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Issue: *Evolution of Human Handedness***Primate laterality and the biology and evolution of human handedness: a review and synthesis**W. Tecumseh Fitch¹ and Stephanie N. Braccini²¹Department of Cognitive Biology, University of Vienna, Vienna, Austria. ²Department of Anthropology, Washington University and Saint Louis Zoo, Saint Louis, Missouri

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We review evidence for and against lateralization of manual control, communication, visual processing, and auditory processing in nonhuman primates. Compared to humans and some other vertebrate species, manual specialization in nonhuman primates is relatively weak. A right-bias in chimpanzees may exist, but is so weak that many studies using simple tasks fail to reveal it. Slightly stronger biases may exist in baboons and chimpanzees for communicative signals in the manual and facial domains. Several studies have found robust visual side biases that depend on the object being viewed, in primates including chimpanzees. Evidence for lateralization of auditory processing remains inconclusive. We conclude that the robust, species-wide lateralization that exists in humans is unusual, and perhaps unique among primates, and discuss several possible evolutionary explanations for this strong asymmetry. In particular, we consider the hypothesis that preexisting hemispheric asymmetry for perception and language processing drove the evolution of human handedness.

Keywords: cognitive biology; laterality; comparative biology; asymmetry; handedness

Introduction

Geschwind¹ argued long ago that the “remarkable” phenomenon of left cerebral dominance for human language had no known parallel in nonhuman mammals. He dismissed neural asymmetries known in birds as independent and irrelevant. This influential paper fueled a great deal of research on human brain asymmetry, much of it based on the presumed uniqueness of lateral asymmetry (*lateralization*) in our species. It also spurred a more speculative theoretical literature in which manual dominance (*handedness*) and language were seen as closely interlinked in human evolution. However, in the last two decades these ideas seem to have lost their luster: it is now clear that many vertebrates have clear species-typical lateralization patterns, and that the link between handedness and linguistic lateralization is tenuous at best. Despite increasing awareness of these developments, the literature on animal laterality remains sprawling, inconsistent, and plagued by problematic assumptions.

In this paper, we synthetically review the primate lateralization literature, with the goal of understanding the evolution of human lateralization. Our perspective is comparative, with a focus on primates and apes in particular, but interpreted in the context of the broader vertebrate literature. We attempt to separate solid, multiply confirmed findings from the many tenuous and inconsistent reports in the primate literature. To remain concise, we cite comprehensive reviews whenever available, and confine overviews of the primary literature to three tables.

Lateralization: one phenomenon or many?

Lateral asymmetry (lateralization) is a many-faceted phenomenon. Although the most obvious example in humans is manual lateralization (handedness), other behavioral examples include footedness, eye preferences (eyedness), or acoustic orienting asymmetries. Typically, such behavioral asymmetries are assumed to reflect neural lateralization of the corresponding function to the opposite brain

hemisphere (due to the partial or complete crossing of most body–brain connections).

Much has been made of the potential link between the strong human tendencies to both right-handedness, and left-hemisphere dominance for language.^{2–4} The possibility that this correspondence reflects pure coincidence is rarely considered. However, given that chance predicts the side of lateralization at 0.5 in bilateral organisms, the possibility that n functions end up on the same side is $P = 0.5^n$, which gives 0.25 for two functions, or 0.125 for three. Indeed, more than four functions would need to be colateralized to reach a conventionally significant probability less than 0.05, suggesting that the null hypothesis should be that multiple facets of lateralization are independent, barring convincing arguments or evidence to the contrary.

Based on these statistical observations, this review adopts a divide and conquer strategy, separately considering motor lateralization (both manual and vocal) and perceptual lateralization (visual and auditory). We start by summarizing core findings and open questions in the human and vertebrate literature, before giving a more detailed consideration of the primate literature.

Human lateralization: manual and linguistic

As a species, humans are typically 90% right-handed,⁵ with a range of 85–95% across studies. This strong tendency does not appear culture specific (i.e., caused by writing and literacy): it is true across cultures^{6,7} and over long time periods (i.e., in art from cave paintings to the present).^{8,9} Although early studies reported a few outliers (e.g., the Eipo of New Guinea showing only 75% right-handedness),^{9,10} these were based on rough estimates from photographs or films, and more rigorous tests of actual handedness, with large sample sizes, show the Eipo to be, if anything, *more* right-lateralized than Westerners.⁷ Human species-wide lateralization is disproportionately strong compared to any other primate species. Early studies concluded that, although individual nonhuman primates (NHPs) typically have hand preferences, there is no overall species-level asymmetry.^{11,12} Even those later studies that reported population asymmetries in NHPs find them to be much weaker than in humans, around 65% right-biased.^{13,14} Human right-handedness, indicating a left-hemisphere

(LH) bias for manual control, is thus the first unusual fact to consider about our species.

Second, human language is LH-biased to an even greater extent: 96% of aphasics suffer from LH damage, and functional magnetic resonance imaging (fMRI) data show that 96% of right-handers and 76% of left-handers have LH language dominance.¹⁵ This shows that the rough correspondence between right-handedness and language lateralization does not reflect any tight causal linkage between hand preference and language dominance. Despite the population LH bias for language and right-handedness, lefties typically have uncrossed language dominance, and nonetheless have normal language capabilities and lead normal lives.

Recently, brain imaging research has complicated our understanding of the degree to which language is strongly lateralized.¹⁶ Traditional clinical tests for aphasia typically rely upon quick, easy tasks (e.g., counting backward from ten), and thus consistently underestimate the degree to which more subtle linguistic abilities, such as understanding of pragmatics, analogy, and humor, rely on the right hemisphere.^{17,18} Contemporary fMRI data clearly indicate that many linguistic tasks elicit bilateral activity, and that semantic comprehension tasks elicit more balanced activity than speech or syntactic tasks.^{16,19} Thus, the anterior regions involved in speech (e.g., Broca's area) appear to be more strongly lateralized than posterior comprehension regions (e.g., Wernicke's area, temporal lobes). Keeping this caveat in mind, it remains clear that there is a strong population-level tendency for many linguistic functions to be LH-biased, and that this is both disproportionate to our ~90% handedness, and also causally disconnected from it (since most left-handers retain LH-biased language). This type of dissociation will emerge as a theme in the animal work reviewed below.

Vertebrate laterality

Traditional studies of *nonhuman limb specialization* (a term we will use to include pawedness and footedness) found that while individuals often show manual preferences, these generally are roughly evenly distributed between sides in non-human populations. Possible exceptions include toads and parrots.^{20–22} There are also intriguing suggestions of strong side-biases in walrus and whales.^{23,24}

However, it has become increasingly clear that many vertebrates exhibit clear population-level asymmetries at the perceptual level.²⁵ The evidence for visual asymmetry is very strong, and eye preferences have now been repeatedly demonstrated in all five vertebrate classes.²⁶ For example, most pigeons show a right eye/left hemisphere advantage for visual object and pattern recognition, and those birds with stronger asymmetry perform better at discriminating grain from grit in a pecking task.²⁷ Similar phenomena have been reported in so many vertebrate species that Geschwind's dismissal of bird lateralization as convergent evolution now seems premature, suggesting that such neural asymmetry is a basic feature of the vertebrate brain.^{28,29} Thus, perceptual lateralization appears to be an evolutionarily primitive feature, and represents a homology present in most extant vertebrate species.

Most documented vertebrate side-biases are context dependent: they depend on the situation (e.g., predator avoidance versus prey capture), item perceived (e.g., conspecifics or other species), and emotional valence (e.g., fearful versus appetitive). These are not across-the-board preferences to use the right eye or ear, but rather seem to reflect underlying specializations for processing particular types of events or sounds. The precise way to characterize these different categories remains debated,²⁸ and it seems likely that several different dimensions (e.g., species, goal, and valence) need to be considered, perhaps with different emphases in different species. Empirical work in the perceptual domain requires testing multiple stimuli in multiple contexts. While the evolutionary function of asymmetry remains debated, the most plausible current hypotheses agree that unilateral specialization allows fast, effective processing without the need for input from, or possibility of disruption by, the other hemisphere.^{30,31}

Two further points clearly emerge from this broader vertebrate literature. Firstly, there is often a dissociation between manual laterality, and perceptual or cognitive lateralization.^{32–35} More specifically, population- or species-level asymmetries are commonly evident at the perceptual level, but are not reflected in limb specializations. This makes functional sense: while there may be clear perceptual advantages in a computational division of labor among the neural hemispheres, the physical world itself is generally symmetrical: predators do not al-

ways appear on the right side, and food on the left. Thus, an organism strongly side-biased in its actions would be disadvantaged relative to more balanced conspecifics.^{28,31}

A second point is nicely illustrated by recent research on foot preferences in parrots.^{21,36} Parrots often show strong species-typical biases to hold food with one foot while manipulating it with the beak. These biases may be either to the right or left foot (with left being more typical). A study of 23 parrot species in four main clades, with each species represented by 5–20 individuals and 10 reaches per individual, found side biases that ranged from 100% left foot in *Cacatua galerita* to 92% right foot in *Alisterus scapularis*.³⁶ Some smaller species, like the budgerigar *Melopsittacus undulatus*, were split 50/50. Although strength of asymmetry increases significantly with body size, and appears to correlate with feeding ecology, both factors were confounded by phylogeny, and the authors concluded that a strong “phylogenetic inertia” exists for the side of asymmetry, while evolution acts rapidly to tune the strength of asymmetry. The evolutionary timespan for parrot evolution is roughly 60 myr, equivalent to the roughly 60–80 myr for extant primate diversification.³⁷ This strongly suggests that the common assumption of a continuous “phylogenetic progression” in laterality from primitive prosimians through monkeys, to apes and humans, is unrealistic.

Nonhuman primates: manual biases

The literature on manual laterality in NHPs is large, and full of inconsistencies (illustrated by the selection in Table 1). Early researchers found little evidence of species-typical asymmetries,^{11,12} leading to a long research hiatus. This was eventually changed when MacNeilage *et al.*³⁸ provided evidence for left-handed reaching preferences in multiple primate species. They also presented a theoretical framework, the postural origins theory (POT), predicting an evolutionary progression from food reaching with the left hand, to food manipulation with the right, eventually leading to human tool-based right-handedness. This paper played an important role in sparking a revival of research on primate laterality. However, a recent comprehensive meta-review provided little support for the details of POT,³⁹ concluding that evidence for population-level laterality in

Table 1. Summary of manual laterality studies in primates (chronological order)

Reference	Species tested	N	Tasks and results	Interpretation
Finch ¹¹	Chimpanzees	30	<ul style="list-style-type: none">• Individual biases in most individuals• No group-level bias to right or left	Chimpanzees show idiosyncratic individual hand preferences, but no species-level handedness comparable to humans.
Warren ¹²	Rhesus macaques	84	<ul style="list-style-type: none">• Simple food-reaching task• 120 trials over five days• 63% showed strong hand preference (evenly to right or left)	Rhesus macaques show idiosyncratic individual hand preferences, but no species-level lateral bias comparable to humans.
Fagot and Vauclair ⁸³	Gorillas	10	<ul style="list-style-type: none">• Unimanual and bimanual tasks• Equal lateral distribution• Left preference for spatial tasks	Task affects hand preference, especially for reaching, novel and complex tasks.
Forsythe <i>et al.</i> ⁸⁴	Black and white ruffed lemurs	5	<ul style="list-style-type: none">• Food reaching• Left-hand preference for reaching on land	Whole body postural adjustments critically influenced the expression of hand preference.
Larson <i>et al.</i> ⁸⁵	Lesser bush babies	10	<ul style="list-style-type: none">• 8 conditions all requiring altered postures• Individual preferences (7 left and 3 right)	Bipedal postures facilitated the use of the dominant hand; whereas other manipulated conditions did not have a significant effect on hand use.
Steenhuis and Bryden ⁸⁶	Human under-graduate students	942	<ul style="list-style-type: none">• Self-report for variety of manual activities• Preference for tool use and manipulation strongly lateralized	Hand preference is task-dependent. Factors such as precision and heavy lifting alter lateralization.
Olson <i>et al.</i> ⁸⁷	Gorillas	12	<ul style="list-style-type: none">• Floor and mesh retrieval tasks• Gibbons showed left-hand preference• Gorillas showed right-hand preference• No preference shown by orangutans	Posture affects hand preference, reflecting differences in species locomotion.
	Orangutans	13		
	Bonobos	9		
Byrne and Byrne ⁸⁸	Gorillas (wild)	44	<ul style="list-style-type: none">• Observations of natural foraging• Individual preferences	Hand preferences are dependent on food processing tasks.
Hopkins ⁸⁹	Chimpanzees	40	<ul style="list-style-type: none">• Food reaching• Population preference for right hand during upright reaching	Posture is an important factor in the exhibition of hand preference.
	Orangutans	6		
Hopkins <i>et al.</i> ⁹⁰	Bonobos	11	<ul style="list-style-type: none">• Natural observations• Left-hand preference for carrying• Right-hand preference for eating	Posture is a key factor determining hand use.
Hopkins ⁹¹	Chimpanzees	140	<ul style="list-style-type: none">• Bimanual ‘tube’ task• Right-hand preference	Using an easy bimanual task, a population-level right-hand preference was reported.

Continued

Table 1. Continued

Reference	Species tested	N	Tasks and results	Interpretation
Colell <i>et al.</i> ⁹²	Chimpanzees	31	<ul style="list-style-type: none">• Food-reaching task in addition to feeding observations• Right-hand preference for all species	Postural adjustment and direction are influenced by manual laterality.
	Bonobos	2		
	Orangutans	3		
Hopkins and DeWaal ⁹³	Bonobos	10	<ul style="list-style-type: none">• Variety of unimanual and bimanual tasks• Left-hand preference for carrying and holding food	Bonobo results are consistent with those of other ape species.
McGrew and Marchant ⁹⁴	Chimpanzees (wild)	44	<ul style="list-style-type: none">• 44 different wild chimpanzee behavior patterns• Tool-use excluded• Comprehensive ambilaterality observed	Manual laterality sometimes observed in captivity may result from human influence.
Corp and Byrne ⁹⁵	Chimpanzees (wild)	51	<ul style="list-style-type: none">• Bimanual fruit manipulation by Mahale chimpanzees• 29 adults• Most individuals showed a strong hand preference• 73% of males used left hand to manipulate; 67% of females used right hand	Statistically significant sex difference in side of manual bias, with strong and consistent individual component
Fletcher and Weghorst ⁹⁶	Chimpanzees (captive, semi-free-ranging)	26	<ul style="list-style-type: none">• Both tool and nontool behaviors observed in Chester Zoo animals• No population-level manual bias for nontool activities• Half of animals were significantly left-biased for tool-use activities	Individual preferences increase with age; behavior involving contact with water elicited stronger lateralization.
Lonsdorf and Hopkins ⁹⁷	Chimpanzees (wild)	17	<ul style="list-style-type: none">• Full day focal observations• Population-level lateralization	Directionality of hand preference is task-dependent. After combining all of the published data on tool use in wild chimpanzees, a pattern of heritability was presented.
O'Malley and McGrew ⁹⁸	Orangutans	8	<ul style="list-style-type: none">• Simple reaching and manual tool use• Individual preferences reported	Hand preference is dependent on the complexity of the task.
Marchant and McGrew ⁹⁹	Chimpanzees (wild)	37	<ul style="list-style-type: none">• Observations of ant fishing• No preference	The evolutionary transition from a primarily arboreal species to terrestrial may have been a key enabler for the origins of human laterality.

Continued

Table 1. Continued

Reference	Species tested	N	Tasks and results	Interpretation
Harrison and Nystrom ¹⁰⁰	Bonobos	22	<ul style="list-style-type: none">• Tool-use tasks• Only individual preferences reported	Inconstant preferences among species may be a precursor for human handedness. Species-level handedness evolved after <i>Pan</i> and <i>Homo</i> lineages diverged.
Chapelain and Hogervorst ¹⁰¹	Bonobos	29	<ul style="list-style-type: none">• Bimanual “tube” task• Only individual preferences reported	Complexity of task may alter manual specialization.
Humle and Matsuzawa ¹⁰²	Chimpanzees (wild)	31	<ul style="list-style-type: none">• 5 hand measures and 4 tool-use tasks observed• Population-level right-lateralization	Hand preference dependent on task and age (immatures less lateralized than adults)
Pouydebat et al. ¹⁰³	Gorillas	3	<ul style="list-style-type: none">• Grasping small versus large food items• Individual preferences reported	The complexity of the task does not necessarily induce a right-hand bias; there is considerable variability for hand preference in great apes.
Hopkins et al. ¹⁴	Chimpanzees	536	<ul style="list-style-type: none">• Bimanual “tube” task• Population-level right-lateralization for chimpanzees, gorillas, and bonobos• Left-hand preference for orangutans	Population-level preferences are evident for great ape species. The species preference is a result of ecological adaptations associated with posture and locomotion.
	Gorillas	76		
	Bonobos	118		
	Orangutans	47		
Llorente et al. ¹⁰⁴	Chimpanzees (captive, large outdoor enclosures)	100	<ul style="list-style-type: none">• Tube task with finger extraction by animals at Chimfunshi Wildlife Orphanage, Zambia• Age ranges 0–33 years• 86% animals show significant individual bias, 48% RH, 38% LH -> weak right-bias at population level• Females more biased to right than males	Females, but not males, show population-level right-bias in tool use; task complexity important. Humanization does not affect laterality.
Chapelain et al. ¹⁰⁵	Bonobos (zoos, rainforest sanctuary)	77	<ul style="list-style-type: none">• 48 bonobos in Lola Ya sanctuary (+29 previously studied zoo-housed¹⁰¹)• Tube task with finger extraction• Analyzed bouts and events• 42 of 48 sanctuary animals were significantly lateralized, 22 to right, 20 to left	No population-level manual bias found for bonobos (zoo, sanctuary, or combined).

NHPs remains tenuous at best. The same conclusion was also reached by several other meta-reviews.^{40–42}

The main counterpoint to these negative conclusions has come from research by Hopkins *et al.*, who have repeatedly and consistently reported small, but significant, right-hand biases in chimpanzees and gorillas,^{13,14,43} and a left-hand bias in orangutans. Several factors may underlie this inconsistency. The first is a direct statistical consequence of the weakness of the underlying asymmetry, at approximately 65% right-bias. This leads to small or moderate effect sizes (Cohen's d 0.2–0.4) that require large samples (>50 animals), to reach statistical significance.¹⁴ Such samples are rarely available from wild populations, so if studies on captive populations represent the “true” effect size, field studies are typically unlikely to reveal significant asymmetries.¹³

A second contributing factor is the well-documented effect of context and task on lateralized behavior.⁴⁴ In 1991, Fagot and Vauclair suggested that task and task difficulty are major factors influencing the degree of lateralization observed in a species,⁴⁵ a suggestion borne out by considerable subsequent research.⁴¹ This means that even subtle experimental differences influencing task difficulty may lead to inconsistent results within the same species.

A recent study⁴⁶ from our group highlighted this task effect for captive chimpanzees by inducing subjects to perform the same task in three different postural conditions: seated (the most comfortable), fully bipedal (quite difficult), and bipedal, but supported by the other hand (intermediate). The task was a variant of the tube task introduced by Hopkins: with peanut butter smeared within a long pipe, a provided stick is used to extract the food. We found that increasing postural demands significantly increased the degree of asymmetry but not its directionality: animals with a previous left-hand bias became more strongly left-handed, and equivalently for right-handers. Bimanual (no preference) individuals, common in the seated variant, became rare in the bipedal posture. However, no overall increase in right-bias was observed.

A final methodological factor concerns disagreement about the proper unit of analysis to achieve the requirement of statistical independence between data points, first emphasized by McGrew and Marchant.⁴⁰ In the tube task, where an animal grasps

a tube with one hand and then repeatedly removes food from it with the other, each action is not independent of the others. Thus, the proper N is not these individual food-removing motions (events), but rather each separate event of picking up the tube or tool (bouts). Research on primate laterality often reports counts of events, thus inflating sample sizes.^{47,48} The importance of this statistical issue remains controversial.^{44,49}

In conclusion, the primate laterality literature is somewhat inconsistent, but suggests a trend toward right-hand bias for some tasks, at the species-level in chimpanzees. Frequent failures to replicate this bias may result from small sample sizes and methodological differences. Given the large number of left-biased and bimanual chimpanzees, the question of whether the trend is statistically significant remains open. Furthermore, given that the same tasks and methods reveal left-hand biases in orangutans,¹⁴ whatever right-bias exists in chimpanzees might be of recent evolutionary origin. Finally, in contrast with several nonprimate species, such as parrots, the biases in African great apes are weak relative to humans. Thus, these comparative data compellingly suggest that the evolution of strong species-level right-handedness was an important event in human evolution, occurring after our evolutionary split from chimpanzees. The chimpanzee data suggest that a seed for this right-bias may have predated this split, but they do not explain the subsequent strengthening of right-handedness.

Nonhuman primates: communicative biases

Despite a long tradition of considering primate communication to be involuntary or reflexive,^{50,51} at least two classes of communicative actions in apes appear to show intentional control, are learnable, and are deployed in a strategic manner. These are manual gestures^{52–54} and nonphonated, orally produced sounds.^{55,56} This is in marked contrast to species-typical vocalizations that, although informative,⁵⁷ appear to be difficult to inhibit,⁵¹ and exhibit little intentionality (but see Ref. 58). In two species, communicative gestures are biased toward the right hand, including gestures to conspecifics in baboons and chimpanzees,^{59,60} and human-directed food begging in chimpanzees.⁶¹ In both species, communicative biases were stronger than those observed in noncommunicative actions.

Table 2. Summary of studies examining eye preferences in primates (chronological order)

Reference	Species tested	N	Tasks and results	Interpretation
Miles ¹⁰⁶	Humans	600	<ul style="list-style-type: none">• Various eye preference tasks and handedness self-report• 64% R-eyed• 34% L-eyed• 2% no preference• No hand–eye relation	Right-handed humans had a higher report of right-eye preference than left-handed humans, implying a similar operating process.
Kounin ¹⁰⁷	Rhesus macaques, spider monkeys, Cebus monkeys	4 1 3	<ul style="list-style-type: none">• Viewing food through a tube• Individual eye preference• No hand–eye relation	Hand preference was task-dependent and related to greater tendency toward investigation and manipulation.
Cole ¹⁰⁸	Pig-tailed macaques	7	<ul style="list-style-type: none">• Viewing food through a tube• L-eye preference• No hand–eye relation	Although crossed laterality in the limbs is exceptional, it is not related to eye dominance.
Smith ¹⁰⁹	Rhesus macaques	1	<ul style="list-style-type: none">• Binocular viewing• Left-eye preference• Left-hand preference	Ocular dominance and hand preference are related and possibly a distinguishing trait of rhesus macaques.
Kruper, Boyle, and Patton ¹¹⁰	Rhesus macaques	19	<ul style="list-style-type: none">• Viewing food through a mounted tube• Group level L-eye preference• Individual hand preferences	Lack of correlation between hand and eye preference suggests preferences are not mediated by a simple common factor.
McFerran ¹¹¹	Cotton top tamarins	38	<ul style="list-style-type: none">• Food viewing through a hole• No eye bias, slight individual preferences	The subjects had either a left-eye preference or no preference, suggesting some adaptive quality independent of other primates.
Rogers, Ward and Stafford ¹¹²	Bushbabies	6	<ul style="list-style-type: none">• Viewing various stimuli through a grid• Group level L-eye preference• No correlation with handedness	Increased arousal or fear altered eye preference, suggesting lateralization for both processes.
Hook-Costigan and Rogers ¹¹³	Common marmoset	8	<ul style="list-style-type: none">• Trained to look through a slit• Group-level right-eye preference• No correlation with individual handedness	Eye preference, independent of other motor behaviors, represents an independent form of hemisphere specialization, possibly related to perceptual processing.
Westergaard and Suomi ¹¹⁴	Capuchin monkeys	48	<ul style="list-style-type: none">• Food viewing through a hole• No group-level bias, but strong individual bias	Distribution was symmetrical, suggesting equal adaptive advantages for both eyes.

Continued

Table 2. Continued

Reference	Species tested	N	Tasks and results	Interpretation
Porac ¹¹⁵	Humans	387	<ul style="list-style-type: none">• Self-report for eye preference and handedness• Strong individual preferences for eye and hand• L-eye preference more frequent with L-hand	Results are consistent with idea of a common mechanism underlying limb and eye lateral preferences, but unknown which is driving force.
Hook-Costigan and Rogers ⁶⁷	Common marmoset	21	<ul style="list-style-type: none">• Viewing food through a hole• Group-level right-eye preference• No relationship with manual laterality	Eye preferences may reflect hemispheric specializations for perceptual processing, according to the emotional valence of the stimulus.
Chapelain and Blois-Heulin ¹¹⁶	Campbell's monkeys	14	<ul style="list-style-type: none">• Food viewing through tube• 8 right-eyed• 6 left-eyed	Early emergence of lateralization for perceptual processing compared to manual motor functions explains eye preference in the absence of other limb preferences.
de Latude et al. ¹¹⁷	Red-capped mangabeys	14	<ul style="list-style-type: none">• 2 methods (tube and box) with 5 different stimuli• Group-level left-eye preference	Palatability of stimuli affected preferential eye use supporting the theory of valence and the hemispheric processing of emotion.

Equally intriguing results come from a class of sounds chimpanzees generate with the lips and mouth, but which apparently lack laryngeal phonation: lip smacks, buzzes, and jaw clacks. Because apes have direct cortical connections to facial motor neurons, but not to those controlling the larynx,⁶² such sounds may involve greater cortical control than species-typical vocalizations. Facial asymmetries during production of such sounds exhibit a clear right-face bias.⁵⁶ This contrasts with a left-face bias for species-typical vocalizations (barks and pant-hoots), as also observed in other primate species.^{63–65} These results suggest that chimpanzees may have a left-hemisphere bias for cortically controlled, intentional communication, as opposed to midbrain-controlled, species-typical vocalizations, and that this bias is stronger than those observed for manual control.

Nonhuman primates: visual lateralization

Compared to primate manual asymmetry, there is surprisingly little work on perceptual lateral-

ity in NHPs (especially considering the strong evidence for perceptual asymmetry in other vertebrates^{26,27,66}). The primate research is summarized in Tables 2 (visual eye preferences) and 3 (acoustic orienting), which again illustrate the considerable variance in samples sizes, species, and findings in this literature.

Regarding eye preferences, several NHP studies in which an animal must look through a small peep-hole with one eye reveal strong biases dependent on the object being viewed. For example, 9 of 10 common marmosets preferred their right eye when viewing food, but switched to a left, or no, bias when viewing two model snakes.⁶⁷ Such context dependence is typical, although the direction of asymmetry differs across species. We recently conducted the first study of eye preferences in chimpanzees,³⁵ and observed a similar context dependence: there was a strong right-eye bias across 45 subjects to view bananas (highly preferred food type), while a realistic model snake was preferentially viewed with the left eye. Crucially, as for humans,⁶⁸ no individual

Table 3. Summary of studies utilizing the orienting asymmetry paradigm (chronological order)

Reference	Species tested	N	Tasks and results	Interpretation
Hauser and Andersson ⁷³	Rhesus macaques	80	<ul style="list-style-type: none">• Species-specific affiliative, fearful, aggressive calls result in right-turn bias in adults, but not infants• Heterospecific alarm call of ruddy turnstone.• Result in L-turn bias in adults, but not infants	Adult, but not infant, rhesus macaques process conspecific calls in the left hemisphere and heterospecific calls in the right hemisphere.
Hauser <i>et al.</i> ¹¹⁸	Rhesus macaques	26–31	<ul style="list-style-type: none">• Species-specific affiliative, alarm, and mating calls• Temporarily manipulated affiliative and alarm calls resulting in left-turn bias or no bias• Temporarily manipulated mating call resulting in right-turn bias	Temporal cues are used to classify affiliative and alarm calls, but not mating calls as conspecific.
Ghazanfar <i>et al.</i> ⁷⁴	Rhesus macaques	10–20	<ul style="list-style-type: none">• Species-specific alarm and food calls• Resulted in right-turning bias• Time-reversed alarm and food calls• Resulted in left-turning bias	Temporal cues are used to classify alarm and food calls as conspecific.
Gil-da-Costa and Hauser ⁷⁵	Vervet monkeys	5	<ul style="list-style-type: none">• Various species-specific vocalizations produced by familiar and unfamiliar individuals• Left-turning bias reported• Familiar and unfamiliar heterospecific vocalizations from various primate species• No bias was reported.• Nonbiological sounds failed to produce a 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 <i>et al.</i> ¹¹⁹	Barbary macaques	55	<ul style="list-style-type: none">• Various species-specific and heterospecific calls• No bias reported	Authors questioned the validity of the orienting paradigm to track lateralized acoustic processing.

Continued

Table 3. Continued

Reference	Species tested	N	Tasks and results	Interpretation
Scheumann and Zimmermann ¹²⁰	Grey mouse lemurs	38	<ul style="list-style-type: none">• Species-specific calls with positive valence• No turning bias reported• Species-specific calls with negative valence• Females did not exhibit any preference.• Males showed a right-turning bias.• No turning bias for various heterospecific calls• No turning bias for nonbiological sounds	A sex-specific left hemisphere lateralization for acoustic processing of species-specific calls with a negative valence.
Fischer <i>et al.</i> ⁷⁶	Adult humans	22 paired adults in a lab, 224 independent field study	<ul style="list-style-type: none">• Functional MRI response lateralized to left hemisphere in response to speech stimuli• Species-specific speech sounds• Left-turn bias reported for 1 sample (Germany), but not the other (UK)• No turning bias reported for nonbiological sounds	There is no direct relationship between lateralized acoustic processing and asymmetries for orienting behaviors.
Basile <i>et al.</i> ¹²¹	Campbell's monkeys Human girls (eight to nine years old)	7 monkeys; 13 girls	Monkeys: <ul style="list-style-type: none">• Species-specific calls, positive and negative valence• No turning bias reported• Heterospecific calls with negative valence• No turning bias reported Human girls: <ul style="list-style-type: none">• Familiar and unfamiliar species-specific vocalizations, both positive and negative• Right-turning bias for negative valence vocalization by familiar classmate• No other biases reported	Lateralized auditory processing exists only for familiar vocalizations with a negative valence. Processing in Campbell's monkeys is lateralized to the right hemisphere while human girls process in the left hemisphere.

Continued

Table 3. Continued

Reference	Species tested	N	Tasks and results	Interpretation
Lemasson <i>et al.</i> ¹²²	Japanese macaques	6	<ul style="list-style-type: none">• Familiar species-specific contact calls• Left-turning bias reported• Familiar chimpanzee calls• Left-tuning bias reported• Additional familiar primate and familiar nonbiological sounds• No bias reported• Various unfamiliar primate and nonbiological calls• No bias reported	Japanese macaques process species-specific and some other familiar sounds in the right hemisphere, indicating that lateralized auditory processing is influenced by previous experiences.

correlation between hand and eye preference was observed.

In conclusion, the few NHP studies of eye preferences suggest stronger species-level asymmetries than observed in most studies of manual preferences, and typically report no correlation between eyedness and hand preference. This suggests that primate perceptual biases may be stronger and more fundamental than manual biases, as consistently observed in the wider vertebrate literature. This has interesting implications for human evolution (see below). More research on primate eye preference, especially in a wider range of species, is clearly warranted.

Primate auditory lateralization

Turning to auditory laterality, early brain lesion studies suggested that coo vocalizations by Japanese macaques are preferentially processed by the left hemisphere.^{69,70} When positron emission tomography (PET) was used to view brain images of rhesus macaques listening to conspecific calls, one recent study suggested an LH bias,⁷¹ whereas another study reported an RH bias in the same species.⁷² Based on these data, it seems premature to draw conclusions regarding brain asymmetry in macaques.

More data are available for the behavioral measure of acoustic orienting, often thought to reflect hemispheric asymmetry for perception of vocalizations. This task involves playing various sounds from a loudspeaker situated directly behind a sub-

ject, and then recording over which shoulder the animal looks. Hauser and Andersson⁷³ found that 61 of 80 rhesus macaques turned their right ear toward the speaker when a conspecific vocalization was played, but favored the left ear when heterospecific calls were broadcast. Several later studies corroborated this effect,⁷⁴ suggesting that rhesus macaques show a left-hemisphere bias for species-typical vocalizations. However, numerous applications of this technique yield conflicting results (see Table 3). For example, a similar study on vervet monkeys revealed the opposite, left-ear bias for conspecific vocalizations.⁷⁵ Several studies have found no species-level bias, and convincingly challenged the validity of the orienting paradigm.³⁴

A recent study with humans provides further strong grounds for skepticism about the overall validity of this paradigm.⁷⁶ Subjects at supermarkets showed an overall left-ear turning bias for all classes of sounds (whether speech or other sounds). However, when the same sounds were played to 22 participants in a brain imaging study, the expected left-hemisphere activation was observed for speech, but not for other sounds. Thus, even within our own strongly left-biased species, orienting asymmetries do not reflect cerebral specialization. The authors concluded, and we agree, that the entire corpus of results from acoustic orienting must be viewed with considerable caution, and that no strong cognitive or neural conclusions are warranted by the existing data.

Conclusions

In conclusion, there is little evidence of causal links between handedness and other forms of laterality. A large body of research shows that lateralization phenomena are relatively weak in NHPs, and some other nonprimate vertebrates, compared to humans. This strongly suggests that both our species-typical right-manual preference, and left-hemisphere language bias, represent derived traits. What was the driving force behind this evolutionary change?

One possibility is that human handedness actually derives from deeper perceptual (particularly visual) lateralization,^{26,28} rather than preexisting manual biases in primates. A preference for using the right eye/left hemisphere for routine activity might have driven a corresponding right-hand advantage for tool use, supported by a general left eye/right hemisphere superiority for spatial processing. This may have simultaneously selected the left hemisphere for automatized speech motor control and syntactic processing.^{46,77}

A second possibility, not incompatible, is that an underlying left-hemisphere bias for social and communicative functions provided the seed for the very strong LH language bias in humans, but that the strength results from the drive among individuals in a communicating population to align their cognitive biases for effective linguistic use.²⁸ Support for this hypothesis comes from recent neural data comparing humans and chimpanzees. The human brain is asymmetrical both functionally and anatomically. In particular, expansion of Broca's area (left BA 44/45; involved in speech and syntax) is massive and asymmetrical: sixfold greater in humans relative to chimpanzees.⁷⁸ This is twice the threefold overall increase in brain size. The connectivity of this region has also changed significantly between humans and chimpanzees.⁷⁹ Although a PET study of chimpanzees listening to vocalizations revealed a weakly left-lateralized activation in a comparable frontal region,⁸⁰ other brain regions were more strongly, and bilaterally, activated. These new cytoarchitectonic and functional brain imaging data provide little backing for earlier claims that superficial anatomical asymmetries in chimpanzee brains are relevant to language evolution,^{81,82} instead suggesting that Broca's area, and its connective network, has undergone computationally relevant expansion and rewiring during our recent evolution.

Either way, the comparative data suggest that the long-standing focus on handedness, along with its presumed connection to language lateralization, is misplaced. Human handedness, rather than being a driving force, may be a by-product of more fundamental perceptual and cognitive asymmetries, particularly those involved in language evolution, but with potentially deeper roots in vertebrate-wide perceptual asymmetries. Handedness per se may turn out to be a red-herring. Future comparative research should be broadened to incorporate perceptual asymmetries in NHPs, along with the asymmetries in neural tissue and connectivity that presumably underlie them.

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Conflicts of interest

The authors declare no conflicts of interest.

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