Chapter Six

A comparative multimodal perspective on the evolutionary origins of tool use and handedness

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Abstract

Laterality and the evolution of handedness have been of significant scholarly investigation across a wide variety of disciplines, including animal behaviour, neurobiology, developmental psychology, archaeology, and language evolution. Despite the longstanding array of attention, there remains no clear consensus on how and why laterality, and by extension handedness, evolved. Here I review comparative research on handedness in nonhuman primates to draw attention to the leading theories in the evolution of laterality as they relate to tool use and language origins. In doing so, I aim to provide an overview of our current understanding of the factors influencing handedness and the potential insight further study of nonhuman primates, particularly wild great apes, could contribute to ongoing discussions. Moreover, drawing on recent studies in both human knapping and chimpanzee stone tool use behaviour, I advocate for a multimodal approach to investigations of handedness, one where sound is integrated into existing paradigms examining laterality in tool use behaviour. Such a perspective has the potential to reveal novel insights into the auditory information that may have aided our hominin ancestors at the advent of their lithic technical revolution.

INTRODUCTION

Contemporary human populations exhibit a population-level right-handed bias for manual actions. Although there is some variability across cultures and the type of action (for excellent recent reviews see McManus 2019; Prieur et al. 2019), the overwhelming predominance of right-handedness among humans remains a complex and multifaceted trait with significant implications for the evolution of brain lateralization, particularly with regards to left hemispheric specialization for language (Stout et al. 2008). Both the language production and perception centers of the brain are predominantly found in the left hemisphere of the human

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brain although, again, there is variability (Fitch and Braccini 2013; McManus 2019; Prieur et al. 2019; Stout and Chaminade 2012). Since brain imaging techniques, including recent scanning advancements, are considerably more invasive than observations of hand-use, handedness remains one of the principal means by which researchers can have easy access to investigations of laterality. It is therefore unsurprising that much of the handedness research on nonhumans has been in mice where invasive brain imaging techniques are often applied (McManus 2019; Warren 1980). However, there similarly exists a large body of literature on handedness in nonhuman primates, albeit invasive techniques are more difficult to apply to primates due to increased ethical concerns, particularly with regards to wild populations.

The cumulative research on laterality and handedness suggests that genetic, environmental, as well as social and cultural influences likely contribute to the development and persistence of right-handedness among humans (McManus 2019). However, there is still a lack of clear consensus on the relative importance of these factors and exactly how they might interact with one another (McManus 2019; Prieur et al. 2019). Therefore, a comparative approach permits the investigation of the evolutionary selection pressures that may have helped shape laterality and population-level handedness. More specifically, ancestral and living hominids can provide insight into the original contexts and benefits associated with population-level handedness and how this came to be so tightly linked with hemispheric laterality (Cashmore, Uomini, and Chapelain 2008). However, as noted by previous scholars, comparisons across and within species are often hindered by inconsistent application of methods and terminology (e.g., Cashmore, Uomini, and Chapelain 2008; McGrew and Marchant 1997).

In the present chapter, I aim to provide a brief overview of comparative research on handedness of nonhuman primates, with a central focus on great apes, and how they fare in comparison to contemporary humans. In doing so my intention is twofold: 1) highlight the gaps in our knowledge with regards to the evolution of population-level handedness, and 2) present opportunities for future research directions by proposing an integrated multimodal framework for investigating handedness (and by extension laterality) in the tool-use behaviour of humans and nonhumans alike. Importantly, the term laterality can refer to the dominance of one side of the body or brain but in the current chapter, I am primarily concerned with motor lateralization and refer to brain lateralization explicitly in the text where relevant. With regards to motor lateralization, I clearly differentiate whether I am referring to individual-level or population-level laterality in hand use (i.e., handedness). I also use the term hand preference to specify intra-individual hand-use patterns which is altogether quite different from a population-level bias (Cashmore, Uomini, and Chapelain 2008; McGrew and Marchant 1992). Population-level handedness is where the same hand preference is consistently observed across individuals within a specified population or group.

THE EVOLUTION OF HANDEDNESS

Many primatologists have been captivated with the concept of population-level handedness given the obvious insights it might provide regarding the evolution of universal right-handedness amongst humans (Cashmore, Uomini, and Chapelain 2008; Fitch and Braccini 2013; Hopkins 1996). McGrew and Marchant (1997) provided a thorough review of primate laterality studies on both strepsirrhines and haplorrhines which clearly demonstrated that the majority of studies available at that time suffered from methodological and/or statistical constraints, thereby prohibiting robust species-wide inferences. In the studies they were able to assess, McGrew and Marchant (1997) overwhelmingly found little evidence for population-level lateralization in nonhuman primates although chimpanzees showed some tendency for a right-handed population-level bias in captivity. The lack of standardized methods and analyses, as well as the fact that the majority of handedness research involved captive populations, clearly contributed to the inconsistent and variable findings of laterality and handedness. A more recent review by Fitch and Braccini (2013) on the evolution of handedness, still echoes the early concerns highlighted by McGrew and Marchant (1997) regarding small sample sizes and weak statistical effects, to conclude that there is only tenuous evidence for laterality and handedness in nonhuman primates. Therefore, handedness continues to draw great research interest due to the often contradictory and inconsistent results of previous studies (Fitch and Braccini 2013).

One of the leading hypotheses for the evolution of motor lateralization is the "postural origins" hypothesis whereby the right hand is postulated to have been the dominant grasping hand during locomotory and positional behaviours of an ancestral arboreal primate. With increasing terrestriality in the evolution of primates, the right hand would have been subsequently co-opted as the flexible gripping hand, where bimanual actions and object manipulation would have become more frequent (MacNeilage, Studdert-Kennedy, and Lindblom 1987). The hypothesis might then predict that left-handed bias is the ancestral condition (more likely to be found in the basal strepsirrhines) and right-handed bias the derived condition yet recent studies, including phylogenetic comparisons of a large number of primate species, do not support this (Caspar et al. 2021). However, a recent cross-species comparison did find that primarily arboreal primate species tend to have a left-hand population-level bias whilst species that are primarily terrestrial (i.e., the African apes, baboons, macaques, as well as humans) tend to have a right-hand population-level bias, therefore, a species' ecology was important to consider (Meguerditchian, Vauclair, and Hopkins 2013). Overall then, terrestriality is likely to have played a significant role in the evolution of right-handed population bias in primates.

Relevant to discussions on the adaptive utility of laterality is the 'task complexity' hypothesis originally developed by Fagot and Vauclair

(1991). The authors distinguished between low and high-level tasks whereby the latter were more cognitively taxing and involving precise and/or novel movements and are therefore more likely to be associated with hand preferences and ultimately, population-level handedness (Fagot and Vauclair 1991; but see McGrew and Marchant 1997 for reasons why the novel aspect can be difficult to operationalize). In contrast, low-level tasks were considered to be more routine, familiar tasks (e.g., reaching for food). Task complexity explained some, but not all, of the variation in results across the primate studies reviewed by McGrew and Marchant (1997). More recently, however, task complexity has gained support in a number of primate studies comparing unimanual versus bimanual actions, where only the latter demonstrates consistent lateralization in hand-use (reviewed in Meguerditchian, Vauclair, and Hopkins 2013).

Additional theories for the evolution of laterality and handedness stress the significance of social interaction in shaping patterns of hand-use (Ghirlanda, Frasnelli, and Vallortigara 2009), and the evolution of bipedalism (Westergaard, Kuhn, and Suomi 1998) or tool use (Stout and Chaminade 2012). In particular, theories involving tool use integrate aspects central to the postural (e.g., freeing up the hands) and task complexity hypotheses (e.g., complex object manipulation) for the emergence and adaptive significance of handedness. I will therefore primarily focus on tool-use-related studies for the remainder of this chapter.

POPULATION-LEVEL HANDEDNESS IN CAPTIVE NONHUMAN PRIMATES

Since McGrew and Marchant's (1997) formidable review, research on nonhuman handedness has attempted to address many of the concerns plaguing the earlier studies they examined by using larger sample sizes, variable types of tasks, studies done on wild populations (see next section), and by applying more stringent and comparable methods for analyses of data. For example, using a large sample size of chimpanzees, Hopkins and colleagues have consistently found that captive chimpanzees show a population-level right-hand bias for unimanual (e.g., reaching for food) and bimanual coordination tasks (e.g., tool use or solving the 'tube task' described below), as well as for communicative, manual gestures (Hopkins, Mareno, and Schapiro 2019; Hopkins, Russell, Freeman, et al. 2005; Hopkins, Russell, Hook, et al. 2005). However, many studies fail to find population-level biases in ape hand-use, including chimpanzees, even when employing similar methods (Brand et al. 2017; Lambert 2012; Motes-Rodrigo, Hernandez-Aguilar, and Laska 2019; Prieur et al. 2018)

The significance of the corpus of captive research on primate handedness lies in its rich set of cross-species experiments whereby a standardized set of tasks and methods permits robust inferences. For example, a comparison of 777 captive great apes, including gorillas, bonobos, chimpanzees and orangutans found population-level right-hand bias in all apes for a bimanual coordinated task, excluding the orangutan (Hopkins et al. 2011). Instead, orangutans showed a left-hand population bias, consistent with at least one previous study (Brésard and Bresson 1983) but not a more recent study where a population-level bias in orangutans was not found (O'Malley and McGrew 2006). The strength of these captive experiments, however, is in testing the nonhuman primates with the same 'tube task', facilitating cross-species comparisons. Originally designed by Hopkins (1995) as a bimanual coordinated task, a tube containing food is provided where one hand grasps or stabilizes the tube while the other extracts the food item, hence necessitating the use of both hands. Longitudinal studies of captive populations are also noteworthy for demonstrating some degree of heritability of handedness in chimpanzees, as well as performance asymmetries, whereby right-handed individuals were more efficient in solving a tool-use task with their right hand than their left (Hopkins, Mareno, and Schapiro 2019). Handedness heritability in primates has also been suggested for the unimanual reaching actions of a troop of captive Japanese macaques that showed a left-handed population bias (Kubota 1990). However, these studies are generally limited in sample size compared to the strong evidence for heritability in human handedness (McManus 2019; Warren 1980).

The majority of captive studies on ape handedness have been overwhelmingly focused on bimanual coordination and tool use tasks and did not consider the potential role or influence of communication on hand preference. More recently, however, researchers have investigated laterality for both communicative and non-communicative actions. For example, investigations of handedness for communicative gestures have shown a population-level right-hand bias in baboons, gorillas, chimpanzees and bonobos (reviewed in Meguerditchian, Vauclair, and Hopkins 2013). Other studies report right-hand population-level bias for gestures involving tool use only (Prieur et al. 2018) and another study investigating the gestural repertoire of wild chimpanzees found no population-level bias but an individual-level right-hand bias for gestures involving object manipulation (Hobaiter and Byrne 2013). Therefore, the inclusion of an object into the communicative action may be a significant factor in driving lateralization.

Recent studies analyzing gestural laterality in-depth have provided further insight into mediating factors, such as features of the target of the actions being done. More specifically, whether actions are directed at an inanimate (e.g., an object), rather than an animate target (e.g., a conspecific or human), has been shown to influence hand preference. For example, one study found that young children demonstrate a right-hand bias only towards actions directed at inanimate rather than animate targets (Forrester et al. 2013). It is argued by Forrester and colleagues (2013) that this is in line with what is reported for tool-use tasks in wild chimpanzees where a right-hand population-level bias has been shown for some tool-use tasks (but see next section). However, animate targets are likely to be highly relevant for communicative gestures, where a right-hand population bias has been observed in multiple species. Therefore, this target distinction cannot account for all the variation we observe in primate handedness, particularly if we include human infants and toddlers who have also shown a right-hand population-level bias for gestures in other studies (Cochet and Vauclair 2010). Additionally, for communicative gestures, whether the conspecific is in the left or right visual field of the signaller can further influence hand preference (Prieur et al. 2017). Overall then, despite the decades of research on primate handedness, we still lack a consensus regarding if, and to what degree, species exhibit population-level handedness, and if yes, how specialized this is for a particular task or type of action, whether communicative or not.

Generally speaking, captive studies are powerful due to their clear experimental design and standardized tasks, but they also lack natural socio-ecological contexts to provide insight into the evolutionary drivers of handedness (McGrew and Marchant 1997). These studies have been further criticized for the influence of captive rearing environments and the effects of learning (McGrew and Marchant 1997; Palmer 2003; Warren 1980; see also Hopkins and Cantalupo 2005). However, these latter concerns seem generally unfounded given that nonhuman primates in the wild have also exhibited population-level biases suggesting handedness is not unique to captive settings. For example, some studies on wild chimpanzees report population-level right-handedness for certain tool-use tasks similar to captive studies (e.g., Lonsdorf and Hopkins 2005) although there is considerable variability in these findings (see next section). It is therefore prudent to find parsimony between captive and wild studies with regards to handedness when possible.

A WILD PERSPECTIVE ON HANDEDNESS: WHY IT MATTERS

While research on captive primates provides much-needed experimental control, research in the field gives us the behavioural contexts in which primates naturally exhibit handedness and have evolved to do so. Of particular relevance here, are the variety of tool-use behaviours wild primates show in foraging but also socio-communicative contexts. Much of the tool-use repertoire of wild primates has been shown to be socially influenced, and even cultural (Sanz, Call, and Boesch 2013), therefore there are stark ontogenetic differences in behaviours that are part and parcel of a species evolved repertoire in comparison to artificial tasks that they might be trained to do in captivity. We know for humans how developmental and environmental factors can be critical to establishing population-level handedness, including social and cultural influences, even from a young age (McManus 2019). Hence, data on wild primate populations provides a critical and necessary perspective for our understanding of the origins and development of population-level handedness within the Primate order. It is also worth noting that the majority of handedness studies in wild nonhuman primates are on chimpanzees; therefore, much of the rest of this chapter focusses on chimpanzees.

Some of the first studies on laterality in wild primates were conducted via behavioural observations of wild chimpanzees using tools. Here we find an often convoluted stream of research findings where for the same population of wild chimpanzees early studies may have failed to find population-level handedness but later studies, with the inclusion of more behaviours and/or more individuals, would confirm population-level handedness (e.g., the chimpanzee nut cracking studies described below). Importantly, hand preference, whereby individuals demonstrate the consistent use of either the left or right hand for a task, has been consistently observed in chimpanzees in both captive and wild contexts from even the earliest investigations of handedness (e.g., Finch 1941; Boesch 1991). However, individuals may differ in their preferred hand across tasks, and most importantly, results for population-level handedness have been inconsistent as described in the following section.

The Bossou chimpanzees of Guinea and the Mahale chimpanzees of Tanzania have arguably provided the most in-depth studies in wild chimpanzee handedness, given the number of behaviours investigated and the longitudinal nature of their datasets. Other populations, such as Taï, Gombe and Goualougo, have also contributed significant works on handedness in wild chimpanzees, especially for tool use behaviours. Overall, these studies provide mixed results. With regards to nut-cracking behaviour, whereby chimpanzees use wooden or stone tools to crack open various species of nuts in the wild (Boesch and Boesch 1981), we have inconsistent findings on handedness. Studies on the Bossou chimpanzees where they crack open nuts with not only hammer tools but also employ moveable anvils have found individual-level hand preferences for holding the hammer but no significant population-level bias for the left or right hand (Humle and Matsuzawa 2009; Sugiyama et al. 1993). Similarly, there was no population-level hand bias found for nut cracking in the Taï chimpanzees of Côte d'Ivoire (Fig. 1) (Boesch 1991). However, a later study conducted by Lonsdorf and Hopkins (2005) where nut-cracking data was pooled from two populations (Taï: Boesch 1991; Bossou: Biro et al. 2003) found support for a population-level right-hand bias, implying that a larger sample size of individuals was necessary for detecting a population-level bias. However, it is then debatable to what degree combining two distinct chimpanzee communities represents a naturally occurring population-level phenomenon. Notably, this study also found evidence for heritability in hand preferences when examining mother-offspring hand use (Lonsdorf and Hopkins 2005).

Besides nut cracking, termite fishing is perhaps the best-studied tool use behaviour in wild chimpanzees. Termite fishing is a behaviour that exhibits clear cultural variation among different populations but can be generally described as chimpanzees using herbaceous vegetation or stick tools by inserting them into termite nests to collect the insects for eating (Boesch et al. 2020). Lonsdorf and Hopkins (2005) reported a left-

Fig. 1.
An adult female Taï chimpanzee nut cracking with a stone hammer as her daughter watches. Credit: Liran Samuni/ Taï Chimpanzee Project.

handed population bias for termite fishing in the Gombe chimpanzees, for which McGrew and Marchant (1992) had also documented a trend toward a left-hand bias at the population-level. Similarly, the Fongoli chimpanzees of Senegal show a trend toward population-level left handedness for termite fishing (Bogart et al. 2012). However, the Goualougo chimpanzees of Central Africa do not show a clear population-level hand bias despite strong hand preferences at the individual level, as well as documented performance asymmetries. For example, chimpanzees with a right-hand preference had a faster stick tool insertion time than those with a left-hand preference (Sanz, Morgan, and Hopkins 2016). McGrew and Marchant (1999) also reported that lateralized individuals were more efficient at gathering termites compared to individuals that did not show a clear hand preference.

A number of other chimpanzee tool use behaviours have also been investigated with regards to handedness. Bossou chimpanzees have shown population-level right-hand bias for an extractive foraging behaviour called ant dipping where herbaceous stalks or sticks are used as tools to collect army ants for eating (Humle and Matsuzawa 2009). No significant population-level bias was found for other tool use behaviours, namely algae scooping and pestle pounding (Humle and Matsuzawa 2009). There was also no population-level hand bias found for aimed throwing (of various naturally occurring objects) using a long-term dataset of the Mahale chimpanzees despite some clear hand preferences at the individual level (Nishida, McGrew, and Marchant 2012). The Taï chimpanzees had clear individual-level hand preferences for wadge dipping, where individuals use one hand to repeatedly dip chewed-up wadges of a particular fruit into water, but again showed no population-level hand bias (Boesch 1991). Combined, these studies provide mixed support for the task complexity hypothesis given that nut cracking is arguably considered the most complex behaviour and clearly involves bimanual coordinated actions of all the tool use behaviours investigated in the wild.

Research on the handedness of wild monkey species is relatively rare, despite baboons and macaques being highly terrestrial and generally easy to observe and identify. One notable study by Leca and colleagues (2010) on the stone handling behaviour of free-ranging Japanese macaques compared unimanual and bimanual actions during stone manipulation and found lateralization for the more complex bimanual actions only (note no population-level handedness was found when looking across multiple tasks). These results lend additional support to the task complexity hypothesis although additional studies of other wild populations are desperately needed. Handedness research in the wild may be complicated by observational conditions but also the lack of individuals engaging with the exact same behaviour frequently enough to calculate robust handedness indices within a population, let alone across. Still, this is where a complementary perspective, combining both captive and field work, can be fruitful for constructing larger frameworks in which to investigate the evolution of handedness.

TOOL USE, LANGUAGE & LATERALITY COME HAND IN HAND

Functionally, it has been suggested that laterality likely conveyed an evolutionary benefit whereby hemispheric specialization via co-evolution mechanisms for tool use and language, facilitated by handedness and performance asymmetries, would permit faster and more efficient cognitive processing (Hopkins, Mareno, and Schapiro 2019; Prieur et al. 2019; Stout et al. 2008). Such an evolutionary pathway would have become particularly important for tasks involving complex bimanual actions and enhanced dexterity, especially for a bipedal primate (MacNeilage, Studdert-Kennedy, and Lindblom 1987; Meguerditchian, Vauclair, and Hopkins 2013; Prieur et al. 2019; Westergaard, Kuhn, and Suomi 1998). Tool use and tool manufacture (the latter for hominins only) have therefore been of significant focus when it comes to theories of the evolution of handedness (Gabrić, Banda, and Karavanić 2018; Stout and Chaminade 2012). Generally speaking, current theories for how laterality and handedness may have evolved in our species coincide on themes of a tool-using biped whose social and ecological environment would have favoured intentional communication with conspecifics. The strongest evidence for this evolutionary scenario comes from neuroanatomical studies which show similar brain asymmetries for hand motor tasks (e.g., tool use) and communicative actions, such as gestures (for detailed reviews see Hopkins, Mareno, and Schapiro 2019; McManus 2019; Prieur et al. 2019; Stout and Chaminade 2012). Such an evolutionary scenario therefore links the emergence of left hemispheric specialization in the primate lineage with the emergence of bipedalism and tool use, as primers for language to evolve by co-opting the pre-existing neuro-architecture of a left hemisphere specialization. Details and the order of emergence are still up for debate, but many (though definitely not all) scholars can agree that these traits appear to be highly interconnected and linked in their neurobiological origins and development.

Unlike tool use and bipedalism, language does not leave behind archaeological evidence that can be examined and dated to reconstruct evolutionary histories. It is therefore not a coincidence that the origins of language have perplexed scholars for centuries, and continue to do so (Corballis 2017; Fitch 2010). The search for the origins of language among nonhuman primates has generally favoured a gestural origin given that gestures, particularly well studied in the great apes, have consistently demonstrated clear communicative intent, greater control, increased flexibility and innovation relative to a limited vocal repertoire (Arbib, Liebal, and Pika 2008; Call and Tomasello 2007; Christiansen and Kirby 2003; Fröhlich et al. 2019; Liebal et al. 2013; Pika et al. 2005). Yet others would argue that the framework used to evaluate gestures has typically not been applied to vocalizations therefore the bias towards gestures is partly a result of methodological discrepancies (Townsend et al. 2017; but see also Fischer 2017). However, the gestural theory for language origins also has strong support from disciplines other than primatology, namely neuroscience. The discovery of mirror neurons in the F5 brain region of monkeys, a homologue of Broca's area, one of the critical language centers in the human brain, has lent strong support for gestural motor theories of language origins (Rizzolatti and Arbib 1998). As mentioned previously, this research supports that the neurobiological substrates responsible for motor coordination were co-opted for the evolution of language within the primate lineage (Arbib, Liebal, and Pika 2008; Corballis 2003; Kohler et al. 2002; Rizzolatti and Arbib 1998). Importantly, mirror neurons are activated not just when an individual performs an action, but also when watching others perform that action (Arbib 2005; Kohler et al. 2002). This suggests mirror neurons may facilitate social learning mechanisms such as imitation, a cognitive skill argued to be necessary for developing uniquely human traits such as language (Arbib 2005; Corballis 2017) and cumulative culture (Henrich and Tennie 2017). Importantly, the gestural theory of language evolution has some overlapping neurobiological support with the technological or tool-use hypothesis for language evolution, although slight differences are also recognized (for a detailed review see Stout and Chaminade 2012).

More recently, a multimodal origin for language evolution has become increasingly supported in the literature, again primarily via detailed studies of great ape communication, given that auditory, orofacial and gestural signals are often combined with one another by both humans and nonhuman primates (Arbib, Liebal, and Pika 2008; Fröhlich et al. 2019; Liebal et al. 2013; Taglialatela et al. 2015). Studies on multimodal communication, particularly in chimpanzees, have revealed significant associations with both motor coordination and sound processing. For example, a study on captive chimpanzees found that individuals who combined vocalizations and orofacial movements to produce attention-getting sounds had a higher deposition of gray matter in brain regions associated with motor control, compared to individuals that did not produce these signals (Bianchi et al. 2016). Similarly, other researchers have proposed that oropharyngeal motor coordination, such as lip-smacking in primates, creates rhythmic sound utterances that may have provided the ancestral basis for human speech (Bergman 2013; Ghazanfar and Takahashi 2014). These slight movements of the mouth, tongue and larynx are thereby argued to have facilitated the transition in language evolution from a primarily gestural mode to the acoustic channel (Corballis 2017). Despite the clear relevance to theories of language evolution, multimodal investigations of primate communication remain relatively understudied with researchers usually focussing on a single modality (Slocombe, Waller, and Liebal 2011).

Similarly understudied yet relevant to the multimodal origins of language evolution are the incidental sounds produced by manual actions that can potentially serve as sources of information to both producers and listeners. Previous scholars have remarked that incidental sounds, produced by chewing or locomotion (Larsson 2014; MacNeilage 1998), or by the manual acts of using tools (Larsson 2015), all rely on motor coordination and likely stimulate mirror neurons. Moreover, mirror neurons can be activated by simply hearing these incidental sounds alone (Kohler et al. 2002). In sum, there is some evidence to suggest that tool-use sounds which necessitate manual dexterity are linked to the neurobiological substrates of language perception and production in humans (Arbib 2005; Bianchi et al. 2016; Corballis 2003; Larsson 2015; Rizzolatti and Arbib 1998). However, other neurobiological studies do not show an overlap between motor control brain regions involved in object manipulation with language area homologs (Becker et al. 2022; Fitch and Braccini 2013). Nevertheless, the incidental sounds and the role of auditory (non-vocal) signals have generally not been factored into these studies and are usually ignored for their relevance to both tool use and communication. I suggest that these auditory signals need to be examined in greater detail, particularly for their ability to provide critical information not only to the tool user or producer, but also to any bystander or listener. In this sense, they may play a role in the learning and transmission of manual actions such as tool use or manufacture, and importantly, provide a pathway that intimately connects auditory channels of perception and processing with hand-eye motor coordination and left-hemispheric specialization, potentially significant for language origin theories.

THE (NEGLECTED) ROLE OF IMPACT SOUNDS

Auditory, non-vocal signals, have been of little interest to most primatologists concerned with communication other than recognizing that primates often produce displays whereby objects may be incorporated to some extent to produce sound. Lameira and colleagues (2012) describe an instrumental gesture-call in orangutans, as a call that can "modify oro-laryngeal acoustic production, with or without tools" which, while technically non-vocal is still produced by the animal. Similarly, chimpanzee buttress drumming (Arcadi, Robert, and Boesch 1998) or leaf clipping (Kalan and Boesch 2018), are sounds that are produced by the animals interacting with an object in their environment and are therefore also non-vocal. Although interesting behaviours for animal communication, in the present context I am particularly concerned with sounds produced by nonhuman primates as they interact with stone tools, given the obvious parallels and implications for hominin lithic technology and its evolution.

The sound produced when a stone makes contact with another object can be referred to as an impact sound. Impact sounds are significant in that their acoustic properties will be dependent upon, and characteristic of, both the material properties of the impactor and the object being impacted (Kalan et al. 2019). We are surrounded by impact sounds in our daily lives, from the musical instruments we hear or play to the mechanical noise of machines and vehicles. Although archaeologists have long remarked on the potential importance of impact sounds while making stone tools (i.e., flint knapping), the sounds themselves have rarely been featured in thorough investigations until recently. Researchers have suggested that the knapping sound may provide information regarding the accuracy of the strike or quality of the knapping material (cf. Patten 2009 in Smith et al. 2021). In a one-of-a-kind study, a controlled hammer machine was used to impact various lithic materials and demonstrated significant differences in sound duration, pitch and loudness (DeForest and Lyman 2022), suggesting ancient knappers would have been able to use impact sounds to assess lithic quality. Additionally, knapping sounds may offer information such as the size of the flake, or the level of expertise of the knapper (Smith et al. 2021). In their recent study, Smith and colleagues (2021) trained musicians to process the sounds produced by human flint-knappers and found significant differences in pitch and octaves produced due to raw material and knapper skill-level, but no differences in sound could be attributed to flake size (Smith et al. 2021). Of course, we cannot directly observe the ancestral hominins who first started to make and use stone tools and instead must rely on staged, experimental settings with contemporary humans. Here, a comparative approach can once again be of value given that a number of nonhuman primate species use stone tools naturally in the wild, including one of our closest living relatives, the chimpanzee (for knapping experiments done with nonhuman great apes see Motes-Rodrigo and Tennie chapter in this book).

Although chimpanzees do not make stone tools, they do use stone tools, for both cracking open nuts (Boesch and Boesch 1981) and for a unique communicative behaviour where they repeatedly throw stones at particular trees, referred to as accumulative stone throwing (AST) (Kühl et al. 2016). I recently investigated the impact sounds produced by AST, namely the sounds of stones hitting the trees being used as AST sites by the chimpanzees. I found that the tree species used for AST had a resonant timbre (i.e., a longer lasting, lower frequency sound), in comparison to other trees widely available but not used for this behaviour (Kalan et al. 2019). Were the chimpanzees drawn back to these particular AST trees just because they found the sounds they produced to be pleasant to the ear? Unfortunately, we do not know and this remains to be investigated. Similarly, this research has reignited my interest in the sounds produced by nut-cracking chimpanzees that I personally observed in the Taï forest of Côte d'Ivoire (Fig. 2). Are chimpanzees paying attention to nut-cracking impact sounds? If so, what kind of information are they extracting and potentially using? One way in which we might begin to address these questions is by incorporating the sounds produced during stone tool use into the robust frameworks of handedness and laterality research described in this chapter. Specifically, we can make predictions regarding the degree of laterality expected if sounds are produced. For example, we may predict that tool use behaviours that produce impact sounds may be more likely to activate a left hemispheric specialization (i.e., 'language areas of the brain', Stout and Chaminade 2012), and therefore present a greater likelihood to observe population-level right-handedness. Most importantly, such a prediction allows us to compare patterns in both humans and nonhuman primates using the same framework, given that instructions in the form of speech or gestures would not be necessary. Impact sounds themselves can be acoustically described via spectral and temporal properties of the sound signal (Kalan et al. 2019), and acoustic patterns can be characterized in relation to the fine-grained manual actions of the tool use behaviour. Sounds themselves could also be mod-

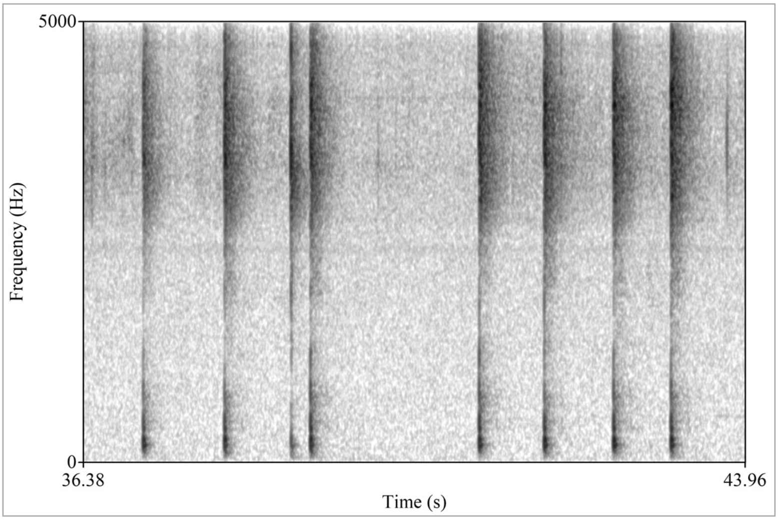

Fig. 2.
Spectrogram of the impact sounds produced by a nut cracking chimpanzee in the Taï forest of Côte d'Ivoire. The audio signal has been extracted from a remote camera trap (Bushnell Trophy Cam) video which has a sampling rate of 11kHz and 24 bits/s. Credit: MPI-EVA/PanAf/TCP.

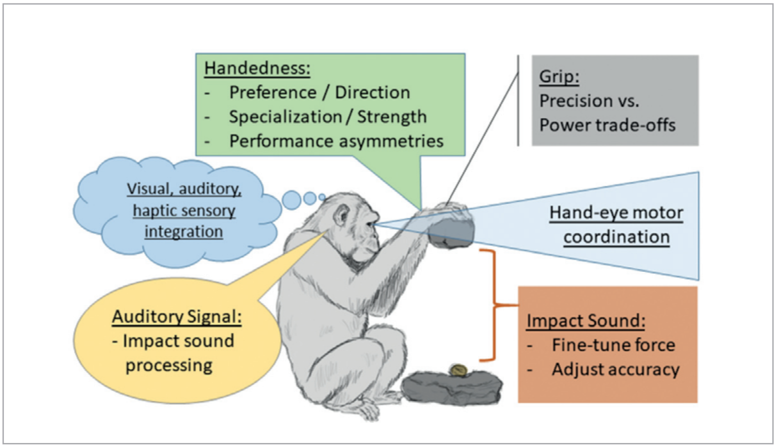

Fig. 3.
Diagram illustrating multisensory components relevant to tool use and the evolution of handedness, particularly the auditory information available via tool use impact sounds. Tool-use impact sounds are expected to be processed in the auditory cortex of the brain and integrated with visual and haptic sensory information, to subsequently guide variations in hand-use and specialization via adjustments in grip, force and accuracy for the task. Credit: chimpanzee drawing in the center by William B. Snyder.

ified or altered, either artificially or by introducing novel materials. Importantly, the auditory component of tool use should only be considered alongside the significant haptic and visual-motor sensory components of tool use. For example, analyses of grip type and grasping style, along with the fine-grained hand movements required to achieve a particular task, which are suggested to affect hand preference, specialization and handedness (Hopkins, Cantalupo, and Wesley 2002; Lambert 2012). For example, in humans, the dominant hand for right-handed individuals demonstrates greater grip strength (Incel et al. 2002; but see Bardo et al. 2021 for a recent review on the topic). Trade-offs between power and precision grips are significant for the evolution of hominin technology given their influence over the control of manual actions involved in processes like tool manufacture and tool use (Karakostis et al. 2018). Temporal integration of grip variation alongside sounds could therefore provide insight into potential mechanisms by which auditory signals mediate, or provide feedback, during processes such as knapping or other stone tool use behaviours in humans and nonhumans alike (Fig. 3).

CONCLUSION

Current research leaves us with mixed results and a lack of consensus on the origins of handedness, particularly given the growing number of intrinsic and extrinsic factors that appear to influence population- and individual-level handedness. Therefore, by adopting a broad, multimodal perspective we may gain new insights to help clarify the evolutionary relationships between manual dexterity for complex tasks, tool use, handedness and the emergence of language in humans. To achieve this, future comparative research will benefit from bridging the gap between communication research and tool use research when it comes to questions regarding handedness and hand-use. In particular, a focus on the common auditory component to both communication and tool use could provide a fruitful way forward. There is always the possibility that there is not much to be gained by listening to the impact sounds of tools (i.e., little to no information added beyond the visual and haptic senses). Yet given the ease with which observers of human knapping experiments, or observers of wild chimpanzee nut cracking, can attune their ears to the slight variations in the sounds produced when a stone strikes another object (Boesch and Boesch 1981), it is definitely an area of investigation that deserves more attention. Research on the evolution of handedness will further benefit from a greater focus on comparative studies conducted using natural observations and behaviours, especially for wild nonhuman primates, rather than relying primarily on captive experiments which currently dominate the literature on this topic.

REFERENCES

Arbib, M.A. 2005. From Monkey-like Action Recognition to Human Language: An Evolutionary Framework for Neurolinguistics. *The Behavioral and Brain Sciences* 28: 105–124; discussion 125-167.

Arbib, M.A., K. Liebal, and S. Pika. 2008. Primate Vocalization, Gesture, and the Evolution of Human Language. *Current Anthropology* 49: 1053–1076.

Arcadi, A.C., D. Robert, and C. Boesch. 1998. Buttress Drumming by Wild Chimpanzees: Temporal Patterning, Phrase Integration into Loud Calls, and Preliminary Evidence for Individual Distinctiveness. *Primates* 39: 505–518.

Bardo, A., T.L. Kivell, K. Town, G. Donati, H. Ballieux, C. Stamate, T. Edginton, and G.S. Forrester. 2021. Get a Grip: Variation in Human Hand Grip Strength and Implications for Human Evolution. *Symmetry* 13: 1142.

Becker, Y., N. Claidière, K. Margiotoudi, D. Marie, M. Roth, B. Nazarian, J.-L. Anton, O. Coulon, and A. Meguerditchian. 2022. Broca's Cerebral Asymmetry Reflects Gestural Communication's Lateralisation in Monkeys (Papio Anubis). *eLife* 11: e70521.

Bergman, T.J. 2013. Speech-like Vocalized Lip-Smacking in Geladas. *Current Biology* 23: R268–R269.

Bianchi, S., L.D. Reyes, W.D. Hopkins, J.P. Taglialatela, and C.C. Sherwood. 2016. Neocortical Grey Matter Distribution Underlying Voluntary, Flexible Vocalizations in Chimpanzees. *Scientific Reports* 6: 34733.

Biro, D., N. Inoue-Nakamura, R. Tonooka, G. Yamakoshi, C. Sousa, and T. Matsuzawa. 2003. Cultural Innovation and Transmission of Tool Use in Wild Chimpanzees: Evidence from Field Experiments. *Animal Cognition* 6: 213–223.

Boesch, C. 1991. Handedness in Wild Chimpanzees. *International Journal of Primatology* 12: 541–558.

Boesch, C., and H. Boesch. 1981. Sex Differences in the Use of Natural Hammers by Wild Chimpanzees: A Preliminary Report. *Journal of Human Evolution* 10: 585–593.

Boesch, C., A.K. Kalan, R. Mundry, M. Arandjelovic, S. Pika, P. Dieguez, E.A. Ayimisin, et al. 2020. Chimpanzee Ethnography Reveals Unexpected Cultural Diversity. *Nature Human Behaviour* 4: 910–916.

Bogart, S. L., J. D. Pruetz, L. K. Ormiston, J. L. Russell, A. Meguerditchian, and W. D. Hopkins. 2012. Termite Fishing Laterality in the Fongoli Savanna Chimpanzees (Pan Troglodytes Verus): Further Evidence of a Left Hand Preference. *American Journal of Physical Anthropology* 149: 591–598.

Brand, C.M., L.F. Marchant, K.J. Boose, F.J. White, T.M. Rood, and A. Meinelt. 2017. Laterality of Grooming and Tool Use in a Group of Captive Bonobos (Pan Paniscus). *Folia Primatologica* 88: 210–222.

Brésard, B., and F. Bresson. 1983. Handedness in Pongo Pygmaeus and Pan Troglodytes. *Journal of Human Evolution* 12: 659–666.

Call, J., and M. Tomasello. 2007. *The Gestural Communication of Apes and Monkeys*. Mahwah, New Jersey: Lawrence Erlbaum Associates.

Cashmore, L., N. Uomini, and A. Chapelain. 2008. The Evolution of Handedness in Humans and Great Apes: A Review and Current Issues. *Journal of Archaeological Science* 86: 7–35.

Caspar, K.R., F. Pallasdies, L. Mader, H. Sartorelli, and S. Begall. 2021. *The Evolution and Biological Correlates of Hand Preferences in Anthropoid Primates*. Preprint: http://biorxiv.org/lookup/doi/10.1101/2021.12.30.474462.

Christiansen, M.H., and S. Kirby. 2003. *Language Evolution*. Oxford, UK: Oxford University Press.

Cochet, H., and J. Vauclair. 2010. Pointing Gesture in Young Children: Hand Preference and Language Development. *Gesture* 10: 129–149.

Corballis, M.C. 2003. From Mouth to Hand: Gesture, Speech, and the Evolution of Right-Handedness. *The Behavioral and Brain Sciences* 26: 199–208; discussion 208-260.

Corballis, M.C. 2017. Language Evolution: A Changing Perspective. *Trends in Cognitive Sciences* 21: 229–236.

DeForest, D.S., and R.L. Lyman. 2022. Characteristics of Lithic Sound to Assess a Rock's Predictability of Flaking. *Lithic Technology* 47: 221-230.

Fagot, J., and J. Vauclair. 1991. Manual Laterality in Nonhuman Primates: A Distinction between Handedness and Manual Specialization. *Psychological Bulletin* 109: 76–89.

Finch, G. 1941. Chimpanzee Handedness. *Science* 94: 117–118.

Fischer, J. 2017. Primate Vocal Production and the Riddle of Language Evolution. *Psychonomic Bulletin & Review* 24: 72–78.

Fitch, W.T. 2010. *The Evolution of Language*. Cambridge University Press.

Fitch, W.T., and S.N. Braccini. 2013. Primate Laterality and the Biology and Evolution of Human Handedness: A Review and Synthesis. *Annals of the New York Academy of Sciences* 1288: 70–85.

Forrester, G.S., C. Quaresmini, D.A. Leavens, D. Mareschal, and M.S.C. Thomas. 2013. Human Handedness: An Inherited Evolutionary Trait. *Behavioural Brain Research* 237: 200–206.

Fröhlich, M., C. Sievers, S.W. Townsend, T. Gruber, and C.P. van Schaik. 2019. Multimodal Communication and Language Origins: Integrating Gestures and Vocalizations. *Biological Reviews* 94: 1809–1829.

Gabrić, P., M. Banda, and I. Karavanić. 2018. Palaeolithic Toolmaking and the Evolution of Cognition and Language. In *Proceedings of the 21st International Multiconference*

Information Society – IS 2018. Volume B: Cognitive Science, B:12–16. https://urn.nsk.hr/urn:nbn:hr:131:602951.

Ghazanfar, A.A., and D.Y. Takahashi. 2014. Facial Expressions and the Evolution of the Speech Rhythm. *Journal of Cognitive Neuroscience* 26: 1196–1207.

Ghirlanda, S., E. Frasnelli, and G. Vallortigara. 2009. Intraspecific Competition and Coordination in the Evolution of Lateralization. *Philosophical Transactions of the Royal Society B: Biological Sciences* 364: 861–866.

Henrich, J., and C. Tennie. 2017. Cultural Evolution in Chimpanzees and Humans. In *Chimpanzees and Human Evolution*, 645–702. Cambridge, Mass: Belknap Press.

Hobaiter, C., and R.W. Byrne. 2013. Laterality in the Gestural Communication of Wild Chimpanzees: Laterality in Chimpanzee Gestural Communication. *Annals of the New York Academy of Sciences* 1288: 9–16.

Hopkins, W.D. 1995. Hand Preferences for a Coordinated Bimanual Task in 110 Chimpanzees (Pan Troglodytes): Cross-Sectional Analysis. *Journal of Comparative Psychology* 109: 291–297.

Hopkins, W.D. 1996. Chimpanzee Handedness Revisited: 55 Years since Finch (1941). *Psychonomic Bulletin & Review* 3: 449–457.

Hopkins, W.D., C. Cantalupo, and M.J. Wesley. 2002. Grip Morphology and Hand Use in Chimpanzees (Pan Troglodytes): Evidence of a Left Hemisphere Specialization in Motor Skill. *Journal of Experimental Psychology: General* 131: 412–423.

Hopkins, W., and C. Cantalupo. 2005. Individual and Setting Differences in the Hand Preferences of Chimpanzees (Pan Troglodytes): A Critical Analysis and Some Alternative Explanations. *Laterality: Asymmetries of Body, Brain and Cognition* 10: 65–80.

Hopkins, W.D., M.C. Mareno, and S.J. Schapiro. 2019. Further Evidence of a Left Hemisphere Specialization and Genetic Basis for Tool Use Skill in Chimpanzees (Pan Troglodytes): Reproducibility in Two Genetically Isolated Populations of Apes. *Journal of Comparative Psychology* 133: 512–519.

Hopkins, W.D., K.A. Phillips, A. Bania, S.E. Calcutt, M. Gardner, J. Russell, J. Schaeffer, E.V. Lonsdorf, S.R. Ross, and S.J. Schapiro. 2011. Hand Preferences for Coordinated Bimanual Actions in 777 Great Apes: Implications for the Evolution of Handedness in Hominins. *Journal of Human Evolution* 60: 605–611.

Hopkins, W.D., J. Russell, H. Freeman, N. Buehler, E. Reynolds, and S.J. Shapiro. 2005. The Distribution and Development of Handedness for Manual Gestures in Captive Chimpanzees (Pan Troglodytes). *Psychological Science*: 487–493.

Hopkins, W.D., J.L. Russell, M. Hook, S. Braccini, and S.J. Schapiro. 2005. Simple Reaching Is Not So Simple: Association Between Hand Use and Grip Preferences in Captive Chimpanzees. *International Journal of Primatology* 26: 259–277.

Humle, T., and T. Matsuzawa. 2009. Laterality in Hand Use across Four Tool-Use Behaviors among the Wild Chimpanzees of Bossou, Guinea, West Africa. *American Journal of Primatology* 71: 40–48.

Incel, N.A., E. Ceceli, P.B. Durukan, H.R. Erdem, and Z.R. Yorgancioglu. 2002. Grip Strength: Effect of Hand Dominance. *Singapore Medical Journal* 43: 234–237.

Kalan, A.K., and C. Boesch. 2018. Re-Emergence of the Leaf Clip Gesture during an Alpha Takeover Affects Variation in Male Chimpanzee Loud Calls. *PeerJ* 6: e5079.

Kalan, A.K., E. Carmignani, R. Kronland-Martinet, S. Ystad, J. Chatron, and M. Aramaki. 2019. Chimpanzees Use Tree Species with a Resonant Timbre for Accumulative Stone Throwing. *Biology Letters* 15: 20190747.

Karakostis, F.A., G. Hotz, V. Tourloukis, and K. Harvati. 2018. Evidence for Precision Grasping in Neandertal Daily Activities. *Science Advances* 4: eaat2369.

Kohler, E., C. Keysers, M.A. Umiltà, L. Fogassi, V. Gallese, and G. Rizzolatti. 2002. Hearing Sounds, Understanding Actions: Action Representation in Mirror Neurons. *Science* 297: 846–848.

Kubota, K. 1990. Preferred Hand Use in the Japanese Macaque Troop, Arashiyama-R, during Visually Guided Reaching for Food Pellets. *Primates* 31: 393–406.

Kühl, H.S., A.K. Kalan, M. Arandjelovic, F. Aubert, L. D'Auvergne, A. Goedmakers, S. Jones, et al. 2016. Chimpanzee Accumulative Stone Throwing. *Scientific Reports* 6: 22219.

Lambert, M. 2012. Hand Preference for Bimanual and Unimanual Feeding in Captive Gorillas: Extension in a Second Colony of Apes. *American Journal of Physical Anthropology* 148: 641–647.

Lameira, A.R., M.E. Hardus, and S.A. Wich. 2012. Orangutan Instrumental Gesture-Calls: Reconciling Acoustic and Gestural Speech Evolution Models. *Evolutionary Biology* 39: 415–418.

Larsson, M. 2014. Self-Generated Sounds of Locomotion and Ventilation and the Evolution of Human Rhythmic Abilities. *Animal Cognition* 17: 1–14.

Larsson, M. 2015. Tool-Use-Associated Sound in the Evolution of Language. *Animal Cognition* 18: 993–1005.

Leca, J.-B., N. Gunst, and M.A. Huffman. 2010. Principles and levels of laterality in unimanual and bimanual stone handling patterns by Japanese macaques. *Journal of Human Evolution* 58(2): 155–165. DOI: 10.1016/j.jhevol.2009.09.005.

Liebal, K., B.M. Waller, K.E. Slocombe, and A.M. Burrows. 2013. *Primate Communication: A Multimodal Approach*. Cambridge, UK: Cambridge University Press.

Lonsdorf, E.V., and W.D. Hopkins. 2005. Wild Chimpanzees Show Population-Level Handedness for Tool Use. *Proceedings of the National Academy of Sciences* 102: 12634–12638.

MacNeilage, P.F. 1998. The Frame/Content Theory of Evolution of Speech Production. *Behavioral and Brain Sciences* 21: 499–511.

MacNeilage, P.F., M.G. Studdert-Kennedy, and B. Lindblom. 1987. Primate Handedness Reconsidered. *Behavioral and Brain Sciences* 10: 247–263.

McGrew, W. C., and L.F. Marchant. 1992. Chimpanzees, Tools, and Termites: Hand Preference or Handedness? *Current Anthropology* 33: 114–119.

McGrew, W. C., and L.F. Marchant. 1997. On the Other Hand: Current Issues in and Meta-Analysis of the Behavioral Laterality of Hand Function in Nonhuman Primates. *American Journal of Physical Anthropology* 104: 201–232.

McGrew, W.C., and L.F. Marchant. 1999. Laterality of Hand Use Pays off in Foraging Success for Wild Chimpanzees. *Primates* 40: 509–513.

McManus, C. 2019. Half a Century of Handedness Research: Myths, Truths; Fictions, Facts; Backwards, but Mostly Forwards. *Brain and Neuroscience Advances* 3: 239821281882051.

Meguerditchian, A., J. Vauclair, and W.D. Hopkins. 2013. On the Origins of Human Handedness and Language: A Comparative Review of Hand Preferences for Bimanual Coordinated Actions and Gestural Communication in Nonhuman Primates. *Developmental Psychobiology* 55: 637–650.

Motes-Rodrigo, A., R.A. Hernandez-Aguilar, and M. Laska. 2019. Preferential Hand Use by Captive Chimpanzees (Pan Troglodytes) in Manual and Tool Digging. *Primates* 60: 367–373.

Nishida, T., W.C. McGrew, and L.F. Marchant. 2012. Wild Chimpanzees at Mahale Are Not Manually Lateralised for Throwing. *Pan Africa News* 19: 21–23.

O'Malley, R.C., and W.C. McGrew. 2006. Hand Preferences in Captive Orangutans (Pongo Pygmaeus). *Primates* 47: 279–283.

Palmer, A.R. 2003. Reply to Hopkins and Cantalupo: Chimpanzee Right-Handedness Reconsidered? Sampling Issues and Data Presentation. *American Journal of Physical Anthropology* 121: 382–384.

Pika, S., K. Liebal, J. Call, and M. Tomasello. 2005. Gestural Communication of Apes. *Gesture* 5: 41–56.

Prieur, J., A. Lemasson, S. Barbu, and C. Blois-Heulin. 2019. History, Development and Current Advances Concerning the Evolutionary Roots of Human Right-Handedness and Language: Brain Lateralisation and Manual Laterality in Non-Human Primates. *Ethology* 125: 1–28.

Prieur, J., S. Pika, S. Barbu, and C. Blois-Heulin. 2017. Intraspecific Gestural Laterality in Chimpanzees and Gorillas and the Impact of Social Propensities. *Brain Research* 1670: 52–67.

Prieur, J., S. Pika, C. Blois-Heulin, and S. Barbu. 2018. Captive Chimpanzees' Manual Laterality in Tool Use Context: Influence of Communication and of Sociodemographic Factors. *Behavioural Processes* 157: 610–624.

Rizzolatti, G., and M.A. Arbib. 1998. Language within Our Grasp. *Trends in Neurosciences* 21: 188–194.

Sanz, C.M., J. Call, and C. Boesch. 2013. *Tool Use in Animals: Cognition and Ecology*. Cambridge, UK: Cambridge University Press.

Sanz, C.M., D.B. Morgan, and W.D. Hopkins. 2016. Lateralization and Performance Asymmetries in the Termite Fishing of Wild Chimpanzees in the Goualougo Triangle, Republic of Congo. *American Journal of Primatology* 78: 1190–1200.

Slocombe, K.E., B.M. Waller, and K. Liebal. 2011. The Language Void: The Need for Multimodality in Primate Communication Research. *Animal Behaviour* 81: 919–924.

Smith, H.N., A. Perrone, M. Wilson, M.A. Raghanti, C.O. Lovejoy, M.J. Rosen, S.J. Shanbhag, D.S. DeForrest, R.L. Lyman, and M.I. Eren. 2021. Rock Music: An Auditory Assessment of Knapping. *Lithic Technology* 46: 320–335.

Stout, D., and T. Chaminade. 2012. Stone Tools, Language and the Brain in Human Evolution. *Philosophical Transactions of the Royal Society B: Biological Sciences* 367: 75–87.

Stout, D., N. Toth, K. Schick, and T. Chaminade. 2008. Neural Correlates of Early Stone Age Toolmaking: Technology, Language and Cognition in Human Evolution. *Philosophical Transactions of the Royal Society B: Biological Sciences* 363: 1939–1949.

Sugiyama, Y., T. Fushimi, O. Sakura, and T. Matsuzawa. 1993. Hand Preference and Tool Use in Wild Chimpanzees. *Primates* 34: 151–159.

Taglialatela, J.P., J.L. Russell, S.M. Pope, T. Morton, S. Bogart, L.A. Reamer, S.J. Schapiro, and W.D. Hopkins. 2015. Multimodal Communication in Chimpanzees. *American Journal of Primatology* 77: 1143–1148.

Townsend, S.W., S.E. Koski, R.W. Byrne, K.E. Slocombe, B. Bickel, M. Boeckle, I.B. Goncalves, et al. 2017. Exorcising Grice's Ghost: An Empirical Approach to Studying Intentional Communication in Animals. *Biological Reviews* 92: 1427–1433.

Warren, J.M. 1980. Handedness and Laterality in Humans and Other Animals. *Physiological Psychology* 8: 351–359.

Westergaard, G.C., H.E. Kuhn, and S.J. Suomi. 1998. Bipedal Posture and Hand Preference in Humans and Other Primates. *Journal of Comparative Psychology* 112: 55–64.