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ACCEPTED VERSION BEFORE THE PROOF CORRECTIONS

Running title: Laterality, from living humans to fossil hominins

Title: Lateralized behaviors in living humans: application in the context of hominin brain evolution

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ABSTRACT

The left and right hemispheres of our brains differ subtly in structure, and each is dominant in processing specific cognitive tasks. Our species has a unique system of distributing behavior and cognition between each cerebral hemisphere, with a preponderance of pronounced side biases and lateralized functions. This hemisphere-dependent relationship between cognitive,

sensory or motor function and a set of brain structures is called hemispheric specialization. Hemispheric specialization has led to the emergence of model systems to link anatomical asymmetries to brain function and behavior. Scientific research on hemispheric specialization and lateralized functions in living humans focuses on three major domains: (1) hand preferences, (2) language, and (3) visuospatial skills and attention. In this chapter we present an overview of this research with a specific focus on living humans and the applications of this research in the context of hominin brain evolution. Our objective is to put into perspective what we know about brain-behavior relationships in living humans and how we can apply the same methods to investigate this relationship in fossil hominin species, and thus improve our understanding of the emergence and development of complex cognitive abilities.

Keywords

Hominins, Paleoneurology, Neuroimaging, Brain asymmetry, Lateralized behaviors, Behavioral experiments, Brain endocast, Interdisciplinarity

1. INTRODUCTION

Laterality refers to the preference humans and many other vertebrates show for one side of the body over the other. This may relate to the preferential use of one arm or leg relative to the one on the contralateral side, but it also concerns biological and functional aspects of the brain. Pierre Paul Broca, a 19th century French physician and anthropologist, was one of the founders of research on brain asymmetry. He studied the relationship between language disorders and brain damage, and showed also asymmetry in the brains of great apes (Broca, 1865). The early discoveries of Paul Broca and Carl Wernicke (1910), a German

neuropsychiatrist, highlighted that the left hemisphere was specialized for language and verbal functions in humans (i.e., Broca's area and Wernicke's area of the brain). Since then, new approaches and methodological improvements have enhanced our knowledge of the biology and the functioning of our brain, showing the complexity of this structure. Major recent advances came from functional imaging while available databases of extant human brains combine morphological and functional imaging for thousands of individuals (Balzeau and Mangin, 2021).

The existence of brain and behavioral asymmetries among many other vertebrates had been acknowledged since the late 1970s or early 1980s (Rogers et al., 2013; but see as well Güntürkün et al., 2020 for a detailed history of comparative research on lateralization in animals), highlighting that lateralization is not a trait unique to humans (Ocklenburg et al., 2013). There is much evidence about functional brain asymmetries in many different species of animals, mostly related to vocalization systems and limb preferences (Ocklenburg et al., 2013, Ströckens et al., 2013). For example, recent neuroanatomical research has found that great apes (Cantalupo et al., 2003; Spocter et al., 2010), macaques (Shepherd and Freiwald, 2018) and baboons (Marie et al., 2018; Becker et al., 2022) have brain regions in the left hemisphere homologous to the speech and language areas in the human brain. Moreover, non-human animal forelimb asymmetries were found for different actions such as for manipulation of inanimate objects, living targets and communicative gestures (see recent review by Boulinguez-Ambroise et al., 2022).

Lateralization is important for the survival of an organism. In certain vertebrates, the right hemisphere responds to emergency situations whereas the left hemisphere is involved in processing routine and/or familiar stimuli (MacNeilage, 2008). This can vary between vertebrates, for example, it was found that fish keep track of a predator using their right eye (i.e., left hemisphere dominance for avoiding a predator) while most mammalian, reptilian and

amphibian species use their left eye and so show a right hemisphere bias (Leliveld et al., 2013; and see Rogers et al., 2013). This last has been suggested to be associated with an increase in processing capacity (Rogers et al., 2013). Indeed, it has been hypothesized that hemispheric specialization increased in hominins (i.e., *H. sapiens* and its extinct relatives of the genera *Homo*, *Australopithecus*, *Paranthropus*, *Kenyanthropus*, *Sahelanthropus*, *Orrorin* and *Ardipithecus*, which split off from the *Pan sp.* ~6-8 million years ago; Patterson et al., 2006; Wood and Harrison, 2011) along with the emergence of handedness (i.e., hand preference), tool using and making, and language (Rogers et al., 2013). However, as we still lack a general consensus on the relationship between handedness, anatomical asymmetries and functional lateralization in living humans, it is difficult to characterize when or how *H. sapiens* shifted away from ancestral patterns of laterality (Uomini and Ruck, 2018). Moreover, the available information on lateralization for fossil hominin species is scarce and hardly comparable between specimens and with detailed information obtained directly on living humans.

It is essential today to search the fossil record for possible traces of variations in cerebral asymmetries in fossil hominins in order to re-examine previous conclusions that may have been based on speculative reasoning or inappropriate methodologies. It is crucial to perform qualitative assessments of bilateral variation of fossil endocasts and to compare with the existing contemporary archeological material. Methodologies should be developed to investigate the fossil record that does not exclusively rely on proxies and speculative reasoning. Even if some specific features are visible in our species and linked functionally with behaviors, we cannot assume that the relationship was similar in fossil species. In this chapter we describe a research framework devoted to hemispheric asymmetry and laterality with a specific focus on living humans and the applications of this research to the reconstruction of hominin brain evolutionary history. Despite much research dedicated to the study of hemispheric asymmetry and laterality in recent decades (see Hugdahl and Westerhausen, 2010; Rogers et al., 2013), our

theoretical understanding of the relationships between brain asymmetries and lateralized behaviors remains limited. Our objective is to use what we know about brain-behavior relationships in living humans and apply the same concepts and methods to understand these relationships in fossil hominins.

This chapter has three parts:

1. A review of functional asymmetry of the human brain and the relationship with lateralized behavior.
2. A review of the methods used to infer functional asymmetry of fossil hominins.
3. A presentation of our current project PaleoBRAIN in which we are studying living human brain-behavioral asymmetries. By investigating possible relationships between behaviors and brain biology in living people, we aim to provide a context for understanding hominin brain evolution as represented by fossil remains.

2. FUNCTIONAL ASYMMETRY OF THE HUMAN BRAIN AND LATERALIZED BEHAVIORS

The relationships between functional asymmetry of the human brain and behavioral asymmetries can be investigated through indirect and direct observations. Behavioral experiments enable researchers to demonstrate indirect relationships between well-documented brain asymmetries and lateralized behaviors, by observing which part of the body responds to specific stimuli (Rogers et al., 2013). Through noninvasive neuroimaging approaches, such as PET (positron emission tomography), MRI (magnetic resonance imaging), and DTI (diffusion tensor imaging), it is possible to map anatomical asymmetries onto brain and neuronal structures and functions in living humans (Herve et al., 2013). This section of the chapter

discusses current research findings on brain lateralization, from behavior to anatomy, and the structure-function relationship in living humans. The main body of research on lateralized functions in living humans is focused on language, hand preferences and visuospatial skills and attention. An important question to tackle is to which extent structural differences between left and right hemispheres underlie the lateralization of function, and whether this structural lateralization reflects the degree of functional lateralization from one person to another.

2.1. Language

Two key anatomical areas in the left hemisphere of the human brain are involved in speech production and processing; the Broca's and Wernicke's areas (Broca, 1865; Wernicke, 1910; and see Benjamin et al., 2017; Hagoort, 2017 for a recent review of those original works). Broca's area is located on the left inferior frontal gyrus and Wernicke's area is in the posterior area of the left superior temporal gyrus (Benjamin et al., 2017; Hagoort, 2017). Moreover, the planum temporale, located in the temporal lobe and related functionally to auditory areas close to Wernicke's area, is volumetrically larger in the left than the right hemisphere (Goldberg et al., 2013). It has long been stated that humans, in the sense recent *H. sapiens*, would have a specific pattern for the general organization of the brain and specifically for those particular functional areas. However, there are asymmetries of the planum temporale and Broca's area in the brains of great apes (Gannon et al., 1998; Cantalupo et al., 2003; Spocter et al., 2010), macaques (Shepherd and Freiwald, 2018) and baboons (Marie et al., 2018; Becker et al., 2022).

By comparing bilateral variation in the endocast of hominids (i.e., great apes, including *H. sapiens*) it is possible to reconstruct the evolution of asymmetrical structures. An endocast is a cast of the internal aspect of the cranial vault that reflects the imprints of the brain left on the internal surface of the bone. The average spatial asymmetry pattern on endocasts is shared

among current hominids for the antero-posterior expansion of the frontal and occipital lobes, namely the petalial pattern (Balzeau et al., 2012; Neubauer et al., 2020), or for the third frontal convolution (Balzeau et al., 2014). However, living *H. sapiens* show a pattern of asymmetry more variable than in the great apes (Balzeau et al., 2014). This was suggested to reflect increased functional and developmental modularization of the human brain (Neubauer et al., 2020). Nevertheless, the endocast is only a partial reflection of the morphology of the brain and the homology of cortical areas between species that is based on their supposed position relative to brain sulci. One limitation is that any region defined according to surface features could be made up of multiple different Brodmann areas (Brodmann, 1909) and so it is difficult to determine the correspondence to histologically and functionally defined cortical regions (de Sousa et al., 2010). Recent research has shown that the asymmetric pattern of the Broca's and Wernicke's areas is not specific to *H. sapiens*, or even to any *Homo* species (see 3.1.). Anatomically homologous areas have been identified in extant apes (Palomero-Gallagher and Zilles, 2019). Moreover, these areas are difficult to define and to compare between extant hominids (Keller et al., 2009; Balzeau et al., 2014).

The most common behavioral test used to assess hemispheric dominance for language processing, without using neuroimaging techniques, is the dichotic-listening paradigm (Westerhausen and Samuelson, 2020). For this task, pairs of verbal stimuli (words or consonant-vowel syllables like /DA/ and /GA/) are presented simultaneously to the participant via headphones, with one specific stimulus used for each ear. Participants have to report which stimuli (word or syllable) they heard best. This indicates which ear is dominant (for example, if there is /DA/ in the left ear and /GA/ in the right ear and the participant says that they heard /GA/, the right ear is dominant). This operation is repeated on average a hundred times because a recent review showed that high reliability of this test seems expected for 90 to 120 trials (Westerhausen, 2019). Participants report significantly more of those syllables that had been

presented to the right ear than those presented to the left ear, a phenomenon termed the right-ear advantage. The right-ear advantage is thought to reflect left hemispheric language lateralization (Ocklenburg and Güntürkün, 2018; Westerhausen and Samuelsen, 2020).

2.2. Human handedness

One of the most robust behavioral indicators of hemispheric specialization in humans, as well as in nonhuman primates (see the recent review by Nelson, 2022) and other species (Rogers et al., 2013), is handedness (i.e., side preference for the right or the left hand) (Ocklenburg and Güntürkün, 2018). The human population presents approximately 90% right-handers while left-handers constitute approximately 10% (Papadatou-Pastou et al., 2020; but see Faurie et al., 2005, who found 26.9% of left-handers among the Eipo in Papua New Guinea). Nonhuman primates also show population-level laterality for manipulative tasks but not in the same proportions as in humans (i.e., not 90% of right-handers or left-handers), and the extensive literature on the subject seems even to show conflicting results (see the meta-analysis by Papademetriou et al., 2005). Moreover, nonhuman primate laterality can vary according to the complexity of the task (Bardo et al., 2015). Handedness is thought to have played an important role in the human brain lateralization and the emergence of language (Corballis, 1998) and other complex cognitive functions, including tool use (Corballis, 2003; Uomini, 2009), manual gestures (Corballis, 2003; Meguerditchian et al., 2013), and throwing (Calvin, 1983). A predominance of right-hand use has been reported in communicative gestures in humans (Kimura, 1973a, b; Grossi et al., 1996), as well as in non-human primates (Meguerditchian et al., 2022), indicating a greater dominance of the left-hemisphere for gestural communication. It has been suggested that the motor sequencing for tool use (i.e., dexterous hierarchical motor activities) facilitated the emergence of language in humans with likely manual gesture as a first form of language (Greenfield, 1991). This theory proposes that tool

use abilities and language evolved together. The neural circuits in both tasks are superimposed (see for more details a recent study in humans, Thibault and al., 2021; and in chimpanzees, Hopkins et al., 2007) and may have facilitated an increase in hemispheric specialization. A limitation to this possible general trend is that the currently used definitions and methods for quantifying handedness do not take into account the full complexity of this trait. Fully understanding handedness in living humans is fundamental to discussing hand preferences in fossil hominins.

Handedness in living humans is indicative of preference and/or performance. For example, a person can prefer to use the right hand to write but can be more skillful with the left hand for another task. The usual method to measure hand preference is to ask via a questionnaire what is the preferred hand during different activities (e.g., the Edinburgh Handedness Inventory developed by Oldfield (1971) at Edinburgh University). However, most questionnaires used to measure handedness focus on the manipulation of specific objects and tools (e.g., a pen, a toothbrush) rather than on more comprehensive ethological measures that include non-object-manipulatory, self-directed and socially communicative patterns of behavior. Moreover, the problem with questionnaires is that people do not always answer reliably. Measuring handedness with performance measures is necessary to quantify different skills and test which hand is better for specific activities. Performance can be measured for example with grip strength (Bardo et al., 2021), the time needed to perform a task (Bardo et al., 2022), or the speed of the hand (Peters and Durdin, 1978). The degree of hand preference varies depending on the task being tested (Annett, 1972; Bishop, 1989). For example, by studying manual activities in three traditional societies (G/wi San of Botswana, Himba of Namibia and Yanomamo of Venezuela), Marchant and colleagues (1995) found a right-handedness bias only for tool use, while other manual actions showed mixed results (used of both right and left hand without preference) at both individual and population level (Marchant et al., 1995). However, a large

part of the studies only analyzes the dominant hand (i.e., the preferred hand use for specific manual action such as writing) while both hands are important in daily activities, for living *H. sapiens* and fossil hominins (Steele and Uomini, 2009; Bardo et al., 2021). Numerous manual activities involved bimanual coordination during Paleolithic times. Tool production and tool use behaviors (Marzke et al., 1998; Williams-Hatala et al., 2018; Shaw et al., 2012) and having two strong upper limbs would likely be positively selected for through hominin evolution (Cartmill, 1985; Preuschoft, 2022; Kappelman et al., 2016). Pre-industrial lifestyle certainly induces less highly specialized lateralization compared to more sedentary humans (Bardo et al., 2021). When studying hand laterality, it is necessary to investigate both hands' performance to better understand the effect of handedness on human daily life according to lifestyle factors (e.g., occupation, practice of sport and music) and the potential clinical implications of this, but also to provide a broader evolutionary understanding. Indeed, population-level hand asymmetry has been related to advances in technological and cultural innovations (Uomini, 2009; Provins, 1997), or more generally, to task complexity (Fagot and Vauclair, 1991; Cashmore et al., 2008; Bardo et al., 2015). In return, increase in hemispheric specification could have been favored by a more frequent use of the dominant hand during diverse activities, rather than both hands, and vice versa. However, as early hominins (e.g., *Australopithecus*) were still likely using their hands for arboreal locomotion, they may have been under stronger selection for bimanual abilities and strong grip force, as in extant non-human hominids (Cashmore et al., 2008). Moreover, Steele and Uomini (2009) highlighted the importance of studying the complementary role of both hands during bimanual Paleolithic tools behaviors to better understand the evolution of hand laterality.

Linking handedness with specific brain anatomical asymmetries seems complex and recent studies have shown inconsistent findings. For example, some studies have found a correlation between handedness and the widths of right-frontal and left-occipital petalias, with

petalias seemingly more prominent, in term of magnitude, in right-handers (LeMay and Kido, 1978; Kertesz et al., 1986; and more recently by Kong et al., 2021). However, other studies showed that left-handedness does not involve any broad or substantial alterations or cortical asymmetry compared to right-handedness (Guadalupe et al., 2014; Maingault et al., 2016; Kong et al., 2018). After testing more than 17,000 healthy individuals, Kong and colleagues (2018) found no significant associations between handedness and cortical asymmetries although there were some significant associations for several traits with lateralized functions, including language and visuospatial processing. Finally, the same authors (Kong et al. 2021) on a larger sample of over 40,000 individuals, found an association between torque pattern – i.e., the tendency of the brain to show opposing right-left asymmetries of frontal and occipital regions in the antero-posterior directions– and handedness. A limitation of those studies is that they considered handedness as a categorical trait (i.e., supported by the bimodal distribution of overall hand preference). But as discussed above, it will be more accurate to also define handedness with different manual measurements, such as manual performance and preference, to provide more information of potential association between brain anatomical asymmetries and handedness. Moreover, it should be noted that handedness seems to correlate more strongly with functional asymmetries in language structures than with asymmetries in the motor cortex (Toga and Thompson, 2003). For example, the planum temporale appears much larger in the left-hemisphere for right-handed individuals (Geschwind and Levitsky, 1968), and is often reported as reduced or more frequently reversed in left-handers (Herve et al., 2006; Narr et al., 2007).

2.3. Visuospatial skills and attention

Visuospatial attention is a cognitive skill involving the capacity to process stimuli around us, and to interpret spatial relationships (Posner and Petersen, 1990). The most common

behavioral experimental technique to investigate laterality in visuospatial skills and attention is the divided visual field paradigm (Banich, 2003). During this experimental task, participants are seated in front of a computer monitor and asked to focus on a fixation cross that is presented in the center of the screen. A stimulus is then presented very briefly on either the left or the right side of the fixation cross, and the participant is asked to respond to the stimulus (e.g., telling what they see). Due to the anatomical organization of the visual system, stimuli on the left side of the fixation cross are processed in the right hemisphere and vice versa. The divided visual field paradigm utilizes this principle to test whether one hemisphere is more efficient (e.g., by quantifying response time) in processing a specific type of stimuli (e.g., words, faces, or images showing emotional states) than the other one (Güntürkün et al., 2020). It was found that visuospatial attention is a function of the right hemisphere (e.g., Mesulam, 1981), that depends on a bilateral (i.e., processing between the two hemispheres) parieto-frontal network (De Schotten et al., 2011).

Different brain areas are involved in vision and processing of the information. Several visual areas are common between mammals, including primates. Some specific visual areas are shared within primates only, while others vary among primate species (Kaas, 2020). The sophisticated visual processing capacities of primates are linked to an increase in the area of cerebral cortex that processes visual information, expanding to areas of the occipital, parietal, temporal, and even frontal lobes, as well as other specializations such as changes in color vision and high cortical neuronal numbers (see the recent review by Haas et al., 2020). Goldberg et al. (2013) demonstrated that, in humans, these regions involved in visual processing show rightward volumetric asymmetries in humans, consistent with other findings on rightward cortical surface and thickness differences (Luders et al., 2006; Lyttelton et al., 2009). These results are consistent with a right hemispheric dominance for visuo-spatial processing in humans (Goldberg et al., 2013). The parietal association cortex appears to play a major role in

the representation of objects and their movements (Van Essen et al., 2001), more precisely, the right posterior parietal cortex (Rushworth et al., 2001a). Moreover, there is a distinct form of attention related to motor processes, involving the hands, as opposed to oculomotor processes. Such motor attention depends on a network of areas that are lateralized to the left rather than the right hemisphere (Rushworth et al., 2001a). The left parietal region, the supramarginal gyrus, is an important part of this network and its role cannot be explained as merely the consequence of the left hemisphere's dominance for language; an interconnected ventral premotor region by the inferior precentral sulcus may also be important for motor attention (Rushworth et al., 2001b). Therefore, these attentional processes are lateralized; the angular gyrus region (right parietal region) is critical for orienting attention and the more anterior supramarginal gyrus (left parietal region) is essential for motor attention.

3. HOW TO INFER FUNCTIONAL ASYMMETRY OF FOSSILS HOMININS?

Studying extant non-human primates is a prerequisite to understanding and contextualizing the characteristics of brain lateralization in humans. It is therefore important to investigate whether lateralization and hemispheric asymmetry is shared since an ancient evolutionary stage (Güntürkün et al., 2020), and for this reason evidence of lateralization in fossil hominins can improve our understanding of the emergence of complex cognitive abilities in human evolution (Steele and Uomini, 2009). The anatomy of living *H. sapiens* may provide important clues to document the behaviors of fossil hominins. The cognitive capacity of *H. sapiens* is said to be associated with characteristics in terms of brain size, cortical proportions, histology, connection patterns, and metabolic functions (Preuss, 2017). Comparative neuroanatomy and paleoneurology are therefore necessary to formulate hypotheses about the hominin brain, integrating information from extinct and extant species. Paleoneurology is a research field applying functional brain imaging techniques in living *H. sapiens* to identify the

cerebral regions involved in the conception of artefacts produced in the past by hominins (Salagnon et al., 2020). Using different imaging techniques (e.g., PET, functional or structural MRI, Functional Near-infrared spectroscopy, fNIRS), paleoneurology elaborates hypotheses about the evolution of cognition by making inferences about hominin cognitive function with regards, for example, to language and cognitive control learning domains (Salagnon et al., 2020). The behaviors of fossil hominins may also be documented by direct evidence. As summarized in Uomini and Ruck (2018), evidence of lateralization in fossils hominins can be found through: 1) identification of hand preference from stone tool manufacture and use, from hand prints found on rocks and cave walls, and from the direction of striations on fossil teeth; and 2) by measuring functional asymmetries in fossil skeletons.

3.1. Paleoneurology and endocasts

In the absence of brain tissues preserved in the fossil record, we refer to the superficial imprints that the brain forms on the internal cranial surface: the endocast. Endocasts constitute a critical proxy for qualifying and quantifying variations in brain shape and organization in extinct taxa and provide the only direct evidence of brain evolution (Dumoncel et al., 2020). The development of advanced imaging techniques (such as computed-tomography, CT, and MRI) and analytical methods (e.g., geometric morphometrics) in neuroscience and paleoneurology offers a unique opportunity to study the brain-endocast relationship. More specifically, shape analyses of endocasts are based either on anatomical landmarks that represent endocranial surface features homologous to cortical convolutions (impressions of brain gyri and sulci) or on dense meshes of semi-landmarks that capture overall endocranial shape (Borne et al., 2020), or on diffeomorphic approaches (Beaudet et al., 2019; Dumoncel et al., 2020). However, debates on whether or not information inferred from the study of endocasts reflects brain shape and organization have polarized discussions in paleoneurology since the

earliest descriptions of cerebral imprints in fossil hominin crania. Indeed, the endocast is only a partial reflection of the morphology of the brain and the homology of cortical areas between species is based on their relative position to brain sulci. Of course, the resulting anatomical region may not correspond directly to a Brodmann area, which is based on histology (Brodmann, 1909) and may not be fully functionally comparable. Nonetheless, Dumoncel and colleagues (2020) provide critical evidence supporting the invaluable contribution of the brain imprints left on the fossil endocranial surfaces to our understanding of the human brain evolutionary history and for discussing key cerebral aspects in the fossil hominin record. Indeed, they found a close relationship between the shape and the sulcal pattern of the frontal, temporal and occipital lobes as well as in the inferior portion of the parietal lobes. However, the correspondence in terms of morphology and organization between the superior part of the brain and of the endocast is more questionable.

The morphoarchitecture of areas located in the frontal and temporal regions such as Broca's and Wernicke's areas could be inferred from the study of the endocast (Dumoncel et al., 2020). As we previously demonstrated, there is a moderately strong relationship between language comprehension and the brain metrics from Broca's and Wernicke's areas (the cortical thickness of Wernicke's area, in particular), contributed most to this structure-function relationship (Jäncke et al., 2020). The trend during hominin evolution has been suggested to be a reduction in size on the left compared with the right hemisphere (Balzeau et al., 2014). As the third frontal convolution projects more laterally and antero-posteriorly in the right hemisphere, the left Broca's cap looks more globular (Balzeau et al., 2014). An asymmetric third frontal convolution is a feature shared by chimpanzees, bonobos and *H. sapiens*, as well as by fossil hominin species. As a result, the relative development of specific anatomical areas on the endocasts and their degree of bilateral variation in fossil hominins cannot be used to prove/dismiss the presence of an articulated language during human evolution. Further research is needed in this

context, both to clarify the relationships between anatomy and function but also to better characterize the neuroanatomy of fossil hominin specimens. It is still challenging to demonstrate a relationship between the variation in size, shape and bilateral asymmetries of those areas and the origin of language capabilities in hominins. This information must now be considered by researchers comparing homologous brain areas in humans, non-human primates and fossil hominins. Recent results illustrate in particular that the cognitive capacities of *H. sapiens* come from a neuroanatomical substrate deeply rooted in the evolution of hominins (Beaudet, 2017; Albessard-Ball and Balzeau, 2018).

3.2 Hand preference

Stone tools and remnants of knapping are very abundant in Paleolithic sites and the oldest date from 3.3 million years (Harmand et al., 2015), making them the most accessible evidence to assess hand preference in hominins. Different studies attempted to determine hand laterality from stone tool use with different methods (see a review of successful methods applied to the archeological record, Uomini and Ruck, 2018); for example by looking at directional traces of use on the stone flakes (Rodriguez et al., 2020), dorsal cortex position (Toth, 1985), spatial organization of debitage remains (Bargalló et al., 2018), asymmetries of the tool (Brinton, 1896), or with the direction of fractures around the point of percussion (Dominguez-Ballesteros and Arrizabalaga, 2015).

Cave paintings can be used to evaluate the hand preferences of Paleolithic people by comparing the proportions of right and left hands of hand prints and hand stencils (called negative hand stencils) found on cave walls and rock shelters. Through experimentation, it was found that living right-handed humans tend to press their left hand against the wall to make stencils (Faurie and Raymond, 2004). In this context, a high proportion of left hand prints and

stencils have been found in numerous sites, with a majority of right-handed individuals (see details of these studies in Uomini and Ruck, 2018). Moreover, Nelson and colleagues (2017) recently published a study using geometric morphometric techniques allowing to successfully assess the sex of the makers of hand stencils, and opening up new perspectives for identifying individual cave painters (Uomini and Ruck, 2018).

Characteristic diagonal striations can be found on some fossil teeth (Bermúdez de Castro et al., 1988) and these striations are hypothesized to be caused by using the teeth as a third hand (Uomini and Ruck, 2018). These paramasticatory practices involved, for example, processing leather, plants and meat (e.g., Lozano et al., 2008; Uomini, 2011). Evidence of right-handedness bias has been found from the studies of the direction of striations on teeth surfaces for fossil hominins such as *Homo erectus* (Asia), *Homo heidelbergensis* and *Homo neanderthalensis* (Europe), and even geologically older hominins with one *Homo habilis* individual (OH-65) showing predominance of right oblique scratches (see Lozano et al., 2017 for a review). However, it remains unclear as to when population-level handedness first evolved within the hominin clade (Uomini, 2011; Estalrich and Rosas, 2013). Moreover, as discussed above, it is also necessary to fully understand handedness in living humans to better discuss hand preference in fossil hominins.

3.3. Directional asymmetries in arm bones

The behavior of extinct hominins can be also encoded in their skeletons. As muscles grow and are used, they cause the bones to which they are attached to model/remodel themselves (i.e., derives from the concept of bone functional adaptation; Ruff et al., 2006). Using one arm more than the other can thus cause unequal biomechanical loadings of the muscles in both arms, generating one arm bone to become thicker and/or denser than the other

(Uomini, 2015). Directional asymmetries in the upper limb are then used to identify hand preference in fossil hominins, with the dominant arm showing differences in size and robusticity than the other (Shaw, 2011; Uomini and Ruck, 2018). For example, a Pleistocene hominin with a right humerus with larger cortical thickness than the left one was found (Trinkaus et al., 1994; Sládek et al., 2016; Sparacello et al., 2017; Balzeau et al., 2020), providing evidence of right-side dominance. Studies on hand bones showed that articular constraints on the second metacarpal (Lazenby et al., 2008) and trabecular bone in the thumb (Stephens et al., 2016) help to identify hand preference in the fossil record. Surprisingly, little research focuses on directional asymmetries in fingers bones, a part of laterality and morphology research that needs to be further developed. Moreover, the fossil record mainly contains partial and fragmentary hand bones, and in very rare cases bones from both hands, which makes skeletal evidence for handedness from hands much sparser.

4. PROSPECTIVE FROM ANATOMY TO BEHAVIOR: THE PALEOBRAIN PROJECT

The discipline of paleoneurology goes beyond the determination of biological characteristics and morphologies, and can also be used to infer the behaviors of extinct species. Just as neuroscience relates present brain structure to present behavior, paleoneurology relates fossil brain structure to past behavior (Uomini, 2015). Paleoneurological evidence primarily relies on the interpretation of fossil endocasts. As discussed above, the work of Dumoncel and colleagues (2020) represents an important reference for paleoneurological studies insofar as they demonstrated that there is a close correspondence in terms of morphology and organization between the brain and the corresponding endocast. However, there remain discrepancies between the brain and the endocast. Specifically, there is a lack of correspondence between superior regions in the brain and in the corresponding endocast. Less information can be directly

related between the two structures because imprints are not clear on the endocast and the brain imaged with medical equipment is more distant from the cranial bone than other areas, particularly the base. Moreover, this study was conducted on a reduced sample (five extant human individuals; 2 females and 3 males) and through different imaging methodologies for the different analyzed anatomical parts. Future analyses will be needed to determine if their conclusions also apply to large samples of living *H. sapiens*. These analyses will have to include larger samples with a more precise knowledge of all the factors (e.g., age, sex) that are involved in the expression of the analyzed traits. This is particularly true for behavioral lateralization. Moreover, an objective characterization of the relative position of the brain sulci and the resulting imprints of the bone has to be obtained through a unique methodological framework to improve the quality of the results, following previous studies (de Jager et al., 2019, 2022). Only once the brain-endocast relationship has been tested in much detail, will we be able to apply this knowledge to study hominin fossil brain organization and then to approach the question of their cognition. Quantifying the degree of reliability of the endocast in order to enable further credible discussion of brain evolutionary changes in the fossil records is of prime interest.

In this context, a valuable output of the PaleoBrain project will be to provide more details of the correlations between the anatomy, including the asymmetries, of the brain and the endocast within a larger sample of living humans ($N = 60$; ranging in age from 20 years to 45 years; female and male), and with comparisons with the endocasts of fossil hominins. Another objective will be to investigate the potential correlation between hand preference, anatomical asymmetries of the arm and brain anatomical lateralization at the individual scale among our sample. It will open opportunities for investigating the details of the correlations, both in terms of lateralization and of magnitude, for several parameters for hand preference, bone structure of the arms and details of brain asymmetries.

4.1. Complexity of human laterality

As mentioned in Uomini and Ruck, (2018, p. 306) “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”. In order to have a robust individual profile of laterality and to better understand the functional interaction between the different parts of the body, we have to consider other lateralized behaviors in addition to handedness. But, so far, investigations of laterality have not taken this into account, handedness being the most studied lateralized behaviors. A recent *Live science* project at the London Science Museum called “Me, Human”, and directed by Gillian Forrester, explored a variety of lateralized behaviors and cognitive performance in more than 1,600 individuals throughout the lifespan, as well as the relationship between hand form and function (Bardo et al., 2021, 2022). However, this “Me, Human” project was limited by the rules of the *Live Science* scheme (i.e., a project in which scientists can carry out research in the museum using visitors as volunteers) of the London Science Museum with a specific amount of time in which the participants could do the experiments. As a result, the data set does not provide complete individual profiles of laterality and dexterity. In our upcoming project, we will explore the potential relationship between different organization profiles (i.e., laterality profiles such as right-hand, left-eye and right-ear dominance) and performance of participants (ranging in age from 20 years to 65 years; N = 120 females and males). At first, they will be asked several lifestyle-related, multiple-choice, binary questions with regards to their laterality (wide variety of questions about daily life), occupation, and whether they play manual sports or musical instruments. Then, they will also take part in several experiments: (1) experiments measuring hand strength (grip and pinch strength) and shape (both hands of each participant will be digitized for measurements using a flatbed scanner); (2) experiments measuring dexterity in

both hands; (3) the ‘dichotic-listening test’ (see 2.1); and (4) the ‘visual test’ to determine the dominant eye. Our aim is to detail as much as we can the different behaviors in relation to the anatomy of hands and arms of participants as well as in relation to their lifestyle factors. Indeed, the effect of lifestyle factors on dexterity, manual strength and laterality on the human hand needs to be further investigated to fully understand if manual laterality is really important in our daily life and if manual laterality is plastic and thus varies according to our personal life experiences (Bardo et al., 2021, 2022). Finally, this data will be considered in relation to anatomical features of the endocast/brain. In summary, participants will provide corresponding behavioral and neuroanatomical data as they answer the handedness survey, do the experiments on brain and body function, and we will also obtain structural MRIs of their brains (described below). These exploratory analyses will be essential to fully understand the relationship between functional asymmetry of the human brain and behavioral observations.

4.2. Endocasts: from living humans to fossil hominins

In this section, our main objectives are to (1) explore the relationship between the brain and the endocast in living humans in order to (2) evaluate if the brain endocast is a reliable proxy for studying the evolution of the brain. To do so, our laboratory is currently combining analysis of the brain and the corresponding endocast of a sample of living humans (N = 60; selected among the participants of the behavioral experiments explained above). Concerning the MRIs, multiple sequences will be used, including T1-weighted (produced by using short time to echo and short repetition time) and UTE (ultra-short time to echo; used to characterize the cortical bone). The brain is segmented from the T1 and the endocast from the UTE, and sulci will be detected and identified on the brain and endocast (Figure 1), using the freely distributed software BrainVISA (Geffroy et al., 2011). The shape of the brain and the endocast,

as well as the sulcal patterns of the brain and endocasts, will then be directly compared using complementary approaches through qualitative comparison, qualitative evaluation of the variation between individual characterization of both imprints, distance measure between sulci and imprints on the endocasts, and characterization of absence/presence of imprints on the endocranial surface at the exact location of brain sulci. We will then describe the morphology, which means the global (i.e., volume) and regional (i.e., lobes) shape, and structure, which means the position and spatial relationships of the sulci, of the brain and the endocast. This will contribute to the study of the variation in anatomical features, such as the disposition of the lobes and the relative position, extension and expression of the sulci. We will also consider the potential relationships between anatomical features of the endocast/brain and other biological aspects such as sex, age, manual laterality. The obtained knowledge on the relationship between the brain and the endocast will be also used to look at the endocast of fossil hominins under a new perspective to extend previous qualitative studies of these features. Indeed, once we have acquired a better understanding of this relationship within our own species, we will be able to use this model to address the inverse relationship between the shape of the endocast and a reconstructed brain in selected samples of well-preserved specimens that are crucial for characterizing important and debated hominin species (see the website of the project here: <https://paleobrain.jimdofree.com/>).

[INSERT FIGURE 1 HERE]

5. CONCLUSION

As we do not have direct access to the details of the behaviors of fossil hominins, the question of manual laterality in extinct hominins has long been of interest in archeology and

paleoanthropology. This is related to the broader question of when our rightward-biased pattern of hand use emerged in the hominin lineage. Moreover, interest in determining handedness in ancestral species has often been motivated by the question of whether these hominins had language. However, while data exist on living humans, the main limitation is the application of this knowledge resulting from separate studies of the brain, of biological adaptation of the skeleton to lateralized behaviors and hand preference, to fossil specimens. With the PaleoBrain project, we will show that important but complex information may be extracted from the combined study of behavioral lateralization and anatomical asymmetries at the level of the arms and the brain. We hope to bring original data about brain-related capacities such as manual lateralization, language and their emergence during hominin evolution. It is hoped that this overview of multiple disciplines of laterality has provided a greater appreciation of how they can be combined to gain a truly deeper understanding of the evolution of human cognition.

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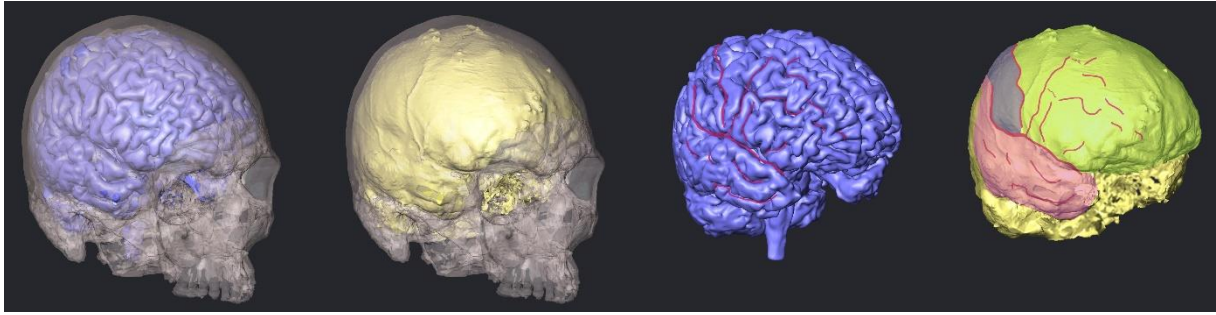


Figure 1. Complementary imaging acquisitions on volunteers. The brain anatomy will be observed using complementary imaging acquisitions on volunteers and the data will be used to extrapolate the correspondence of its surficial features on virtual endocasts. From left to right, the skull is shown by transparency and reveals the brain in blue and the endocast in yellow. The red lines on the brain are the main sulci identified directly on this model, they are projected on the endocast to show the extension of the frontal lobes (in green), of the right parietal lobe (in purple) and of the right temporal lobe (in pink).