Manual laterality and cognition through evolution: An archeological perspective

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Abstract

To understand the evolution of lateralized motor biases and cognitive functions, we rely on archeological methods to give us a window onto the past. Currently, the overwhelming majority of prehistoric data on asymmetry and laterality concern only the hominin lineage, spanning the time period from the presumed evolutionary split with the other great apes around 6–8 million years ago until the present day. We present an overview of these data from paleontology and archeology. Lateralized motor biases and anatomical asymmetries are evident throughout prehistory, showing increases in the predominance of right-handedness over time. Laterality was a key feature of the motor-cognitive development of extinct human ancestors. However, further research in living humans is needed to resolve the extent of colateralization of functions in the human brain, so we urge caution when inferring functional cognitive laterality from behavioral markers of handedness.

Keywords

Archeology, Fossils, Handedness, Hominins, Human evolution, Laterality, Lithics, Stone tools, Paleoanthropology, Paleoneurology

1 INTRODUCTION

Through the ages, laterality has been considered a hallmark of humanity. From the predominance of right-handers in human societies to the functional specialization of the hemispheres in human brains, our salient laterality has captured the attention

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of scholars worldwide. Although lateralized cognition and motor behaviors are widespread in the animal kingdom—as discussed in the other chapters in this volume—and lateralities are also ubiquitous in plants, molecules, and galaxies (McManus, 2004; Myrgorodska et al., 2017; Rosenberg et al., 2008; Shamir, 2012), it is clear that our species has a unique system of distributing behavior and cognition across the midline, with its unusual species-level preponderance of extreme side biases and lateralized functions.

First, it is important to understand the place of humans in the evolutionary tree of biological life, since *Homo sapiens* evolved in continuity with the ancestral species preceding us. Humans are just one species of great ape, in the primate order, belonging to the class of mammals. Our unique evolutionary lineage extends about 6–13 million years back in time (the exact dates are uncertain), starting from the moment when we shared a common ancestor with other living apes, the chimpanzees (*Pan troglodytes*), and bonobos (*Pan paniscus*), who themselves only diverged into separate species 1.6 million years ago (mya). In the last 7 million years of our evolution, dozens of different hominin species appeared and disappeared, many of them living alongside one another (as do bonobos and chimpanzees today). Ultimately, only *H. sapiens* remained into the present day (albeit with a significant proportion of DNA from Neanderthals, Sankararaman et al., 2014). It is still unclear why only our species survived; current theories propose that the success of *H. sapiens* was due to one or more evolutionary adaptations for sociality, tool-use, cumulative culture, language, increased brain size, or intelligence (McBrearty and Brooks, 2000; Uomini, 2008b). Lateralization might also have contributed to our species' evolution, as for example a stable individual hand preference over time facilitates learning difficult bimanual skills (Todor and Doane, 1977), and having a functionally lateralized brain is suggested to improve the ability to perform tasks that involve both hemispheres (Rogers et al., 2004). Thus, knowing the conditions surrounding the evolution of lateralization helps us to better understand why lateralization exists today.

There has now been over 150 years of scientific research on hemispheric specialization and lateralized functions in living humans, with three major domains being hand preferences, language, and visuospatial skills and attention. Owing to its long history, this research includes assessments of behavioral asymmetries, as well as work on anatomical and functional brain asymmetries; it also includes large-scale studies of laterality-related genes and comparative research on nonhuman species. In other words, the literature on laterality is incredibly vast (see Rogers and Vallortigara, 2017; Seghier, 2016). In the next section, we review some key findings from comparative research and provide a broad overview of the evolutionary perspectives which underlie contemporary laterality research today.

1.1 LATERALITY IN THE ANIMAL KINGDOM

The evidence for lateralized cognition, motor biases, and anatomical asymmetries in nonhuman animals suggests that laterality at the level of the individual is actually quite conserved across animal taxa, with various forms of individual asymmetry across the midline being present in a range of species widely separated by evolution to varying degrees. Thus, while laterality itself is not unique to humans, comparative work shows that *H. sapiens* has a much more extreme degree of functional specialization than other species, even when compared to our closest living relatives among the apes (reviewed in Rogers, 2014; Rogers and Vallortigara, 2017), as we discuss later. Owing to various practical limitations—such as a general inability to conduct task-based functional neuroimaging on nonhumans, the contentious nature of work on nonhuman communicative (or linguistic) capabilities, ethical considerations for animal and human research, etc.—much of the work on hemispheric specialization and laterality in other species comes from behavioral data and, when possible, anatomical comparisons between well-established homologous brain areas.

Driven by the early discovery of a relationship between manual motor skill and other lateralized behaviors in humans (Corballis, 2003, 2009), quite a bit of comparative work relates directly to understanding the basis and the evolutionary context of human *hand preferences*. Although some of this work seek to understand hand preferences in themselves, a majority of research publications situate hand preference *as a proxy* for the other lateralities (Bishop, 2013; Rogers and Vallortigara, 2017). The idea of hand preference as a proxy was certainly based on earlier research, but the spread of this idea throughout the literature was likely facilitated due to a relative ease of studying hand preference (a behavioral trait) compared to the complications of studying functional specialization and hemispheric asymmetries directly.

In the specific case of motor biases in lateralized hand use, which, as discussed earlier, have been more thoroughly investigated than other forms of lateralization, humans are at one end of a continuum on which individual-level and species-level hand preferences can be quantified (Forrester et al., 2013). Nonhuman apes—which also execute complex manipulations with their hands and fingers—commonly have individual hand preferences, just as humans do (although some authors hypothesize that hand preferences in primates can be task specific, as for example in western lowland gorillas (*Gorilla gorilla gorilla*) hand actions are more likely to be right-handed if the target is inanimate, compared to animate targets, Forrester et al., 2011). Hand preferences can also be rather consistent within an individual (i.e., some authors argue that individual apes can be right- or left-handed, in much the same way as us, Hopkins, 2004, 2006; Hopkins et al., 2004, 2011). However, unlike humans, the other apes do not have a species-level bias toward *one* hand preference configuration—that is, handedness (Cashmore et al., 2008; McGrew and Marchant, 1997; Uomini, 2009c).

In other words, all human groups (populations) have a statistically significant majority of right-handers, with proportions across various types of human societies ranging from 77.4% to 96.6% right-handers (Faurie et al., 2016; Faurie and Raymond, 2005), and there are no human groups with a majority of left-handers. On the contrary, nonhuman great ape hand preferences are more evenly distributed to the left or right, in adults, such that various groups have a majority of left-handers, a majority of right-handers, or equal numbers of right-, left-, and ambilateral-handers

(Meguerditchian et al., 2015); for instance, the highest proportion of right-handers in a chimpanzee group does not exceed 70% (Neufuss et al., 2017). The comparative data are on adult hand preferences because in humans, children's hand preferences do not stabilize until age 10 (Michel et al., 2013), but we currently lack thorough comparative research on nonhuman primate hand preferences from similar developmental perspectives. Beyond the primates, group-level limb preferences are found in 61 species of vertebrates—mammals, birds, amphibians, reptiles, and fishes (Ströckens et al., 2013). Some other nonprimate species among the whales and dolphins also show behavioral side biases to 90% at the population level (Karenina et al., 2017; MacNeilage, 2014; Rogers, 2009), which indicates that species-level motor biases can evolve independently in species for different reasons (Rogers, 2014; Rogers et al., 2013).

Some authors have also favored hand preference as a proxy for other forms of lateralization due to the well-known overlaps between bilateral anatomical brain areas subserving manual motor functions to those subserving more complex cognitive functions. In living humans, hand preference and other lateralized functions, such as language and visuospatial attention, share anatomical similarities ranging from white-matter pathways (Bernal et al., 2015; Biswal et al., 1995; Figley et al., 2017; Tzourio-Mazoyer, 2016) to cortical area overlaps (Gotts et al., 2013; Guadalupe et al., 2014; Jung-Beeman, 2005; Marzoli et al., 2014; Mayka et al., 2006; Salmelin and Kujala, 2006). Thus, efforts have also been made to explore additional evidence for the evolutionary roots of human lateralization, specifically to assess and compare brain asymmetries between humans and great apes. Although sample sizes are currently smaller than the behavioral work on manual motor biases, as with the hand preference work in apes, some crucial areas—including primary visual and motor cortices, and even language areas like the planum temporale and frontal operculum—show anatomical asymmetries in apes. These asymmetries are often in the same direction as humans, but to a lesser extent both in absolute size disparities and in the number of individuals presenting such asymmetries (Balzeau et al., 2012a; Gomez-Robles et al., 2013; Holloway et al., 2003; Hopkins and Nir, 2010; Sherwood et al., 2003).

Coupled with the broader comparative work, these studies provide evidence that human asymmetries are elaborations of preexisting biases in related taxa, although confirmations of behavioral or anatomical asymmetries do not directly implicate functional similarities (on this, see Striedter, 2002). In summary, laterality itself is not rare in the animal kingdom, but humans' lateralities have evolved to an extreme form which is unique within our primate lineage in both direction and degree. The comparative approaches are certainly of value in understanding the evolutionary context of lateralization, but because we still lack a general consensus on the relationship between hand preferences, anatomical asymmetries, and functional lateralization, we argue that it is hard to characterize when or how *H. sapiens* shifted away from ancestral patterns of laterality, without learning heavily on implied proxies or speculative logic. Despite these limitations, there is broad evidence that the strong right-handed bias, which occurs at the species-level today in humans, has emerged during our evolution, in the course of the last 7 million years. To understand why right-hand predominance evolved in our lineage, the timing of its emergence can give us clues as to the evolutionary conditions surrounding it. It is our view that this information can also provide some insight into the evolution of other human lateralities.

1.2 EVOLUTION OF LATERALITY AND COGNITION

To track the evolution of lateralized motor biases and cognitive functions, we rely on archeological methods to give us a window into the past. Other sources of data, such as genetics, cannot at present resolve the timing of their evolution. The complex genetic underpinnings of human laterality are still being explored (Brandler et al., 2013; Crow, 2002; Faurie and Raymond, 2013; Francks, 2015; Kavaklioglu et al., 2016; Laval et al., 1998; Loffing and Hagemann, 2012; McManus et al., 2013; Paracchini, 2011; Van Agtmael et al., 2001; Versace and Vallortigara, 2015). Recent works have largely refuted isomorphic polygenic theories, which posited that the genes controlling hand preferences would be identical to those controlling other lateralities (McManus, 1985, 1999; McManus and Bryden, 1991), in favor of a "partial pleiotropy" view, which acknowledges that there is *some* overlap between the genes which affect the development of hemispheric asymmetries in the brain and those contributing to hand preference, but it is likely that there are also genes which affect each system independently (Ocklenburg et al., 2014, p. 195). New genetic evidence from large-population studies finds hand preferences are weakly associated with some pathologies like schizophrenia and dyslexia (Brandler and Paracchini, 2014; Francks et al., 2002, 2003, 2007; Giouzeli et al., 2004; Ocklenburg et al., 2014; Priddle and Crow, 2013; Scerri et al., 2011). In our view, these associations are potential indicators that past evolutionary pressures affected specific cognitive skills with tradeoffs, for example that selection for brain laterality created a higher risk of schizophrenia (Crow, 1998). There is a growing literature on the role of the environment with regard to the development of laterality as well, with recent estimates of the heritability of hand preferences as low as 25%, and much higher contributions coming from external factors (Bishop, 2013; Brandler and Paracchini, 2014; Paracchini and Scerri, 2017; Somers et al., 2015). As the results of these large-scale studies show, there has been a general shift from simple models of laterality—whereby the functional specialization of brain and behavior is seen as largely controlled by simple mechanisms—to more complex perspectives.

Inferences of cognitive function in prehistoric species, paleocognition, relies on anatomical evidence of fossil brains to reconstruct the behaviors of past species. To the best of our knowledge, there is currently only one published study of paleocognition in a nonhominin species. Gaetano et al. (2017) used brain shape measurements from endocasts (fossil brain cases) to infer that extinct maniraptors (a common ancestor of birds and nonbird dinosaurs) could have been cognitively equivalent to modern cormorants. Paleocognitive research on hominins is gaining momentum, especially thanks to the advent of paleoneurology (the study of past brain anatomy from fossil endocasts, Bruner, 2014; Holloway, 2014), which has expanded our ability to reconstruct the neuroanatomy of extinct hominins. Paleoneurology and paleocognition have not yet been applied to animal taxa other than maniraptors and hominins. The main challenges in this research arise from preservation, as many fossil cranial bones are fragmentary, distorted, or the surfaces are too worn to reliably identify features. Linking the data with lateralization and cognition is another challenge, as the features that can be measured are limited to those which are large enough to leave imprints on the endocast, such as overall brain size, arteries, vessels, nerves, sinuses, suture closure, sulci, and gyri of the cortex, and the cerebellum (Bruner, 2017; Falk, 2014b). Inferences about cognition thus necessarily occur at the coarse level, drawing on neuroscience data for these features. Laterality, in particular, is relatively easy to identify in complete and partial fossil skulls, based on asymmetries in size and shape between areas on the two halves of the brain, or between the two hemispheres globally (Table S1 in the online version at https://doi.org/10.1016/bs.pbr.2018.06.015). Below we discuss in more detail the fossil endocast data presented in Table S1 in the online version at https://doi.org/10.1016/bs.pbr.2018.06.015. Just as fossil endocasts can give us an insight to brain asymmetries and cognitive lateralities, so do fossil bones provide information about bodily asymmetries and behavioral lateralities.

1.3 VARIETY OF LATERALITIES

Currently, the overwhelming majority of prehistoric data on cognition or laterality concern only the hominin lineage, spanning the time period from the presumed evolutionary split with the other great apes around 6–10 mya until the present day. Below we present an overview of these data from paleontology and archeology.

In this chapter, we focus on behavioral lateralities and related anatomical asymmetries in hominins (i.e., humans, our ancestors, and related extinct human-like species such as Neanderthals, *Homo erectus*, Australopithecines, etc.). As highlighted earlier, reliable preservation is a primary factor which determines the sources of data archeologists can consult in tracking the evolution of laterality in the human lineage (Ruck et al., 2015), and in others. Here we review the major threads researchers have followed in order to assess individual and population-level asymmetries through time. Diverse methods have been used on a wide array of paleoarcheological data, and each provides evidence on the context and evolution of lateralization in our species and our ancestors. Direct evidence of behavioral laterality at one moment in time is found in the artifacts made by people using a right-handed or left-handed manual configuration. Anatomical asymmetries found in the skeleton, due to stronger muscle activity of one arm during the lifetime, provide evidence of more consistently lateralized behavior. Asymmetric neuroanatomy in the brain also indicates directional asymmetries, and these are presumably linked with lateralized *behaviors*, although we do not wish to impose a unidirectional or causal relationship between the two.

These directional asymmetries are canalized genetically and/or developmentally (Fagard, 2013), indicating that hominins experienced selective pressures for the resulting lateralized behaviors during their evolution.

To some degree, cognitive laterality (i.e., functional hemispheric specialization) and manual laterality (i.e., hand preference) should also be treated separately. Although previous work suggested that hand preference was linked directly to brain asymmetries in many other domains, this idea has become more and more contentious over time, and it is heavily debated today (Badzakova-Trajkov et al., 2016; Zago et al., 2016). The central component of contemporary debate revolves around a concept which we term colaterality: namely, that the functional lateralization of one modality—such as language or visuospatial skills—is related in some way to the functional lateralization of another—such as hand preference (Cai et al., 2013; Willems et al., 2014). It is important to note that colaterality does not imply causality, nor does it require that colateralized tasks must be located in different hemispheres; for example, right-handedness and language are both largely subserved by the left hemisphere in living humans, but left-hemisphere dominance for language may also be complementary to right-hemisphere dominance for visuospatial skills (see discussion later; Flöel et al., 2005; Oltedal and Hugdahl, 2017; Zago et al., 2016), with each being a form of colaterality. Thus, the concept simply posits that asymmetry for each of these traits is likely not independent of asymmetry for the others. Although colaterality was widely accepted before researchers had the means to rigorously test it, in recent years a fair amount of research has argued against colaterality. These studies show that language, visuospatial skills, and manual motor behavior are all, indeed, lateralized, but mounting evidence suggests that the three lateralize independently of each other, and thus that no one behavior can be used to infer the laterality of another, as we discuss later.

2 EVOLUTION OF LATERALITY: THE DATA

We now turn to the prehistoric evidence for lateralities. Table S1 in the online version at https://doi.org/10.1016/bs.pbr.2018.06.015 presents the most comprehensive dataset published to date, compiled from numerous sources. We describe the different categories of data available—artifacts, fossilized skeletal materials, fossilized cut-marked teeth, and fossilized brain cases (endocasts). We then discuss the overall patterns in hominin evolution revealed by the data, which show that brain asymmetry and right-handedness increased over time, although data from earlier hominins are too sparse to make any firm conclusions yet. We then briefly describe a few interesting examples that illustrate the significance of laterality in prehistory.

In Table S1 in the online version at https://doi.org/10.1016/bs.pbr.2018.06.015, we present data for hominin lateralities obtained from the bodies of evidence which we believe are the most reliable, according to critical assessments by ourselves and others (detailed in Cashmore et al., 2008; Faurie et al., 2016; Gowlett and Uomini, 2014; Jöris and Uomini, in press; Ruck, 2014a, b; Ruck et al., 2015; Ruck and Uomini, in press; Steele and Uomini, 2005, 2009; Uomini, 2001, 2008a, b, 2009a, b, c, 2011, 2014; Uomini and Ruck, in press; see Table S1 in the online version at https://doi.org/10.1016/bs.pbr.2018.06.015 for specifics on the data and their respective references).

The evidence for behavioral and anatomical hemispheric lateralities consists of:

1. the hand preferences determined—using various methods—from stone tool manufacture and use;
2. the proportions of right- and left-hand prints and stencils found on rocks and cave walls;
3. the right or left diagonal striations on fossil teeth;
4. the measured asymmetries in fossil skeletons, specifically in the arms; and
5. the measured asymmetries in endocasts, which are the imprints left by the brain inside fossilized skulls.

Several methods have been devised and tested experimentally for determining hand preferences from individual stone tools (lithics) or individual flakes, which are the small pieces struck off during stone tool-making. These include reconstructions of the grips used while holding a tool for cutting actions, spatial configuration of the scatter of stone flake waste left behind after making the tool (also called knapping) that shows the seated position of the knapper (stone tool maker), traces of use on stone tools showing directional movement by one hand, asymmetric tool shapes caused by use and resharpening by one hand, microscopic features on stone flakes that indicate striking direction of the fracture while knapping (Bargalló and Mosquera, 2014; Dominguez-Ballesteros and Arrizabalaga, 2015), and diagonal marks on bone pieces that were used to resharpen stone tools using one hand configuration (Semenov, 1964). Stone tools and knapping remnants number millions or even billions around the world, and span nearly all of hominin prehistory, which make them the most accessible evidence to investigate hand preferences and handedness. The real challenge is to develop methods that work reliably for the great diversity of tool types in the archeological record, as each new method needs experimental validation before it can be applied to archeological tools. In Table S1 in the online version at https://doi.org/10.1016/bs.pbr.2018.06.015, we include methods which have been successfully applied to the archeological record, which result in conferred hand preference data and reveal that a few conspicuous left-handers existed among the majority of right-handers for much of human evolution.

Thousands of hand prints and hand stencils made by prehistoric people survive today on cave walls and rock shelters. Our ability to recognize individual cave painters (as opposed to one individual leaving behind many prints) is only just beginning (Nelson et al., 2017), so we currently assess proportions of right- and left-hand stencils to infer a right-handed majority, consistent with the fact that modern-day right-handers tend to press their *left* hand against the wall to make stencils (Faurie and Raymond, 2004). Hand prints are made by pressing a hand—already covered in liquid pigment—onto the rock surface, but they are relatively rare. Hand stencils are by far more frequent; they are made by the more involved method of placing the hand palm-down onto the rock surface and dabbing or spraying liquid pigment around it, leaving a "negative hand" behind. Dabbing can be done with animal fur or soft leather, and spraying can be done directly from the mouth, or blowing through an arrangement of two tubes in a container of liquid pigment (Uomini, 2009a). The data cover numerous single sites and multisite surveys, showing a universal pattern of high proportions of left-hand stencils, consistent with a right-handed majority among the prehistoric artists (Table S1 in the online version at https://doi.org/10.1016/bs.pbr.2018.06.015 and references therein).

Some fossil teeth show characteristic diagonal striations that were caused by cultural practices for using the teeth as a "third hand," such as processing leather, plants, or meat (Bruner and Lozano, 2014; Lozano et al., 2008; Uomini, 2008a, 2011). The only documented ethnographic parallels to such behaviors are found in the practice of eating meat by gripping strips of meat in the front teeth and slicing off bite-sized pieces with a knife—or in the case of hominins, a sharp stone flake (examples from around the world are detailed in Uomini, 2008a, 2011). Although nobody has yet studied the teeth of living humans who practice this meat-cutting activity in order to verify the correlation of hand preference to dental striation direction, experiments with simulated Neanderthal teeth confirmed that right-handed and left-handed meat cutting with stone leaves distinct diagonal marks, whose angles and features can be measured under microscopes (Bermúdez de Castro et al., 1988). All available data from hominins, collected in Table S1 in the online version at https://doi.org/10.1016/bs.pbr.2018.06.015, show that right-handedness comprises the majority of the surveyed individuals, but that some hominins have clear left-handed marks, or a combination of right- and left-oriented striations suggestive of mixed-handedness.

Directional asymmetries in arm bones—in contrast to fluctuating asymmetry, which is caused by developmental stress—relate to regular, unequal biomechanical loading of the muscles in both arms during use. As exemplary cases, athletes who play asymmetric sports like tennis or baseball commonly have a stronger dominant arm and a lesser range of motion in the joints of the nondominant limb (Ellenbecker, 2016; Hagemann et al., 2016), and these differences manifest themselves in the size and robusticity of their arm bones. Directional asymmetry of this form is generally detectable in individuals beyond athletes as well, and the data gathered in Table S1 in the online version at https://doi.org/10.1016/bs.pbr.2018.06.015 show that hominins generally had strong side biases, showing they habitually performed strenuous asymmetrical activities during their hunter–gatherer daily lives (Shaw and Stock, 2013). Although the lack of clearly paired long bones limits sample sizes for this method, the current data suggest that right-handers were more frequent, but also that some left-handers did exist.

Brain asymmetries occur in several areas and can be assessed with several different measurement methods. Some of these anatomical asymmetries are shared with other apes, but are the most extreme in modern humans relative to other apes, which again shows that the evolution of our species is characteristic of our biological, cultural, environmental, and/or epigenetic heritage, while at the same time highlighting features particular to hominins (Balzeau et al., 2012a; Bruner, 2017; Falk, 2014a, b). Relevant to paleoanthropology are the brain asymmetries, which (1) can be seen in the skull and (2) are related to hand preferences. These asymmetries can be reliably measured in fossil endocasts (Fournier et al., 2011). We focus here on the well-known frontal–occipital petalias, although parietal and temporal petalias are also documented and merit more attention in future research (Kitchell, 2015). Petalias are defined as the protrusion of one hemisphere relative to the other, such as forward (in the frontal lobe) or backward (in the occipital lobe), as related to greater size, greater surface area, or brain torque (Balzeau et al., 2012b). Hand preference is probably correlated with petalia asymmetries. While several studies showed that statistically, right-handed individuals are more likely to have right-frontal and/or left-occipital (RF+LO) petalias and left-handers are more likely to have the opposite petalias (LF+RO) or to have a brain tending toward symmetry (Balzeau et al., 2012a; Galaburda et al., 1978; Kertesz et al., 1990; Kitchell and Schoenemann, 2014; LeMay, 1977; Ruck and Schoenemann, 2018), some other studies failed to find a correlation (Good et al., 2001; Herve et al., 2006). However, it is clear that the RF+LO petalia pattern is unique to humans (Balzeau et al., 2012a; Li et al., 2018; Zollikofer and Ponce de León, 2013); thus the interesting question here is when it emerged in the hominin lineage. Although different measurement methods have been used by researchers, Table S1 in the online version at https://doi.org/10.1016/bs.pbr.2018.06.015 shows that in most cases, the endocast classifications from different studies are in agreement. We indicate the few instances when different researchers have found conflicting results. The data show that the right-handed petalial pattern (RF+LO) was common among hominins, but that all of the other possible petalia combinations also occurred.

2.1 INTEGRATING MULTIPLE LINES OF EVIDENCE

In Table S1 in the online version at https://doi.org/10.1016/bs.pbr.2018.06.015, we combine the data from these four categories of evidence, so we can see how they correlate in individuals with more than one type of data. In fact, there are 18 individual hominins with two categories of evidence for hand preference or other forms of laterality. Although these cases would ideally be used to corroborate multiple methods (insofar as multiple assessments of laterality in living individuals, from experimental or comparative work, should result in nonconflicting classifications), the current data are not auspicious. Unfortunately, the data from the two early hominins (OH 16 and OH 7, both from around 1.7 mya) did not yield clearly lateralized results. Out of the eight pre-Neanderthal and *Homo heidelbergensis* specimens (all dated between 200 and 500 kya), three show conflicting results, suggesting potential mixed-handers. Among the eight Neanderthals (dated between 40 and 122 kya), all show data consistent with right-handedness except the adult male Spy 1, who has a left-occipital petalia consistent with right-handedness, but symmetrical arm bones, suggesting he was possibly mixed-handed. No fossils have all four categories of evidence documented, but one individual has three. The adult

Neanderthal of unknown sex, La Quina H5, has two teeth with diagonal right-handed striations and a stronger right arm, although the arm asymmetry might be pathological, and it has a slight left-occipital petalia suggestive of left-handedness, being noted as either symmetrical or slightly rightward by different researchers. Thus, the humeri and endocast data are uncertain and potentially not-right-handed, while the teeth indicate a right-handed use; this individual we have marked as tentatively mixed-handed. As discussed earlier, fossil endocrania are rarely perfectly preserved, but it is possible to reliably measure petalias in many incomplete skulls; in Table S1 in the online version at https://doi.org/10.1016/bs.pbr.2018.06.015, we include specimens for which there are attributed endocast petalias.

We would like to point out some notable left-handers in our dataset. In prehistoric humans, many left-handed individuals showed a clear left-hand preference already as children. Thus, individual hand preferences were established by adolescence in hominins (Jöris and Uomini, in press), much as they are in living humans today. The data in Table S1 in the online version at https://doi.org/10.1016/bs.pbr.2018.06.015 show that, for example, two Neanderthal individuals at Krapina who died at age 10 and 15 years old were left-handed, and the left-handed Vergisson 4 Neanderthal was 7–9 years old when it died. The pre-Neanderthal female Atapuerca Sima de los Huesos X died at 15–17 years old and was possibly mixed-handed, as she had tooth striations in all orientations. Finally, the Indonesian *H. erectus* individual Sambungmacan 3, who was not quite adult at death, had left-frontal and right-occipital brain petalias, suggesting it was left-handed. Were left-handers more frequent among the individuals who died younger? Many of the fossils showing left-handedness or mixed-handedness were of unknown age at death. For instance, two *H. erectus* individuals from Zhoukoudian had left-frontal and right-occipital brain petalias. We note the adult male Shanidar 1, who died at 40–50 years old with severe trauma and disease on his skeleton; he most likely was obliged to use his left hand long enough to cause right-arm atrophy and a stronger left humerus. The adult female Liang Bua LB1 was about 30 years old at death and shows pronounced left-frontal and right-occipital brain petalias, making her possibly also left-handed. Still, the fossil record is full of right-handed children who also died young, such as at Atapuerca Sima de los Huesos, El Sidrón, and Krapina. Thus, hominins generally lived dangerous lives, and the present data (Table S1 in the online version at https://doi.org/10.1016/bs.pbr.2018.06.015 and references therein) cannot tell us whether being left-handed might have contributed to their young mortality.

3 COLATERALITY: IS HANDEDNESS A VALUABLE PROXY?

As the data presented earlier make clear, behavioral and anatomical laterality were key features of motor-cognitive development in extinct human ancestors. However, further research in living humans is still needed: the extent of colateralization of functions in the human brain is still unresolved, so we must advise caution when inferring functional cognitive laterality from behavioral markers of hand preference.

Although much is now known about hemispheric specialization for language, hand preference, and visuospatial skills, there is still very little consensus on whether, or how, functional laterality in one modality may interact with asymmetries for other tasks in living humans—and even less in other species (for a review, see Badzakova-Trajkov et al., 2016). We now turn to this topic, as we believe it is a major issue for future works toward understanding the evolution of such lateralities. We present an overview of both sides of the colaterality debate, beginning with a description of the original large-sample studies, which urged caution with regard to colaterality. We then present studies on both visuospatial skills and language laterality, which *are* compatible with the concept of colaterality, considering open questions and future directions with regard to this debate.

3.1 LARGE-SAMPLE STUDIES ON HEMISPHERIC LATERALIZATION AND HAND PREFERENCE

It has long been known that a stark majority of right-handers—about 95%—show left-hemisphere dominance for language processing in the brain; from the initial scientific inquiries on aphasia and apraxia, to split-brain studies in the late 1900s, to newer lines of enquiry enabled by the explosion of technology and neuroimaging methods, many researchers supported the use of hand preference as a proxy for other lateralities, most notably language (Broca, 2011a [1861], 2011b [1865]; Gazzaniga, 2000, 2005; Geschwind and Galaburda, 1987; Springer and Deutsch, 1985, 1998). However, early probes of hemispheric dominance for language in left-handers (using various brain imaging techniques like the Wada test, positron-emission tomography (PET) scans, functional transcranial Doppler sonography (fTCD) measures, functional magnetic resonance imaging (fMRI), and most recently, functional near-infrared spectroscopy (fNIRS)) showed that many left-handers—between 70% and 85%—were *also* left-lateralized for language, as opposed to being right-hemisphere dominant (Flöel et al., 2005; Knecht et al., 2000; Paquette et al., 2015; Tzourio et al., 1998; Tzourio-Mazoyer and Courtin, 2013). As this finding was a direct challenge to the expected relationship between hand preference and language dominance, subsequent studies sought to identify and characterize left-handers with typical language dominance in contrast to left-handers with atypical language dominance.

Knecht et al. (2000) made an early large-sample study using fTCD on the cued word generation task in 326 participants, who were classed into six hand preference categories and familial sinistrality scores. They found a linear relationship between left-handedness and atypical, or right-hemisphere, language dominance, as well as an effect of familial sinistrality. Only 4% of right-handers showed atypical language dominance, with 15% of mixed-handers showing atypical dominance, and 23% of left-handers showing right-hemisphere dominance for language. The authors conclude that: “degree of handedness is linearly and highly significantly related to the side of language dominance… [but that the complexity of their results suggest that] handedness and language dominance are each determined by multiple factors, some of which have a role in both phenomena” (Knecht et al., 2000, p. 2517).

As McManus et al. (2013) point out, inherited hand preferences involve at least 40 genetic loci; thus it is most likely that the other lateralities also involve similarly complex genetics.

Similar subsequent approaches highlight a few major advances in the study of colateralization, including a shift toward treating hand preference as a categorical, rather than binary variable, and the rise of "degree vs direction" discussions in the literature; assessing effects of familial sinistrality (presence of left-handers in the nuclear family); and including study samples enriched in left-handers in general (Willems et al., 2014). This body of work confirmed that the *degree* of left-handedness characterized language lateralization better than binary classifications; and also that familial sinistrality played a small, but often significant role in explaining rightward shifts of hemispheric specialization for language (in both right-handers and left-handers). Despite these advances, an isomorphic relationship between hand preference and language laterality was still lacking, as additional investigations showed little-to-no improvements from using *degrees* of laterality, as opposed to binary classes.

In the past 5 years, several large-sample analyses of hemispheric specialization and colaterality have been published, many coming from the Brain Imaging of Lateralization by the Groupe d'Imagerie Neurofonctionnelle (henceforth BIL&GIN) database of brain and behavioral laterality, containing a battery of tests on over 450 participants enriched in left-handers ($n = 199$ using self-reports; see Mazoyer et al., 2016). In addition to self-reporting hand preference and familial sinistrality, participants completed the Edinburgh Handedness Inventory (henceforth the EHI, Oldfield, 1971), and a behavioral measure of hand preference by finger tapping (FT) (Mazoyer et al., 2016). We will review these works in some detail below, but it is important to note that hand preference classifications for subjects in these large-scale studies comes from a single, survey-based metric for assessing hand preference. As we will argue below, the claim for *independence* between hand preference and language laterality is underpinned almost entirely by publications with this methodological limitation.

Zago et al. (2016) used the BIL&GIN database to explicitly probe the relationship between laterality for visuospatial cognition with that of language processing. This paper includes a good review of the competing hypotheses regarding colaterality:

H1. The relationship between language laterality and visuospatial laterality is *causal*—i.e., the hemispheric specialization in one modality forces the other task to occupy the other hemisphere (essentially a "crowding" hypothesis; see Bryden et al., 1993; Flöel et al., 2005).

H2. These systems are independent—i.e., the typical left-language/right-visual lateralization pattern is common by chance. On this view, all of the other possible combinations of language/visuospatial hemispheric specializations exist (both in left hemisphere; both in right hemisphere; and right language/left-visual), but in smaller proportions, for an unknown reason (see Flöel et al., 2005).

Zago et al. (2016) showed that the *degree* of rightward lateralization for a visual task corresponded to performance on the line bisection task, with right- and left-handers both showing the well-known "pseudoneglect effect" (i.e., left-biased failures), and persons who were more-lateralized performed better overall. However, the degree of laterality in one domain was correlated to the degree of laterality in the other *only* in strong left-handers. In other words, as visual processing shifted more to the right, language processing shifted more to the left, but only for participants with EHI scores below −55. Thus, we argue that these data support our proposal that different hand preference groups (left-handers and right-handers, or weak- and strong-handers) may simply have different systems governing colaterality.

Somers et al. (2015) conducted a cued word generation fTCD study on 310 participants (166 left-handers) divided into five hand preference groups—strong right-handers, right-handers, mixed-handers, left-handers, and strong left-handers—based on EHI scores. Although their data support the idea that nondirectional *variability* in hemispheric specialization for language increases as left-handedness does, they did not find a mirror relationship with regard to direction. We contend that their results raise the possibility of multiple systems (i.e., modeling one system for left-handers and another for right-handers). Following this general schematic, others have argued similar thoughts against the handedness-as-a-proxy concept (Allendorfer et al., 2016; Corballis and Häberling, 2017; Häberling et al., 2016).

Arguing in support of the causal model for hemispheric colaterality, Badzakova-Trajkov et al. (2010) conducted an fMRI study on 155 participants enriched in both left-handers ($n=48$) and monozygotic twin pairs ($n=94$). Using covert word generation, a line bisection task, and a task involving recognizing repeated face stimuli, the team sought to assess colaterality, in much the same manner as the BIL&GIN studies. As with the early studies, despite the use of a relatively balanced sample, overall leftward asymmetry was found for the language task, with overall rightward asymmetry for both the landmark and the faces tasks (i.e., left-handers did not show mirrored patterns of functional laterality). In terms of degrees of laterality, language lateralization was higher in right-handers, with a significant effect of gender (males more lateralized; no effect for twins). For the faces task, right-handers were also more lateralized, but no significant differences were found in lateralization between hand preference groups for the landmark task. In a subsequent paper (Badzakova-Trajkov et al., 2016), the team reviews genetic, developmental, and neuroimaging studies on human lateralization and, in reversal of their earlier (2010) views, they largely favor the statistical independence hypothesis (that laterality in one domain is independent of laterality in another). Perhaps based on their earlier findings, however, they at least acknowledge that the true scenario is likely a mix of both causal and statistical factors; on this they state: "…causality [indicated by language and visuospatial tasks co-lateralizing to opposite hemispheres] is most likely in individuals lacking the innate disposition to asymmetry… paradoxically, then, causality may be restricted precisely to those lacking innate predispositions" (Badzakova-Trajkov et al., 2016, p. 391). This view is compatible with our suggestion that multiple systems could be governing colaterality, although teasing these systems apart would be difficult, if not impossible, using the approaches outlined earlier. We think the "different systems" concept should be the target of future investigations.

To the best of our knowledge, only a few studies have been conducted directly comparing survey-based hand preference classifications with actual performance measures of hand preference (Brown et al., 2004, 2006; Bryden et al., 2011; Corey et al., 2001; Gonzalez et al., 2007). In contrast to these previous approaches, Gonzalez and Goodale (2009) assessed correspondence between the EHI and hand-performance using more naturalistic tasks—a puzzle task and LEGO-building—in 20 subjects. They filmed subjects' hand movements and created laterality indices (LIs) for how often subjects used each hand, and compared these data to EHI scores. They showed high correspondence between the LEGO and puzzle tasks for all subjects, but these data did *not* match well with the EHI scores, especially for left-handers. Although all 10 left-handers in the sample were classed as strongly left-handed by the EHI, at least half of them used their right hand more frequently than their left in the behavioral task (Gonzalez et al., 2007, p. 277). In a later study probing language laterality with a dichotic listening task, the authors assessed correlations between the EHI scores, grip strength (GS), FT, and the LEGO task in 36 subjects (Gonzalez and Goodale, 2009). They found that the LEGO task measures were the only ones significantly correlated with the dichotic listening task. Although there was significant correspondence between the EHI, GS scores, and FT scores, these measures did not correlate with language laterality. The authors suggest that, in their sample, "there is something about visuomotor control and handedness that does not map onto other measures of laterality in motor control" such as the EHI and more common behavioral tasks (Gonzalez and Goodale, 2009, p. 3187). These studies provide initial evidence that left-handers are not left-handed in the way that right-handers are right-handed in their manual motor behaviors. An important distinction follows from this fact, in that perhaps we should not expect left-handers to be lateralized in their hemispheric activation patterns in the way that right-handers are, and thus, that task-based laterality systems for right-handers and left-handers may need to be considered more thoroughly.

The concept of colaterality is a basic hypothesis that the lateralization of one modality has an effect on the lateralization of another. However, many published studies suffer from various methodological flaws, with the most salient being the use of the EHI as a sole hand preference metric, but they also fail to allow for different forms of colaterality to exist in left-handers and right-handers (i.e., they do not acknowledge that left-handers, and even mixed-handers, should not be modeled as atypical right-handers, but instead should be assessed in their own right). As for *how* or *why* different hand preference groups would have different systems governing language (and visuospatial laterality), there are many possible explanations already present in the evolutionary anthropology and paleoarcheology literature (we will briefly speculate on this in our conclusions). Next we discuss very recent works on hand preference modulation of visual perception, and then briefly relate this to potential applications for studying language.

3.2 CONTEXTUALIZING COLATERALITY: ADDITIONAL EVIDENCE

Marzoli et al. (2014) argued that perception–action studies on the relationship between leftward visual biases and right-hand preferences are largely unacknowledged in the laterality literature, and thus, that there are many opportunities for future collaborative studies. These authors note that the early onset of left-biased visual attention to faces and bodies—of which there is much solid evidence (Nagel et al., 2013), and which may stem from both genetic and environmental factors (Cochet, 2016)—may be related to right-hand predominance in human populations. Important here is that preferential attention to the left visual field in dyadic social interactions equates to biased attention to the actions of the right hand (Verfaellie and Heilman, 1990), which could then lead to social modulation of one's *own* manual motor biases toward the right hand (although modeling causality in such a system would be quite fruitless, particularly in archeological contexts as described earlier, as it is much more likely for the two to be interacting dynamically and continuously). In general, the perception–action literature suggests that early visual perception biases can potentially modulate and enable the development of action asymmetries toward the right hand later in life, although this link needs to be confirmed with longitudinal developmental studies (Buckingham and Carey, 2015), and that hand preference plays a key role in modulating visual attention. Several researchers have found that hand location directly impacts spatial attention and reasoning, and vice versa, such that visual attention biases might determine our patterns of space use for grasping. Generally, there is a complex and reinforcing behavioral relationship between the two behaviors (Abrams and Weidler, 2014; Adam et al., 2012; Cai et al., 2013; Colman et al., 2017; Craddock and Lawson, 2009; de Bruin et al., 2014; Gingras and Braun, 2017; Lawson et al., 2016; Reed et al., 2006, 2010; Stone and Gonzalez, 2014; Thomas, 2015; Uomini and Lawson, 2017). The concept is nicely summed up by the following statement: "the origin of the rightward hemispheric dominance for spatial attention may have a manipulospatial origin, neither perceptual nor motor *per se*, but rather reflecting a mechanism by which a spatial context is mapped onto the perceptual and motor activities, including the exploration of the spatial environment with eyes and hands" (Petit et al., 2015, p. 1151).

The research on praxis and visuospatial asymmetries inherently adopts an affordance-based view of perception–action, and as we have argued elsewhere, embodiment is the only view of cognition which is compatible with evolutionary theory (Ruck, 2014a, b), and so many of the aspects of the perceptuo-motor research can be easily incorporated into evolutionary discourse. The main concept underpinning the colaterality hypothesis is that the areal and asymmetrical similarities for different modalities—despite being complex and difficult to characterize—are likely not independent of each other, because hand preference, visuospatial skills, and language all interact "online" in the real world every day. In order to tie this finding back to hand preference, and to provide further support for seriously considering multiple systems of colateralization, we close with an fMRI study on functional asymmetry. Gotts et al. (2013) used a short resting-state fMRI paradigm to probe intrinsic levels of intra- and interhemispheric connectivity for the right and left brain hemispheres in 62 right-handed participants. They have several ideas which we adopt here in our own conclusion, although their timescale is more developmental, whereas ours considers evolutionary perspectives. Their conclusions are:

1. The left hemisphere shows greater preference for within-hemisphere interactions; this is likely a consequence of white-matter asymmetries present before birth, as measured near birth (Perani et al., 2011), but it is also undoubtedly related to strong right-handed bias and language functions.
2. The right hemisphere, in contrast, has interactions that are strongly bilateral; this both stems from, and underpins, the bilateral nature of visual perception, and the lack of mirror asymmetry between language and visuospatial networks.
3. The findings of improved cognitive performance in more lateralized participants are consistent with the computational efficiency model for hemispheric specialization.
4. In spite of high individual variability in patterns of connectivity, caused both by developmental considerations and plasticity, an overall pattern of lateralization for cognitive tasks can be found in salient task-positive networks, even using resting state data; this has implications for future comparative work.

4 DISCUSSION

Following each of these points, we will conclude by outlining a basic hypothesis for the evolution of human-specific laterality biases, and set a framework for future works which might help further elucidate colaterality. Based on all that we have discussed in this chapter, we hypothesize a model for the evolution of uniquely human lateral biases:

1. Hemispheric specialization has deep roots in vertebrate taxa, and based on existing primate research, it is plausible that early hominin ancestors inherited systems of preexisting lateral biases for vision, praxis, and communication; these systems became elaborated over time in the hominin lineage.
2. Hemispheric specializations have multifactored genetic underpinnings, but downstream effects of developmental biases and epigenetics may have even stronger effects than genetic factors in driving *directional biases*, and multiple systems may be operating in left- and right-handers today (Schmitz et al., 2017; Vallortigara and Rogers, 2005).
3. One especially critical factor in driving the *typical* directional shifts may be the increasing complexity of manual motor actions, including visually guided bimanual coordinative ones, such as tool-use and tool-making, in hominins (as proposed by Bradshaw and Nettleton, 1982; Uomini, 2009b, c; Tabiowo and Forrester, 2013). On this:

   - **a.** It seems that preexisting visual biases, underpinned by differential hemispheric integration/segregation systems, would have more easily enabled right-hand precision and left-hand support roles, at least on an individual level.
   - **b.** These individual hand preferences (which were, again, being increasingly driven to the right, simply via interactions between preexisting asymmetries and higher task complexity) *then* coupled with increased reliance on social learning in hominins (Högberg et al., 2015; Morgan et al., 2015; Uomini and Lawson, 2017), which (via developmental routes) drove populations' hand preferences even more rightward.
   - **c.** Once a right-handed majority was established, a frequency-dependent selection of the left-handed minority was reinforced and maintained by selective advantages linked to close combat and/or interactive contests (Faurie and Raymond, 2005, 2013; Loffing and Hagemann, 2012), which we can speculate occurred as hominin groups encountered each other in competitive territorial situations.

4. As brain size increased, these once-modest patterns of asymmetry grew exponentially in their complexity (as there is a nonlinear relationship between brain size increases and anatomical–functional changes in the brain, Herculano-Houzel, 2009).

Of course, each of these steps would not have proceeded linearly, but instead in a much more nuanced way, feeding backward and forward in a dynamic fashion. As this is just a speculative sketch, many relevant factors are missing in the earlier outline; most notably is the absence of an explanation for atypical laterality patterns, which is not isomorphic with, but is no doubt related to, the persistence of left-handers. However, until more comprehensive work is conducted to pin down the forms and nature of colaterality, our proposed outline remains an open possibility.

In conclusion, multiple incredibly rich lines of evidence suggest that hand preference, visuospatial skills, and language should be related to each other, but there are more open questions than answers. Much more pragmatic work needs to be conducted on even the most fundamental aspects of colaterality, including a more careful consideration of experimental methods. On this, we recommend to focus on a few easy targets. First is to further probe the efficacy of the EHI in characterizing actual manual behaviors, including communicative gestures, developmental trajectories for the formation of hand biases (see Fagard, 2013), and to continue testing right- and left-handers. Second is to cleverly use the data from current large-sample studies—which unfortunately have the EHI (and other simple hand preference metrics) as their only hand preference measures—because even with their hand preference measure potentially confounded by the EHI, they *can* provide higher frequencies of atypically lateralized persons for language and visuospatial skills, as well as cognitive performance data, and other measures. Additional data from studies like Cai et al. (2013), Pool et al. (2014), and Gotts et al. (2013) can be mined to further probe the disparities regarding colaterality without needing to collect new data. Finally, dependent on replication results for the aforementioned studies—and, of course, continued discoveries from comparative, genetic, and developmental research—we can add hand preferences back into the picture, using more rich, dynamic, and naturalistic tasks, should it seem necessary down the line to do so. As Rogers (2014, p. 566) noted: "it is timely for a more integrated approach to the study of lateralization"; we think these are the best steps forward towards this goal.

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