1994). In short, the authors placed a speaker about 10 m behind a food dispenser and launched a

playback as soon as an individual sat facing the food dispenser with its back toward the speaker and its head held straight (facing directly forward). Stimuli were thus broadcasted from 180° behind the monkey, and the animal had to turn its head either to the left or to the right to orient toward the sound source. Care was taken to ensure that the playback occurred when the monkey's head and the speaker were lined up to avoid an intensity bias to one ear or the other. Under these conditions, the rhesus macaques, remarkably,

showed a strong right-turning bias in response to playbacks of natural species-specific vocalizations, but showed a left-turning bias in response to one familiar heterospecific stimulus—the alarm call of the ruddy turnstone (*Arenaria interpres*). Given the mainly contralateral connections of the auditory pathway in the primate brain, the authors argued that turning with the right ear leading indicated a predominant processing in the left hemisphere, and turning with the left ear leading indicated a predominant processing in the right hemisphere. Consequently, the authors concluded that rhesus macaques process species-specific calls mainly in the left hemisphere and heterospecific calls mainly in the right hemisphere (Hauser & Andersson, 1994).

On the basis of this rationale, Hauser and colleagues extended the use of the orienting-asymmetry paradigm further to identify the acoustic features that rhesus macaques use to classify calls as species-specific or heterospecific. In two studies, they demonstrated that when the amplitude envelope (in which temporal cues are embedded) of natural vocalizations is manipulated either by lengthening the interpulse interval of pulsed calls outside the population typical range (Hauser et al., 1998) or by reversing the calls (Ghazanfar & Hauser, 2001), subjects switched from a right- to a left-turning bias. Assuming that vocalizations that are recognized as species-specific are predominantly processed in the left hemisphere and calls that are classified as heterospecific are predominantly processed in the right hemisphere, a shift from a right- to a left-turning bias after manipulation of natural vocalizations indicates that the manipulated stimuli were no longer classified as species-specific. This implies that the manipulated features were crucial in recognizing whether or not a call was species-specific.

The Empirical Puzzle

The initial findings obtained with the orienting-asymmetry paradigm were promising and inspired studies from other laboratories. An overview of the studies applying the orienting-asymmetry paradigm to different species, however, shows an inconsistent—and largely unexplained—pattern of results. In general, none of the studies by other research groups obtained the clear-cut results of the initial studies from Hauser and colleagues (Ghazanfar & Hauser, 2001; Hauser et al., 1998; Hauser & Andersson, 1994). In a study on Barbary macaques (*M. sylvanus*), two different species-specific call types as well as three different categories of heterospecific calls were used as stimuli (Teufel et al., 2007). Despite a sample size large enough to uncover an effect of even smaller magnitude as demonstrated in the studies on rhesus macaques, the Barbary macaques showed no orienting differences in response to any of the broadcasted vocalizations. Similarly, a study on a prosimian species—the mouse lemur (*Microcebus murinus*)—demonstrated neither a right-turning preference for the collective category of species-specific calls (three different vocalizations) nor a left-turning preference in response to seven heterospecific and one nonbiological sounds (Scheumann & Zimmermann, 2008). The authors did, however, find an effect when the two sexes were analyzed separately: Males showed a right-turning bias for two of three species-specific vocalizations but not for any other stimulus category, whereas females did not show any orienting asymmetries. The mouse lemur results clearly cut across the species-specific versus heterospecific comparison, and the authors thus speculated that these biases might reflect lateralized acoustic

processing of negative emotional valence in male animals (Scheumann & Zimmermann, 2008). A more recent study by the same research group did not replicate the sex-specific orienting asymmetry in response to negatively valenced vocalizations (Leliefeld et al., 2010). Rather, this study demonstrated a right-turning bias by mouse lemurs in response to calls by a sender of the opposite sex, independent of valence (see A Note on Statistics for further discussion).

A second study that investigated the influence of emotional valence on orienting asymmetries produced a confusing mosaic of results (Basile, Lemasson, et al., 2009). Similar to the previous study with mouse lemurs, female Campbell's monkeys (*Cercopithecus campbelli*) did not show an overall turning bias in response to species-specific or heterospecific calls. The animals did, however, show a left-turning bias in response to species-specific calls with a negative valence. The authors also reported a significant left-turning bias in response to calls with a negative valence from one of the two heterospecific stimulus categories (red-capped mangabey's [*Cercocebus torquatus*] threat calls, but not de Brazza monkey's [*Cercopithecus neglectus*] threat calls) but only in the *second* block of the experiment, not the *first* block (see A Note on Statistics for further discussion). This result was compared with that for a group of 8- to 9-year-old schoolgirls, although exclusively with species-specific stimuli. Here, the authors found a right-turning bias in response to vocalization with a negative valence produced by a classmate but not from a child of a different class (both children were familiar to the subjects; Basile, Lemasson, et al., 2009).

The most recent orienting-asymmetry study from Hauser and colleagues applied the task to captive vervet monkeys (*Chlorocebus pygerythrus*, formerly known as *Cercopithecus aethiops*), and their findings complicate the picture even further (Gil-da-Costa & Hauser, 2006). The five subjects that participated in this study showed no turning bias for heterospecific or nonbiological sounds, a finding that was not discussed despite it being contrary to the predictions of previous orienting studies of rhesus monkeys by this research group (Hauser et al., 1998; Hauser & Andersson, 1994). More intriguing, the monkeys demonstrated a *left*-turning bias for species-specific sounds, suggesting a *right*-hemispheric dominance for this stimulus class. Note that most previous studies that did find any bias in response to species-specific calls reported a bias in the opposite direction (Ghazanfar & Hauser, 2001; Hauser et al., 1998; Hauser & Andersson, 1994; Scheumann & Zimmermann, 2008; see also studies of sea lions, harpy eagles, dogs, and horses below). According to the authors, the opposite pattern of results from vervets suggests that the organization of the primate brain is destined to lateralize the acoustic processing of species-specific calls, but the direction of lateralization is characterized by a high degree of plasticity and constrained by species-specific patterns of brain development (Gil-da-Costa & Hauser, 2006). This explanation, while superficially reasonable, suggests that vervets alone among Old World primates (and other nonprimate animals) evolved a novel trajectory of brain development and form of hemispheric specialization with an opposite lateralization for no discernable (or even speculated) reason(s). One other study reported a left-turning bias in response to species-specific calls in Japanese Macaques (*Macaca fuscata*); a similar bias was, however, also found in response to familiar heterospecific chimpanzee calls but not to other familiar or unfamiliar biological and nonbiological

sounds (Lemasson et al., 2010). The implications of this study are discussed below (see Comparisons With Established Measures of Lateralization).

Four studies that employed the orienting-asymmetry paradigm in nonprimate species do not help to clarify interpretations. Dogs (*Canus familiaris*) showed a right-turning bias in response to species-specific vocalizations and a left-turning bias in response to a nonbiological sound (Siniscalichi et al., 2008). Six California sea lions (*Zalophus californianus*) demonstrated a right-turning bias in response to species-specific calls but no bias in response to heterospecific calls (Böye et al., 2005). A study on three experienced and four inexperienced harpy eagles (*Harpia harpyja*) identified an altogether different factor responsible for a turning bias: experience (or lack thereof) with hunting a certain type of prey (Palleroni & Hauser, 2003). Finally, a study with domestic horses (*Equus caballus*) demonstrated a right-turning bias in response to species-specific calls produced by a familiar animal that was not member of the subject's group (Basile, Boivin, et al., 2009). The authors found no asymmetry in response to familiar group members, unfamiliar animals, or white noise.

Contextual Factors and Orienting Asymmetries

Behavioral lateralities are widely known to be influenced by contextual factors. For example, in humans, most right-handed individuals report verbal material more accurately when it is presented to the right ear than to the left ear, reflecting the language specializations of the contralateral (left) hemisphere (Kimura, 1961). This right-ear advantage, however, is unreliable. For example, the direction of ear advantage (right vs. left) can change from one session to the next for many subjects (Blumstein, Goodglass, & Tarter, 1975). Remarkably, the state of the vocal tract (whether it is active or not) can also influence the direction of ear advantage in humans (Milberg, Whitman, Rourke, & Glaros, 1981). This suggests that articulatory activity (movements of the jaw, tongue, lips, etc.), which may normally accompany the processing of speech, may serve to activate the left hemisphere, biasing attention to the right side of auditory space (Milberg et al., 1981). In the context of the orienting-asymmetry paradigm, this is quite intriguing. All the field playback studies conducted on rhesus monkeys by Hauser and colleagues were done in the context of feeding (Ghazanfar & Hauser, 2001; Hauser et al., 1998; Hauser & Andersson, 1994). The playbacks were performed while subjects were facing a food dispenser, presumably eating food (this was not controlled for or monitored). Thus, in light of the human study where activity of the vocal tract influences ear advantage, it seems plausible that a similar process may be occurring in these studies of rhesus monkey orienting asymmetries. It would explain the consistency of the result for rhesus monkeys as well as the lack of consistency with other playback studies; however, it fails to explain the supposed left-turn bias toward heterospecific calls under the same "eating" conditions.

Other contextual features, beyond the body state, may also influence orienting asymmetries. The report of vervets showing a left-turning (right-hemisphere) bias for species-specific vocalizations is truly bizarre (Gil-da-Costa & Hauser, 2006), but may be simply explained by the spatial arrangement of the experiment. The vervet monkeys were placed in sound attenuating enclosure; the monkeys came into this enclosure from a door that was on their

left (AAG, personal observations). As all the vervet vocalizations they had ever heard came from that direction, it seems parsimonious to conclude that they expected all vervet (species-specific) sounds to be on the left. Thus, they oriented in that direction. The authors did not control for this spatial confound. All but one of the non-species-specific sounds were unfamiliar to the vervet subjects; thus, there was no spatial association with them and no turning bias.

Given the wide variety of circumstances in which species were tested in the orienting-asymmetry studies described above, context seems to be at least one likely factor that could explain the numerous discrepancies among the orienting patterns across species.

Comparisons With Established Measures of Lateralization

To date, the discussion of the orienting-asymmetry paradigm focused almost entirely on the right-turning bias in response to species-specific vocalizations in some studies. The interpretation of this finding in terms of a predominant processing of species-specific calls in the left hemisphere is consistent with studies that used psychophysical (LePrell, Hauser, & Moody, 2002; Petersen, Beecher, Zoloth, Moody, & Stebbins, 1978), lesioning (Heffner & Heffner, 1984), and brain-imaging techniques (Poremba et al., 2004) to track lateralized acoustic processing in macaques. However, one recent orienting-asymmetry study testing Japanese macaques found a left-turning bias in response to species-specific calls, supposedly indicating a right-hemispheric specialization (Lemasson et al., 2010). This result is particularly puzzling given that the Japanese macaque is the classical nonhuman primate model in psychophysics and neurobiological research for a left-hemispheric specialization in processing species-specific sounds (Heffner & Heffner, 1984; Petersen et al., 1978). Surprisingly, this inconsistency was not discussed by the authors.

Moreover, some orienting studies suggested that processing of heterospecific stimuli is predominantly lateralized to the right hemisphere (Ghazanfar & Hauser, 2001; Hauser et al., 1998; Hauser & Andersson, 1994). There is some weak support for the idea that heterospecific stimuli are mainly processed in the right hemisphere from methods other than the orienting-asymmetry paradigm (Pohl, 1983, 1984), but most other studies using different methods failed to find such lateralization. In a classic psychophysical study by Petersen and colleagues (1978), Japanese macaques and subjects from different Old World monkey species (control subjects) were trained on an auditory discrimination task of two types of Japanese macaques' "coo" vocalizations. The calls were presented monaurally to either the left or the right ear. All Japanese macaques showed a significant right-ear advantage for the discrimination task, indicating a predominant processing of species-specific calls in the left hemisphere. An interesting finding, however, was that the control subjects either failed to exhibit any ear advantage or also showed a right-ear advantage, suggesting that heterospecific calls are processed equally in both hemispheres or in the left hemisphere rather than in the right hemisphere.

Similar results have been obtained by a recent study on rhesus macaques using positron emission tomography (PET; Poremba et al., 2004). The cerebral metabolic activity in response to species-specific calls indicated neural activity mainly in the dorsal tempo-

ral pole of the left hemisphere, whereas equal levels of activation across the two hemispheres were recorded in this same brain region in response to various control stimuli (nonbiological sounds, human voices, white noise, and manipulated species-specific vocalizations; however, it should be noted that this study did not have a control category that was solely heterospecific vocalizations). Finally, lesioning studies that investigated related phenomena like auditory memory and auditory–visual matching with heterospecific stimuli do not support the idea that heterospecific sounds are mainly processed in the right hemisphere (Dewson, 1977; Gaffan & Harrison, 1991).

A PET study using rhesus monkeys and species-specific vocalizations boldly claimed to have identified homologues of Broca's and Wernicke's areas in rhesus monkeys, but reported that there was *right* neural lateralization for species-specific calls in the temporal lobe, specifically in the temporo-parietal junction (area Tpt; Gil-da-Costa et al., 2006; see Ghazanfar & Miller, 2006, for a critique of this study). This, of course, is inconsistent with the orienting-asymmetry results in the same species that used stimuli from the same catalog of vocalizations (Ghazanfar & Hauser, 2001; Hauser et al., 1998; Hauser & Andersson, 1994). These PET activation results are also at odds with an anatomical study demonstrating that the volume of area Tpt is larger in the left hemisphere than the right hemisphere in macaque monkeys (Gannon, Kheck, & Hof, 2008) and the other rhesus monkey imaging study described above that controlled for interhemispheric transfer of auditory information (Poremba et al., 2004).

To our knowledge, there are no studies on lateralized acoustic processing using more established and direct measures in Barbary macaques, mouse lemurs, vervet monkeys, Campbell's monkeys, California sea lions, dogs, harpy eagles, or horses that could externally validate the results of the orienting-asymmetry paradigm and what it reveals about lateralized acoustic processing. It is certainly possible that, in all of the reported cases, the turning biases genuinely reflect a single consistent underlying mechanism. Yet, it would imply puzzling patterns of lateralization of entirely different functions of auditory processing (species-specificity, heterospecificity, familiarity, and emotional valence) within the primate order, with closely related species (e.g., macaques vs. vervet monkeys) showing different patterns of responses in different hemispheres. Such a scenario is unlikely from an evolutionary perspective. Moreover, the fact that the orienting-asymmetry paradigm produced results that are inconsistent with studies using other, more reliable measures of lateralized acoustic processing casts doubt on the utility of the orienting-asymmetry paradigm as a measure of lateralization.

A Note on Statistics

Some of the studies employing the orienting-asymmetry paradigm used very small sample sizes. It is important to consider the likelihood of obtaining a statistically "significant" bias just by chance alone. For instance, the probability of observing a left (or right) bias in five of five subjects is 3.12%; for six subjects, the probability is 1.56%. Now consider that in a number of studies, more than one hypothesis was tested. For instance, Gil-da-Costa and Hauser (2006) tested three hypotheses on five subjects. The likelihood of obtaining at least one significant results at $p < .05$ is $3.12\% \times 3 = 9.4\%$. The study by Basile, Lemasson, et al. (2009)

provides an extreme example of a related statistical problem also found in other orienting-asymmetry studies. In their analysis of monkey head turns, the authors seem to have conducted 24 independent Wilcoxon's tests on the same data set without correcting for multiple testing, thereby massively increasing the likelihood of a false positive. Initially, they tested for a general orienting bias across stimulus categories and then conducted seven analyses separately for the different stimulus categories. For no apparent reason, they subsequently split their analysis by block, conducting one general analysis across stimulus categories for the first and another one for the second block as well as seven separate analyses for the different stimulus categories for each block, respectively. Out of this multitude of tests, only two resulted in a significant effect at the 5% level. Similar criticisms apply to some other orienting studies (Böye et al., 2005). In sum, it is important to be aware of the probability of obtaining "false positives" when testing various hypotheses on small sample sizes without proper corrections.

The Theoretical Puzzle

Besides the empirical problems of the orienting-asymmetry paradigm, there are several unsolved theoretical issues that thwart straightforward interpretation of results obtained with this method. One of these issues—the use of the paradigm to identify the crucial features of call classification—has been discussed elsewhere (Teufel et al., 2007). The most fundamental problem, however, is the fact that a substantive hypothesis about how lateralized auditory processing is translated into a turning bias is currently lacking, despite the fact that the whole rationale of the method relies on this assumption. Even worse, there is now evidence suggesting that there might be no such relationship between lateralization and direction of orienting.

An explicit reference to a possible mechanism that translates the hypothesized lateralized processing into a turning bias is provided by only one article (Hauser et al., 1998; but see critical discussions in Fischer et al., 2009; Hopkins & Fernández Carriba, 2002; Teufel et al., 2007). Here, the authors suggest that when one hemisphere is preferentially activated during processing of a specific acoustic signal, this activation bias might interact with the ipsilateral frontal eye field in the frontal cortex that, in turn, might lead to a visually guided turn toward the contralateral side. One problem with this hypothesis is that it assumes that the lateralized processing leading to the turning bias occurs in the auditory cortex rather than in any other part of the auditory pathway. Serious caution is warranted given the evidence that actions such as head turning in response to auditory stimuli are initiated in the inferior colliculus via strong projection to the cerebellum (Casseday & Covey, 1996). The extremely fast reaction times observed in Barbary macaques (Teufel et al., 2007) might support the idea that such responses are indeed initiated in the midbrain rather than the cortex. Hopkins and Fernández Carriba (2002) raise a second problem, pointing out that the neck muscles responsible for the orienting response are controlled by a ventromedial neural pathway, which projects ipsilaterally in the brain. In other words, an orienting response to the right would be controlled ipsilaterally, that is, by the right hemisphere—not the left hemisphere, as presumed by Hauser, Ghazanfar, and colleagues (Ghazanfar & Hauser, 2001; Hauser et al., 1998; Hauser & Andersson, 1994).

Most problematic, however, is the fact that one recent study that directly addressed the relationship between lateralized acoustic processing and turning biases in humans found no evidence to support the assumptions of the orienting-asymmetry paradigm (Fischer et al., 2009). In a “field” study, speech and nonspeech sounds were played back to human subjects ($N = 224$) shopping in a supermarket. The results showed a slight bias to turn toward the left in response to all sound categories. This finding in itself is inconsistent with what would have been expected on the basis of the extensive evidence indicating that speech is predominantly processed in the left hemisphere (Fischer et al., 2009). Additional experiments using functional MRI ascertained that the speech stimuli used in the orienting-asymmetry paradigm indeed lead to higher left hemisphere activation in BA44 relative to the control stimuli (Fischer et al., 2009). These results suggest that potentially a number of factors other than the lateralization of acoustic processing may affect orienting behavior, most notably the experimental context and the task.

Conclusions

During the past decade, the orienting-asymmetry paradigm has attracted considerable attention from researchers trying to identify lateralized mechanisms in the processing of species-specific acoustic signals in animals and humans. Despite initially promising findings, however, studies employing this method have produced a puzzling pattern of inconsistent results. Moreover, some of the findings of the orienting-asymmetry paradigm clearly contradict results obtained with more established and direct measures of lateralized acoustic processing. Most problematic, however, is the lack of a sufficient understanding of the processes that lead to turning biases. One recent study that attempted to directly address this issue found no indication of a relationship between lateralized acoustic processing and turning biases (Fischer et al., 2009), thus shedding doubt on the fundamental assumption on which the current interpretation of the orienting-asymmetry paradigm rests. In light of these empirical and theoretical inconsistencies, we believe that as long as the processes leading to a turning bias are not understood, results obtained with the orienting-asymmetry paradigm must be treated with greater caution. Future research should be devoted to uncovering how context and lateralized brain functions interact to produce overt lateralization in behavior.

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