Limb Preference in Animals: New Insights into the Evolution of Manual Laterality in Hominids

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Abstract: Until the 1990s, the notion of brain lateralization—the division of labor between the two hemispheres—and its more visible behavioral manifestation, handedness, remained fiercely defined as a human specific trait. Since then, many studies have evidenced lateralized functions in a wide range of species, including both vertebrates and invertebrates. In this review, we highlight the great contribution of comparative research to the understanding of human handedness' evolutionary and developmental pathways, by distinguishing animal forelimb asymmetries for functionally different actions—i.e., potentially depending on different hemispheric specializations. Firstly, lateralization for the manipulation of inanimate objects has been associated with genetic and ontogenetic factors, with specific brain regions' activity, and with morphological limb specializations. These could have emerged under selective pressures notably related to the animal locomotion and social styles. Secondly, lateralization for actions directed to living targets (to self or conspecifics) seems to be in relationship with the brain lateralization for emotion processing. Thirdly, findings on primates' hand preferences for communicative gestures accounts for a link between gestural laterality and a left-hemispheric specialization for intentional communication and language. Throughout this review, we highlight the value of functional neuroimaging and developmental approaches to shed light on the mechanisms underlying human handedness.

Keywords: handedness; grasping; gesture; brain asymmetry; vertebrates; invertebrates; primates; ontogeny; evolution

1. Introduction

Humans exhibit a strong right hand preference for manual actions, which is consistently observed across tasks at the population-level and is so referred as "handedness" [1,2]. Recent meta-analyses assessed more precisely the strong manual bias observed for manipulating items and for different manual tasks. Handedness is usually assessed using questionnaires (e.g., Annett's Hand Preference Questionnaire, Edinburgh Handedness Inventory, Rennes Laterality Questionnaire [3–5]) asking for the preferred hand (right vs. left) when performing a variety of manual tasks: the hand used for writing, for using different tools (e.g., hammer, scissors, toothbrush . . .), performing tasks like unscrewing a lid or threading a needle, or to communicate through iconic, symbolic, or deictic gestures (i.e., physically representing a shape or movement, having arbitrary meanings, or directing other's attention, respectively). While 10.6% of the human population shows a left hand preference, the right-handedness prevalence lies thus around 90% [6]. It is to be noted that values may vary according to the way handedness is measured and exclusion

criteria for certain categories of the population (e.g., elite athletes), as highlighted in the five meta-analyses run by Papadatou-Pastou et al. [6].

However, even if this manual bias exhibited for reaching, grasping, and manipulating objects or even interacting and communicating with conspecifics is being better assessed, the mechanisms underlying human handedness are still widely debated on both theoretical and empirical grounds. The large corpus of studies on this topic suggests that, besides genetic factors, non-genetic environmental factors play a significant role and need further considerations [7–9].

The presence of such a population-level right-side bias (i.e., similar proportions) has been demonstrated in hominin species prior to *Homo sapiens*, namely in *Homo neanderthalensis* [10]; as evidence of this, previous studies investigated asymmetric morphological traits of the fossil record like asymmetries in the humeral shape or dental striations, but also asymmetrical retouch patterns on Paleolithic artifacts (i.e., when producing stone or bone tools [11]). In *Homo habilis*, on a maxilla dated to ~1.8 mya (OH-65, found in Olduvai Bed), Frayer et al. [12] documented the earliest evidence for right-handedness (i.e., oblique labial striations) in the hominin fossil record. Another category of evidence from fossils are the asymmetries of the endocast (i.e., cranial vault) as some authors suggested specific patterns of the petalias (i.e., one of the brain hemispheres protruding towards the other, causing an impression on the inner surface of the skull-that can still be visible in fossil skulls) to be associated with right- or left-handedness [10].

Indeed, the evolution of the human brain led to a cerebral lateralization: while some organs are duplicated (i.e., kidneys, lungs), the two hemispheres of the human brain display a functional specialization associated with structural asymmetries [13–15]. This dissociation of specialized processes of left and right hemispheres permits to optimize the associated functions, for instance the language for the left hemisphere, and emotional signals' processing for the right one [16,17]. As the nerve fibers of the motor cortices are contralaterally innervated, the dominant hemisphere processes can manifest as contralateral motor behaviors [18], such as handedness.

Cerebral lateralization is not specific to humans and has been well established in many other vertebrates such as birds, fishes, and amphibians (see [19] for a review; [20,21]), and forelimb preferences (at the individual or population level, for one specific task or across tasks) have been widely demonstrated among non-human animals [9,22]. Cerebral and associated behavioral lateralizations may be beneficial for animals in terms of cognitive and motor performance, notably permitting spatial gain within the brain [21,23] or the processing of several simultaneous tasks [24–26].

Because of the hemispheric specialization, hand use may be mainly processed by different brain hemispheres according to the action performed, and shows differences in lateralization (right- versus left-hand dominance). In this review, we present the results of studies conducted in a wide variety of species (including both vertebrates and invertebrates) that allow us to discuss the potential mechanisms underlying human handedness by identifying three categories of "manual" actions: (1) towards inanimate targets, (2) towards animate targets (i.e., self, conspecific)—that may involve emotion processing, and (3) communicative gestures—involving language-related functions. Comparative research done in the past years has been a real opportunity to better understand the different functions in which limb use is lateralized, and thus better assess the adaptive explanations for the evolution of limb lateralization by better understanding the different selective pressures that may have driven this evolution. Recent studies have also further considered that—besides adaptive explanations—the acquisition of handedness may be related to variations in developmental trajectories in other traits across ontogeny.

2. Current Developmental and Evolutionary Hypotheses on Object Manipulation Laterality

2.1. Is Handedness Genetically Determined?

In humans, as hand preferences run in families, many studies in the past worked on a genetic model [27–30], but no gene has been linked to the expression of handedness. Running genome-wide association analyses (GWAS) with large sample sizes, recent studies investigated more precisely how many loci are involved in determining handedness: the results of the GWAS showed only a handful of significant associations [31–33]. For instance, Cuellar-Partida et al. [31] analyzed data collected on a considerable sample of 1,766,671 individuals (right-handed: 86.88%; left-handed: 10.99%; ambidextrous: 2.13%) and GWAS revealed only 48 statistically significant variants. Furthermore, a meta-analysis on handedness in twins showed that the rate of handedness concordance was higher in monozygotic twins compared to dizygotic twins [34], supporting the idea that genetic factors do play a role in the determination of handedness. However, the heritability of handedness in humans has been evaluated around 24% [30], which is a relatively modest value showing that genetic factors explain less than one quarter of the variance in human handedness, thus contributing only partially to handedness. Also in mice, if the degree of paw preferences is under the influence of genetic effects, these effects only drive the direction of the preference a little; it is to be noticed, however, that some studies brought out that different strains of mice differ in strength and direction (for a meta-analysis in mice, *Mus musculus*, *Apodemus agrarius*, and rats, *Rattus rattus*, see [35]).

These results suggest that other nongenetic factors may also play a significant role in the development of handedness, explaining the remaining variance. In this regard, investigating limb preference in animals brings further elements to better picture all the factors that may affect the development of this trait.

2.2. The Insights of Ontogeny

As nongenetic factors that may influence the acquisition of handedness, a growing number of studies investigate early life parameters. For instance, still in the mice animal model, it has been reported that prenatal stress can affect paw preference pattern, even transgenerationally via epigenetic mechanisms [36,37]. As the mother acts on the immediate developmental environment of the fetus and then of the infant [38], some works focused on potential effects of mother-infant interactions during ontogeny. Since the maternal intrauterine environment is asymmetric [39], it has been suggested that the position of the fetus may play a role in the development of lateralization in the motor system [40,41], such as handedness. In humans, according to Ververs et al. [42], there is a clear lateral bias at 38 weeks of pregnancy for a rightward head turning. A majority of human fetuses seem to place their back on the left side of the mother because of asymmetries of the pregnant uterus shape. For cephalic fetuses (i.e., positioned head-down, which is the majority case) lying on the left maternal side, a rightward head turning could be explained by the fact that it allows them to face maternal movements when walking, or also because the maternal front part is clearer, exposing the fetus to more light but also to more tactile and auditory stimulations [43]. Ultrasound scans made it possible to demonstrate that limb movements emerge during fetal life: young human fetuses already grab the umbilical cord, push the uterine wall, and even repeat hand-mouth contacts [44,45]; while unimanual movements are visible between 8 and 10 weeks of gestation, hand face contacts are recorded from 12 weeks [46,47]. A consequence of the asymmetry in head position for hand use may be that in case of a rightward head turning, the fetus' right hand is more likely to touch the mouth than the left one, which may consequently "encourage movements of the right arm more than the left (...) as the fetus becomes sensitive to sensorimotor contingencies" [43]. Thumb sucking, with a rightward bias, is a very early demonstration of manual asymmetry, observed in utero [48].

Just like in humans, some non-human primate species such as chimpanzees (*Pan troglodytes*), gorillas (*Gorilla gorilla*), and olive baboons (*Papio anubis*) show an interesting

asymmetry in maternal cradling behavior. Not only do mothers show a bias at individual-level but also a left-side bias at population-level, which means the use of left arm is favored over the right arm to cradle the infant in a majority of individuals [49,50]. In chimpanzees, Hopkins et al. [51] have found an inverse relationship between this maternal ventro-ventral cradling bias and the offspring hand preference for simple reaching at the age of 3 years. In olive baboons, if cradled on the left, the infant embraces and holds onto the left side of the mother with its right arm, the left hand being free, and vice versa. The hand that is not recruited for clinging on the fur is free for reaching and fine manipulative grasping actions, involving potentially greater motor and neurological stimulation than the other hand. In fact, in this species, early postnatal individual hand preference for unimanual grasping within the first months of age has been positively correlated with the maternal cradling lateralization (infants cradled on the left side of the mother are left-handed, and vice-versa; [52]). Hand preferences assessed later in the development, from 9 to 10 months of age, are less dependent on maternal cradling bias and less consistent with the earlier developmental stages, especially in infants initially cradled on the right maternal side. These findings suggest that maternal cradling behavior might be the first environmental factor that affects the development of early handedness in infant monkeys before being weaned from the mother and letting other mother-independent factors change its onto-genetic trajectory. As maternal left-cradling bias likely reflects brain right hemisphere specialization for emotion [53–55], the early emergence of handedness in baboons might be indirectly related to emotion processing. In Barbary macaques (*Macaca sylvanus*) as well, early life asymmetries in mothers' and infants' behavior seems to affect the development of hand preference: while maternal cradling is lateralized at individual-level, the infants' nipple preference is correlated with their hand preference [56]. However, early postnatal infant lateralization remains poorly investigated in non-human primates. In human and chimpanzee neonates, the only few data available so far reported manual performance asymmetries in the strength of grasping responses [57,58]. In a few other primate species, data on the development of manual grasping and its early lateralization are available at juvenile stages: in capuchins (in *Sapajus apella*, an individual hand preference by 5–6 months of age [59,60], marmosets (in *Callithrix jacchus*, an individual hand preference for unimanual reaching by 5–8 months [61], and rhesus macaques (in *Macaca mulatta*, a population-level bias for both unimanual reaching and bimanual tasks by 4–11 months [62]). Regarding the ontogeny of limb preferences in non-primate species, Wells and Millsopp [63] investigated the development of paw preferences in the domestic cat (*Felis silvestris catus*) and reported a significant effect of age: while individuals were more ambilateral at 12 weeks of age than at later developmental stages, paw preferences at 6 months and at 1 year of age were positively correlated. In marsupial species, the red-necked wallaby (*Macropus rufogriseus*) and the eastern gray kangaroo (*Macropus giganteus*) show a left-forelimb preference (for manipulating food) at population-level as soon as the pouch young stage (approximately 6–7 and 7–9 months old, respectively) [64]. In the eastern gray kangaroo, the authors compared limb-preferences in manipulative behavior at different developmental stages, namely before and shortly after individuals display the bipedal posture (young-at-foot, approximately 11–15 months old): as they observed no difference between these two juvenile stages and the adult stage, the authors concluded that "manual lateralization in bipedal marsupials is not determined by the acquisition of habitual bipedality" but precedes it in the course of ontogenesis [64] (p. 1). Interestingly, in the American lobster crustacean species (*Homarus americanus*), while normal differential claw use during on-togeny induces one claw to transform into the specialized crusher claw, induced insufficient stimulation in laboratory conditions during a specific developmental stage leads to no specialization [65,66], highlighting the strong role that behavioral asymmetry may have "inducing and orienting morphological and subsequently functional asymmetry" [9].

2.3. Brain Correlates of Lateralized Manual Actions

At adult stage, the asymmetric use of the hands for manipulative manual tasks in humans has been correlated to contralateral brain structural asymmetries within a section of the central sulcus related to the motor hand area [67]. Outside the human species, cerebral lateralization has been well established in many other vertebrates such as birds, fishes, and amphibians (see [19] for a review; [20,21,68]. Direction and degree of hand preference for a bimanual task (i.e., tube task, see [69] in nonhuman primates such as baboons, capuchin monkeys, or chimpanzees have been found to be associated—just like in humans—with contralateral neuro-structural asymmetries in the primary motor cortex including the surface of the motor hand area surface, its neuronal densities, or its adjacent central sulcus depth [70–75]). Furthermore, as in humans, the hand preferences tested in a large population of adult olive baboons, for both unimanual and bimanual tasks, are consistent over time [76].

Regarding non-primate species, Australian parrots' footedness is correlated with eye lateralization for discriminating food items, supporting—according to the authors—a functional explanation for the evolution of handedness in vertebrates (Figure 1) [77]. A recent study investigated the association between brain size and parrots' (psittacine) foot preference [78]. It has been shown that cerebral lateralization enhances the brain capacity by allowing parallel processing of sensory information (e.g., to forage efficiently while remaining vigilant for predators) [26]. As the Australian parrot species known for having foot preferences also has a better ability to perform certain manipulative and cognitive tasks compared to species with no foot preference [79], Kaplan and Rogers [78] asked the following question: «Do species with footedness have larger brains, or is footedness a way of compensating for having a smaller brain?» (p. 2). The authors found in several Australian parrots that species with larger brains (i.e., absolute brain mass) have stronger foot preference and that left-footedness is stronger in species with a larger brain. Moreover, the authors found foot preference to be associated with the size of a brain area (i.e., the nidopallium) recruited for higher cognitive tasks, so that species with stronger left-foot preferences have larger brains, with a larger volume of the nidopallium (compared to the whole brain) [78].

Figure 1. A blue-and-yellow macaw (*Ara ararauna*) opening a box to retrieve a food reward (i.e., a nut) using its left foot and its mouth (at the Ménagerie du Jardin des Plantes, MNHN, Paris). See Brunon et al. [80] for a description of the manipulative repertoire of blue and yellow macaws. Photograph credit: Emmanuelle Pouydebat.

Interestingly, even if the eight arms of octopuses (*Octopus vulgaris*) were traditionally thought to be equipotential, Byrne et al. [81] demonstrated a preference for frontal arms in reaching and exploring objects, as well as a preference for a specific arm to reach into a maze and retrieve a food item. Given the structure of the octopus neural network with each arm possessing its own network operating it (i.e., all arms being coordinated by a central hub in the head), it would be interesting to investigate whether cerebral asymmetries related to limb preference are shaped in these species.

Several structural asymmetries have been observed in the fetal brain, during human development [82–86]. Further studies, benefitting from the improvements in MRI technology, should help to determine whether contralateral hemispheric specialization of the brain within the central sulcus is present at early developmental stages, its potential change across ontogeny, and whether it predicts hand preference at later stages.

2.4. Morphological Limb Specialization

A recent study (published in this volume) assessed grip strength—a common indicator of overall muscle strength—in a large sample of humans (i.e., 662 individuals aged 17 to 83 years), testing the effects of hand dominance (i.e., asymmetric use of the dominant vs. the non-dominant hand, without considering the left-right direction) and handedness [87]. The authors found that both males and females are significantly stronger with their dominant hand compared with their non-dominant hand; however, they found no significant difference in grip strength between right- and left-handed individuals [87].

Whether limb preference is associated with asymmetric body traits in the limb morphology is especially visible in crustaceans, namely the brachyuran crustaceans (i.e., crabs) and lobsters. For instance, In American lobsters, if both the left and right claws are initially similar, they transform during a given developmental stage and become morphologically different: one being a large slow-acting (i.e., closing slowly, made of only slaw muscle fibers) "molar-toothed" crusher claw, and the other being a minor fast-acting (mainly fast fibers) "incisor-toothed" cutter claw; both being used when foraging [65,88]. The pattern of this claw asymmetry in American lobsters appears to be random, with half of the population having the major claw on the right and the other half having it on the left side [9]. Such a 1:1 ratio in limb asymmetry suggests no advantage to any of the two groups. Additionally, in fiddler crabs (genus *Uca*), while a few species have been reported to be predominantly right-clawed (i.e., major claw on the right side; with a population-level bias greater than 95%), most species show populations with equal numbers of right-clawed and left-clawed individuals (for a review, see [89]). These differences in limb (i.e., claw) asymmetry between crab species make it difficult to conclude whether this trait is under selective pressure or a bimodal trait [90]. Perhaps, next studies may further investigate the differences observed between these species by carefully taking into consideration the functional context in which asymmetric claws are used: whether there are more recruited in feeding behaviors or in interactions towards conspecifics (i.e., animate targets) like courtship or fights. Interestingly, in the males of the *Uca vocans dampieri* species—which fight using their enlarged major claw—it has been shown that only 1.4% of males are left-clawed, and that being left-clawed was a disadvantage for fighting (i.e., left-clawed males were both less likely to engage in a fight and less likely to win a fight; [91]).

2.5. The Effects of Posture and Locomotion Mode

If several primate species display a right-hand preference for bimanual manipulative tasks that is associated with a left-hemisphere specialization, some other primate species—namely lemur species—show a left-handedness for reaching food items, suggesting right hemisphere prehension specialization (for reviews, see [92,93]). Facing this paradoxical finding of left-handedness in strepsirrhine species (e.g., sifakas, black lemurs, indris), Mac-Neilage et al. developed in 1987 the "Postural Origins (PO) theory" as an evolutionary theory of handedness in primates [93–95]. The PO theory relies on the fact that several strepsirrhines species show a "vertical clinging and leaping" [96] locomotor style and display

unimanual predation: one side of the body ensures anchor to the substrate while the other grabs the prey [93,97]. The authors thus suggested two complementary specializations: a "left hand-right hemisphere specialization for unimanual predatory prehension" and a specialization of the right side of the body for postural support that would be controlled by the left hemisphere [93,97]. Even if the PO theory focuses on primates, it is interesting to report that several parrot species—which are not primate, nor mammal species either—show a similar left-footedness predominance for grasping and holding food items while they use their right foot for perching or climbing (also using their beak to help them climb), (for a review, see [98]).

The PO theory further suggests that given "the greater physical strength of the right side of the body", the right hand would have become "the operative side", favored in object manipulation, in primate species abandoning the vertical clinging locomotor style-giving the forelimbs more freedom with regard to postural support—and showing a more omnivorous diet requiring more manipulative skills for foraging. An interaction between effects of postures and arborealism on the direction of grasping laterality is indeed observable in primate species, being biased in favor of the right hand in terrestrial and bipedal species and of the left hand in arboreal, quadrupedal ones [99–102]. For both a unimanual task (food grasping of grains) and a bimanual task (i.e., tube task: the two hands are used in an asymmetric but complementary matter, e.g., holding a tube with one hand and removing the food inside a tube with the other hand), adult olive baboons, which are mainly terrestrial monkeys, show a right-handedness predominance at population level [76]. Moreover, capuchin monkeys are well known as tool users [103], namely stones to crack nuts, and display a right hand preference for feeding [104] and coordinated-bimanual tasks [105]. Human right-handedness may have then derived from a selective pressure for tool use or coordinated bimanual manipulations [9]; as MacNeilage highlighted in his review, the conclusion of the Hook-Costigan and Rogers [104] study suggested that "tool use and right handedness may have evolved before bipedalism, and well before the apes and, indeed, humans evolved" (p. 195), although bipedalism seem to strengthen right-biased manual laterality consequently to the suppression of the locomotory function of hands [60].

If a large body of literature documents the lateralization of the primate limb motor systems at both individual and population levels [76,93,104,106–108], there is very little comparative research of manual lateralization in non-primate mammals [9,22]. Giljov et al. [109] assessed handedness in marsupial species, one of the other large mammalian lineages. The authors reported a population-level manual preference for multiple behaviors (e.g., unimanual feeding, grooming) in red (*Macropus rufus*) and grey (*Macropus giganteus*) kangaroos, which mainly display a bipedal gait, freeing the hands to perform other tasks. By comparing mainly bipedal and quadrupedal marsupial species, Giljov et al. [109] highlighted the crucial role that postural characteristics (i.e., bipedality), rather than phylogeny, may have play in the origin of handedness in mammals, beyond the order of primates.

These works on lateralization open many perspectives of comparison within tetrapods: the questions addressed and the new ones that arise can be applied to other species outside primates. However, it has to be noted that interspecies comparisons of handedness measured using different tasks has to be done carefully. A task effect related to variation in motor demand has been reported in several studies in both humans and non-human primates: namely, differences between unimanual and bimanual tasks when assessing the hand preference: handedness in unimanual grasping seems to be not as strong as in bimanual grasping [76,110–112], but also less sensitive than bimanual manipulations in detecting population-level bias [113,114]. About the literature focusing on humans, Fagard and Marks [110] highlighted that the use of different tasks to measure handedness (i.e., asymmetric bimanual actions vs. unimanual actions, reaching vs. manipulation) led to contradictory interpretations. To better assess the validity of the PO theory, for instance, handedness in strepsirrhine species should be additionally assessed for a bimanual coordinated manipulation such as in the tube task.

In addition to the above-cited observations suggesting that species locomotory style affects manual laterality, the PO theory is supported by findings on postural effects at the individual level in several mammal species. Indeed, an increased manual preference can be observed in human and non-human primates performing manual tasks in a bipedal compared to quadrupedal posture [60,115–118]. Similar observations have been made in other mammals, such as red-necked wallabies (*Macropus rufogriseus*) [115] (but see absence of postural effect in tree shrews, *Tupaia belangeri* [119], and in cats, *Felis silvestris catus* [120]). This corroborates the hypothesis that the need for postural support acts as a constraint on hand availability for manual actions, and so on manual laterality. The PO theory proposes this as a critical evolutionary mechanism which would have shaped handedness emergence.

2.6. Social Origins of Manual Laterality

The fact that social animals exhibit population-level forelimb preferences [22] also led to the hypothesis that the alignment of individual lateralization may be under specific social constraints. An evolutionary theory has been proposed regarding lateralities at the population level, which postulates that the alignment of individual lateralizations favors the coordination and cooperation between individuals of the same social group [21,121–123]. First supported by observations of population-level behavioral asymmetries in social vertebrates (e.g., of flight behavior in fishes, [124]), this theory is also corroborated by group-level lateralizations of social invertebrates compared to solitary ones (see for review: [125]), suggesting a wide phenomenon in animal phylogeny.

In the case of manual actions, social constraints on laterality may arise from the need for inter-individual coordination to perform complex tasks and from social learning. The acquisition of tool use, for instance, may be facilitated if the learner uses the same hand as the teaching expert [123]. Parental hand preferences have been shown to affect the development of children's handedness, notably through social play involving object manipulation [7]. Diverse other social factors affect individuals' hand preferences [37], resulting in slight variations in the rate of left-handedness across different geographical and cultural regions [6,126,127]. One of the most striking examples of cultural pressures modulating handedness might be the constraints exerted against left-handedness for writing and eating, which directly affects the development of children hand preference [128,129].

In spite of these social constraints and of the advantages of the alignment of individual lateralization for intragroup coordination, one can note that in all species in which we observe a population-level laterality (including humans), there still exist a certain proportion of individuals lateralized in the opposite direction compared to the majority of others. Ghirlanda et al. [130] suggested that the frequency of minority laterality results from a costs-benefits balance of behavioral lateralization. Although the alignment of laterality is beneficial for cooperation, it disadvantages individuals in competition contexts, as their decisions become more predictable [24]. In humans, left-handers are indeed more frequently represented in competitive sports, and seem to benefit from strategic advantages (e.g., in tennis [131]). Recently, a large-sample study on professional boxers evidenced greater success for left-handed subjects [132], supporting the hypothesis that fighting interactions may have constituted an evolutionary constraint in favor of left-handedness in humans [133]. As individual- and population-level behavioral lateralizations amongst a species may result from the relative frequencies of cooperative and competitive social interactions [130,134], it may be hypothesized that the high proportion of right-handedness in humans results from a high need for inter-individual cooperation and coordination in manual tasks [135].

While the process of manipulating inanimate objects involves a left-hemisphere specialization (as shown by the contralateral left-brain asymmetries present in the predominant right-handed individuals), a growing number of studies in vertebrates support the idea that the grasping function when involved in interactions with animate targets (i.e., conspecifics, self) is processed differently, namely in relationship with the hemispheric specialization for emotion processing.

3. Manual Laterality for Living Object Manipulation and the Role of Emotional Lateralization

Along with the hypotheses previously mentioned regarding the origins of manual laterality, behavioral asymmetries in animals suggests that hemispheric specializations for specific cognitive mechanisms, such as emotion processing, might have driven the lateralization of associated manual tasks. In gorillas and chimpanzees, hand preference for manipulative actions has been shown to depend on the living nature of the target objects [136,137]. Although these apes exhibited a right-hand bias for inanimate object manipulation (i.e., objects and environment), they used the left as much as the right hand to act toward animate objects (i.e., self or conspecifics), supposedly because self- or socially-directed actions imply emotional processes in addition to manipulative ones. Recently, Baldachini et al. [138] reported concordant observations in Barbary macaques. Although the animacy of targets did not affect the direction and strength of manual laterality at the population level, individual lateralizations differed depending on whether actions were directed to an object or to a living being. These results are in favor of the hypothesis of (socially-driven) emotions affecting the laterality of manipulative actions.

3.1. Current Hypotheses on Emotional Lateralization

Different theories have been formulated and co-exist regarding emotional lateralization in vertebrates, i.e., to explain the differential involvement of the two brain hemispheres in the processing of emotions (see for reviews [139,140]). The "Right hemisphere theory", which postulates that the right hemisphere is specialized in both positive and negative emotion processing, is particularly relevant to explain the asymmetries which are observed in the expression and perception of emotional signals [16,141,142]. Notably, the facial and vocal expressions of emotions are associated with leftward oro-facial asymmetries in humans and other primates [143–147]. Moreover, behavioral leftward-biases have been evidenced for the perception of emotional stimuli (including intraspecific or interspecific signals) in numerous species ([148]; e.g., in humans [149,150]; chimpanzees [151]; olive baboons [152]; vervet monkeys, *Chlorocebus pygerythrus* [153]; and dogs, *Canis familiaris* [154,155]). Other theories suggest that both hemispheres are involved in emotional processing but that the left and right side of the brain are differently involved depending on the emotional valence or motivation elicited by the context. The "Valence theory" thus proposes that the right hemisphere is involved in the treatment of negative emotions, frequently associated with withdrawal behaviors, and that conversely, the left hemisphere is responsible of the processing of positive emotions, frequently associated with approach behaviors [156–158]. The theory has been supported by behavioral asymmetries expressed by numerous vertebrates in contexts with different emotional valences [148,155]. In the last decades, this assumption has been updated by differentiating affective hypotheses (i.e., the left and right hemispheres are respectively associated with positive and negative emotions) from motivational hypotheses (i.e., the left and right hemispheres are respectively associated with approach and withdrawal/flight motivations). This idea is strengthened by the fact that a positive relation was found between right-handedness and approach motivations in captive chimpanzees in an experimental context [159]. A similar association was observed in Geoffroy's marmosets (*Callithrix geoffroyi*), in which right-handed individuals presented with novel objects seemed less fearful and exhibited more frequent approach behaviors than left-handed subjects [160,161]. Although affective and motivational hypotheses have long been amalgamated, they can result in contrary predictions for some contexts such as aggressivity, which involve both negative emotional states and high approach motivations [139,162–164].

Some authors propose that the affective hypothesis may explain how the valence of a particular situation is experienced by individuals, whereas the motivational hypothesis may account for the decision-making process to approach or avoid an emotional stimulus [162,163,165]. It is to note that these different theories might all be compatible with one another, as they relate to different levels of cerebral processing of emotions [140,166].

As we may assume that self- or socially directed manual actions are more likely than others to be underlined by specific emotional states, the associated hand preferences may be representative of the role of emotional lateralization in the evolutionary and developmental history of handedness.

3.2. The Case of Self-Directed Manual Actions

Behaviors such as scratching or self-grooming may be identified as "displacement activities" in response of social or predatory stress in primates [167–172]. Therefore, several primatology studies have addressed the potential brachio-manual asymmetries in self-directed actions commonly considered as indicators of negative emotional states, but have led to discordant results. Some revealed a left-hand preference for self- touching and scratching in great apes, as expected according to both the "Right hemisphere hypothesis" and the "Valence theory" considering the negative emotional state associated with these behaviors, such as anxiety (in humans, gorillas, chimpanzees, and orangutans [173–175]). Human children exhibit similar leftward bias for actions directed to self [176], and left-handed face touch in fetuses has been evidenced to be associated with maternal stress [177]. Other studies showed a preference for the right hand for self-scratching in squirrel monkeys [178] and for self-rubbing but not scratching in chimpanzees under stressful situations [179,180], highlighting the effect of the type of self-directed on laterality. Bard et al. [181] also evidenced a right-hand preference for self-calming behaviors in young chimpanzees under human care (e.g., "hand-to-mouth" behaviors, such as thumb sucking, and "hand-to-hand" grasps, i.e., holding and pressing one hand with the other). Authors interpreted it as resulting from the left hemispheric specialization for anxiety regulation in mammals, and notably for dopaminergic reward circuits whose activity is affected by stressful stimuli [182–184]. Finally, other research works did not show any lateral bias for self-directed manipulation in primates [173,178,185–187], though it is to be noted that they were based on small samples of subjects, which may prevent the evidence of a population-level bias [188,189]. Very few studies in other animals as in primates reported forelimb laterality for self-directed actions (e.g., no lateral bias for autogrooming in rats and mice: Stieger et al., 2021), but noteworthy results on these topics arose from marsupial studies [109]. Comparably to the leftward lateralization of self-touching observed in great apes, red-necked wallabies (*Macropus rufogriseus*), Eastern grey kangaroos (*Macropus giganteus*), and red kangaroos (*Macropus rufus*) preferentially use their left limb for autogrooming in bipedal position [64,109,115], which suggests similar hemispheric specialization for emotional control in these marsupials than in primates. Interestingly, such lateralization for self-touching has not been reported for the Goodfellow's tree-kangaroos, *Dandrolagus goodfellowi*, which is mainly arboreal, suggesting some effect of species characteristics [109].

3.3. Laterality of Conspecifics-Directed Manipulative Actions

A difference in hand preference between unimanual interactions with inanimate targets (i.e., food, objects) and physical contacts made toward a conspecific has been reported in ape species-chimpanzees and gorillas: in the two studies conducted by Forrester et al. [136,137], while a group-level right hand preference for interaction with inanimate targets was confirmed in these species, no right-handed bias was reported toward conspecifics, further suggesting that manual lateralization reflects right- or left hemisphere processing according to the emotive or functional characteristics of the target. The right hemisphere of vertebrates seems specialized for the processing of social information, notably for the purpose of emotional signal perception [16,141,142] or individual recognition [190]. This may result in a higher involvement of this hemisphere for performing manual actions directed towards conspecifics compared to manual actions directed to inanimate objects, resulting in a higher use of the left side of the body.

Interestingly, forelimb actions directed to conspecifics may also be lateralized in invertebrate species. A greater involvement of the left body part in interactions towards conspecifics has been observed in insects: for instance, in the Mediterranean fruit flies

(*Ceratitis capitata*, "medflies"), Benelli et al. [191] observed a left-biased population level lateralization of aggressive displays executed with their forelegs. In fact, during a fight, when boxing with their forelegs (i.e., the boxing attacker raises a foreleg, hitting the opponent on the head or thorax), a majority of medflies (almost 70%) were "left-handed" (i.e., performing with their left foreleg significantly more than with their right one); moreover, the authors reported that performing aggressive displays with the left body parts (including foreleg and wing) enhanced fighting success compared to those performed with right body parts [191]. This lateralization in insects may not be homologous (i.e., be inherited from a common ancestor) to the left-hand/right-hemispheric preference observed in vertebrates for socially-directed actions, hence it reflects the possibly ubiquitous nature of the constraints that social interactions represent on the lateralization of social animals' behaviors [192].

3.4. The Case of Maternal Cradling

A phenomenon that raised lots of questions is the maternal left-cradling bias that has been demonstrated in humans (66–72% [193]) but also in great apes (chimpanzees and gorillas [50]) and more recently in olive baboons in the same proportions [49]. At the human population-level, inanimate objects (i.e., bags) are carried on the right side for the greatest part [194]. However, just a pillow adorned with a proto-face is enough to elicit a left-cradling bias in children [53]. A study even asked adult humans (including both women and men) to imagine themselves holding in their arms an object (i.e., either an expensive vase or an old shoebox) and then an infant (i.e., about 3 months of age): while a right-cradling bias was reported for both imagined objects, a left-cradling bias (i.e., 66%) was reported for holding the imagined infant [194]. When cradling their baby, mothers hold their infant in their arms close to their body, positioning the infant's face in one of their peri-personal hemispace (e.g., left side of their body) and supporting the weight with the corresponding arm (e.g., left arm), see Figure 2. The maternal left-cradling bias seems not to be related with the mother handedness [53]. Next to the manual preference for manipulating items, the heart position (i.e., soothing sound of heartbeats [195–197]) and cultural considerations [198] do not affect the left-cradling bias. The theory reaching a consensus combines visual field and cerebral hemispheric specialization. The maternal cradling bias would reflect the right-hemispheric dominance for emotional processing [55]. In fact, the brain right hemisphere is specialized in the perception of emotional facial expressions [16,199]. Since left-side cradling exposes the baby face to the left visual field of the mother, which is projected mainly to her right brain hemisphere, this would favor the mother's monitoring of the emotional state of the infant. In parallel, the left-cradled infant looks at the left side of the mother's face, which has been described as being the most expressive [142,200,201]. According to some authors, this direct access to the mother's emotional state would then facilitate creating and reinforcing social bonds within the mother baby dyad [55].

Furthermore, in human mothers, affective symptoms such as stress, depression, and anxiety can alter left cradling, reflecting a reduced ability to be emotionally involved with the infant [54,202–204]. A recent study investigated the link between left-cradling bias and the maternal emotional state in a non-human primate, the olive baboon [49]. The authors found the maternal cradling bias to shift toward a right bias in mothers living in high density groups with higher social pressure, likely involving higher levels of stress for the mothers (e.g., by increased frequency of conflicts and severe aggression). The socially related stress would alter the rightward hemispheric resources allocated to the maternal monitoring and ultimately affect the left-cradling bias [21]. Those results clearly illustrate the phylogenetic continuity between humans and catarrhine monkeys concerning this lateralization and its potential links with hemispheric specialization for emotions, inherited from a common ancestor 25–35 million years ago.
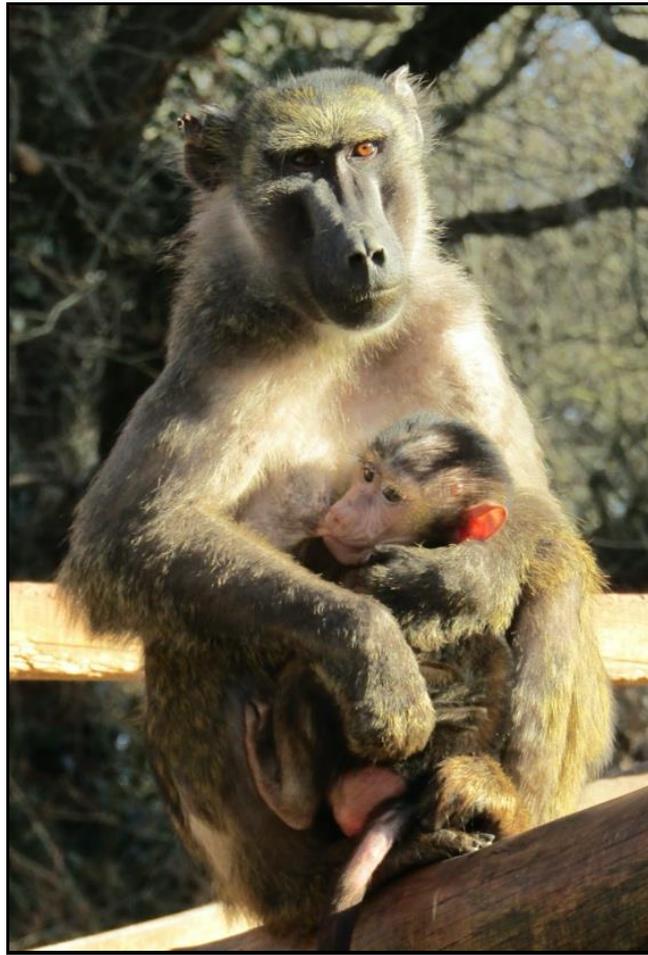
Figure 2. Maternal cradling in olive baboon (*Papio anubis*). A baboon mother cradles her infant on her left side. Photograph credit: Grégoire Boulinguez-Ambroise.

Interestingly, the lateralization of cradling in human mothers is under further investigations to assess the potential of this behavior as a tool to better understand and even early diagnose social disorders in infants, namely autism spectrum disorders (ASD). Several studies have already shown that atypical trajectory in maternal cradling might be one of the early signs of interference in dyadic socio-emotional communication, and thus of potential neurodevelopmental dysfunctions: for instance, right-cradling bias may be associated with a lack of social interactions or degraded interactions within the mother-infant dyad and induce disorders later in life, regarding sociality, namely socio-emotional communication; also, a left-cradling period which lasts too long may reflect the overstimulation in which mothers try to engage ASD infants in response to their lack of responsiveness and social initiative [54,205–209].

Asymmetries in an infant's positioning have been also reported in non-primate species that do not carry their babies. In a wide range of marine and terrestrial mammals, juveniles have a strong preference for keeping their mother on their left side, namely in their left visual field [210]. This has prompted previous authors to propose the idea that the right lateralized "social brain" as described in primates has an ancient evolutionary origin. It would be derived from earlier forms of lateralization in vertebrates, namely lateralization in interactions within the mother-infant dyad that promote bonding and thus maximize the infants' survival.

4. Gestural Laterality and Language Evolutionary Origins

A particular case of socially-directed manual movements are communicative gestures, whose laterality presents specific features compared to manipulative actions and whose characterization in non-human primates provides valuable insights into the evolutive history of human handedness and language.

4.1. A Complex Relationship between Handedness and the Hemispheric Specialization for Language

Humans present a left-hemispheric specialization for language functions, involving in particular the Broca and Wernicke's brain area for the production and processing of speech, respectively in the Inferior Frontal Gyrus and Planum Temporale [211–217]. The strong right-handedness observed in the human species has long been hypothesized to be uniquely related to this brain specialization for language [218,219]. This assumption was based in particular on the mirror neuron system being apparently predominant in the left-hemisphere and driven by neurons of the left Inferior Frontal Gyrus in humans [220,221]. First evidenced in the ventral premotor cortex of rhesus macaques, more specifically in the F5 region which is considered as Broca's area homologue, mirror neurons have the particularity to discharge both during the production of a manual action and during the observation of another individual producing it [222–224]. A large number of studies implying functional neuroimaging in humans have then shown, however, that mirror activity could be evidenced in a wide range of brain regions, both on the left and right hemisphere [225,226]. Moreover, in spite of the above-cited theory, results arising from both neurofunctional and behavioral studies suggest a rather indirect relationship between human language and handedness (see for review [8]). Recent fMRI (functional Magnetic Resonance Imaging) studies revealed independent neuronal circuits for language processing and action observation [227–229]. Häberling et al. [228] notably brought to light three distinct networks within the mirror neuron system which were related to language production and processing, to tool use, and to subjects' handedness, defined in this case as the preferred hand used for writing. Interestingly, among these three networks, only the handedness-linked one was for the most part independent from the Broca's area, and was mainly composed by circuits of the parietal lobe. In addition, it seems that the direction of the laterality for manual actions and the hemispheric specialization for language are relatively disentangled. Indeed, although the incidence of right-hemisphere language dominance is higher among left-handers compared to right-handers, the vast majority of left-handed adults (above 70%) still show a left-hemispheric lateralization for language production [17,230]. The reduced hemispheric lateralization for language production observed amongst left-handed individuals, rather than being due to a reversed asymmetry, might result from a generally weaker lateralization at both the group and individual levels for different cognitive functions [231,232].

By contrast with manipulative actions, the production of communicative manual gestures involves brain regions that are similar to those underlying verbal languages in the left hemisphere [233–238]. Moreover, the tight link between articulated and gestural communication can be observed early in development, the production of pointing gestures playing a key role in the ontogeny of verbal language [239–245]. Population-level right-hand preferences may be observed for the production of communicative gestures in humans, i.e., for co-speech gestures [246,247] (but see [248]), for sign language by deaf adult speakers [249], as well as for deictic and symbolic gestures in preverbal babies, children and adults [3,4,250–254]. Furthermore, even though no significant difference has been found between the direction of manual preference for some communicative gestures and coordinated bimanual actions in adults [251,252], the laterality observed for communicative and non-communicative manual movements seems to be related to different brain region specializations. This is especially underlined by behavioral descriptions in young children, which show that right-hand preference is stronger for gestures (i.e., pointing or signing)

than for non-communicative manual actions, suggesting that these two types of manual laterality develop independently [241,242,250,253–256].

Gestural laterality is thus likely to have an evolutionary history inextricably linked to the emergence of intentional communication. In that respect, the great body of research regarding the gestural communication of non-human primates has shed light upon the evolutionary roots of the left-hemispheric specialization for gestures and language.

4.2. Gestural Laterality in Non-Human Primates

As a matter of fact, brachio-manual communicative gestures are found both in human and non-human primates, in which communication relies strongly on the visual sensory channel [257–265]. The question of whether the gestures of humans and other primates (particularly great apes) are homologous has long been a debate, which has been limited by the heterogeneity of studies' focuses depending on the species (see for reviews [266–268]). However, in addition to recent results showing that human infants share the most part of their gestural repertoire with chimpanzees [269], the fact that the functional definitions of primate gestures have been built based on developmental psychology studies [260] allows us to make relative comparisons. The formal gesture definitions used in primate studies may vary from one study to another (see for review [267,268,270,271], yet the communicative nature of these movements is the core elements which functionally differentiate them from other actions. In that respect, the terms "manual gestures" refer to brachio-manual movements which (i) are directed to a recipient; (ii) receive a voluntary response, i.e., induce a change in the recipient's behavior without acting as a direct physical agent, and thus (iii) are mechanically ineffective. Intraspecific manual gestures which fulfill these criteria have long been thought to be unique to humans and great apes [272–274], but in the last years so-defined gestures have been reported in the spontaneous communication of other catarrhine primates (e.g., in olive baboons [275–277]; bonnet macaques, *Macaca radiata* [278]; red-capped mangabeys, *Cercocebus torquatus* [279–281]). To our knowledge, no such forelimb gestures (i.e., apparently intentional) have yet been demonstrated outside the primate lineage, hence the following discussion will focus on this clade.

Interestingly, a right-biased gestural laterality is observed at the population level in great apes, both for gestures directed to humans in experimental contexts, such as pointing or requesting (e.g., in chimpanzees, *Pan troglodytes*, bonobos, *Pan paniscus*, gorillas, *Gorilla gorilla*, and orangutans, *Pongo pygmaeus* [107,282]) and for intraspecific, spontaneous gestures (e.g., in chimpanzees [283–285]; in gorillas [286–289]). Similar findings were reported in primate species that are more phylogenetically distant from humans, especially in olive baboons whose production of threatening "hand-slap" is preferentially produced with the right hand, in intraspecific as well as interspecific contexts [275,276]. Moreover, this gestural laterality is stable through time at the individual level in baboons and chimpanzees [275,290]. As in the case of children, non-human primates' hand preferences for intraspecific gestures are not correlated with manual laterality for non-communicative actions, whether they are manipulative or self-directed (e.g., in chimpanzees [284,285] and in baboons [291]). Experimental studies also evidenced in other Cercopithecidae species that subjects' hand preference for interspecific communicative gestures (i.e., pointing) was uncorrelated to hand preference for manipulative actions (i.e., food grasping), suggesting different cerebral bases for these two types of laterality (in Tonkean macaques, *Macaca tonkeana* [292]; in Campbell's monkeys, *Cercopithecus campbelli*, and red-capped mangabeys [293]). By contrast, Meguerditchian and Vauclair [291] showed that handedness scores computed for different communicative gestures in olive baboons (i.e., "food-beg" and "hand-slap" gestures) were significantly correlated. Additionally, the manual preferences evidenced for pointing gestures in experimental conditions were shown to depend less on the position of the referent object than in the case of grasping actions (in olive baboons [256,294]; in Tonkean macaques [292]; Campbell's monkeys and red-capped mangabeys [293]), similarly to the pattern of manual laterality observed in human children [256]. Moreover, a divergence between gestural laterality patterns was found

between platyrrhine monkeys (tufted capuchins) and catarrhine species (human infants, olive baboons, and Tonkean macaques) in a comparative experiment involving pointing gestures [295]. These results suggested that the right-biased gestural laterality observed in catarrhine species may be limited to this clade. However, gesture studies in platyrrhine primates are still rare (but see experimental studies on learnt begging or pointing gestures [296–299]) and do not address the potential laterality of spontaneous brachio-manual gestures in these species, which are phylogenetically more distant from humans than African and Asian monkeys [300]. Thus, supplementary research work might be needed in this area in order to assess when gestural laterality emerged in primate phylogeny.

All the above-cited behavioral data suggest that catarrhine primates all share a left-hemispheric intentional communication system, which support their gesture production. This theory is supported by neuroanatomical and neurofunctional imaging studies revealing a relationship between gestural laterality and brain regions homologous to language-related cortical area in African primates (see for reviews [8,301–303]). One of the first key results in this area has been RMI imaging in great apes showing anatomical asymmetries within cortical regions homologous to Broca's area, which were found to be enlarged in the left hemisphere (in chimpanzees, bonobos, and gorillas [304]). A contralateral association was then evidenced between the direction of gestural laterality and the anatomical asymmetries found in the Inferior Frontal Gyrus and Planum Temporale of adult chimpanzees [290,305,306]. The direct link between the production of communicative gestures and the activation of these cortical regions was then brought to light by functional imaging (PET-MRI: Positron Emission Tomography–MRI) [307]. More recently, Marie et al. [308] showed for the first time a population-level asymmetry of the Planum Temporale in a non-hominoid species, olive baboons. Above the 96 study subjects, 62.5% presented an enlarged Planum Temporale in the left hemisphere, consistently with the population-level asymmetry observed in humans and chimpanzees [305,309–311]. A study conducted in the same baboon population then revealed that this leftward planum temporale asymmetry already existed in the early development of individuals, being observable in newborn baboons and getting stronger in their first year of life [312,313]. Comparably, in humans, the asymmetry of the planum temporale can be observed before birth and continuously develop in favour of the left hemisphere [314]. A longitudinal neuroimaging study evidenced that similar leftward asymmetries of the planum temporale as well as of the Inferior Frontal Gyrus may be observed consistently from 1 to 19 months old in another species of catarrhine monkeys, rhesus macaques [315]. A preprint study authored by Becker et al. [316] reported that olive baboons may also exhibit anatomical asymmetry of markers of Broca's homolog, and that the direction and depth of this asymmetry may be associated with a contralateral gestural lateralization but not with laterality for non-communicative, manipulative actions. At this point, it remains to be investigated whether these anatomical asymmetries in baboon brains are functionally associated with a specialization for the control of gestural communication, similarly to great apes [307], in adulthood as well as across development. By contrast with the trend observed in the human gesture literature, very few studies have explored the development of apes and monkeys' gestural communication [267,317], resulting in a scarcity of data related to the ontogeny of gestural laterality. However, the first promising results cited here pave the way for exciting new research perspectives, exploring whether and how monkeys' gestural laterality develop during their early years of life, potentially in line with the development of cerebral asymmetries.

According to all the commonalities between humans and other catarrhine primates regarding gestural laterality and the associated brain asymmetries, several evolutionary hypotheses proposed that a left-lateralized gestural communication system may have already existed in the brain of the common ancestor of African and Asian primates, over 29 million years ago [8,295,300,302,303,318]. The neural substrates of human intentional communication would then have derived from this hemispheric specialization for gestures, under different evolutionary constraints and at different phylogenetic levels [8,303,319]. Notably, ecological changes might have represented significant pressures shaping catarrhine visual

communication, such as a shift from arboreal to terrestrial habitats, associated with an increased visibility and a change of locomotion patterns [320,321]. Moreover, modifications of social systems (and consequently of social complexity) might have affected the extent to which communication relied on brachio-manual gestures, and then on language in the human lineage, depending on the need of sufficiently diverse and flexible communicative signaling to deal with different contexts of cooperation, competition, and cultural transmission [322–326]. Therefore, in line with these theories, the characterization of factors affecting gestural laterality in non-human primates is of great interest for the purpose of depicting the constraints under which humans' gesture and language laterality emerged. We will present, in the following, the main proximate and ultimate causes that have been hypothesized and/or shown to affect the gestural laterality of catarrhine primates.

4.3. Ultimate and Proximal Factors Impacting Primate Gestural Laterality

4.3.1. Effect of Species and Study Population Characteristics

Firstly, the existence of a population-level gestural laterality and its strength appears to depend on the species characteristics, particularly in relation with variation in social systems and ecological characteristics [327]. According to the theory of a social origin of laterality (Section 2.6), it may be predicted that species with high levels of inter-individual cooperation will be more likely to exhibit alignment of individuals' gestural laterality. Moreover, the strength of gestural laterality may depend on social constraints in these species. Observational studies on captive gorillas and chimpanzees brought to light such effects of social dynamics on lateralization of the species' most frequent gestures [288,289,327]. When comparing the production of brachio-manual gestures shared by both species, Prieur et al. [287] found for instance that gorillas were more right-handed than chimpanzees when producing auditory gestures, such as "slap hand". These gestures are more frequent in gorillas probably because of the higher inter-individual distances generally found in this species compared to chimpanzees [328], and are therefore more likely to be socially codified and lateralized. Other species characteristics than sociality might affect gestural laterality, such as the locomotory posture. The theory of a postural origin of manual laterality suggests that the right hand is specialized for complex tasks in terrestrial mammals, the use of one hand or another being less limited by the need for postural stability than in arboreal species [93–95]. In the case of visual communication, it may thus be hypothesized that terrestrial primates are more lateralized when producing brachio-manual gestures than arboreal ones. To our knowledge, there exist no direct comparison of gestural laterality between primate species with different locomotory postures, although comparative studies would be very beneficial to the debate on the origin of primate manual laterality in general [100]. That said, it may be noted that intraspecific gestural laterality has been essentially evidenced at the population-level in terrestrial species, namely chimpanzees, gorillas, and olive baboons [107,275,276,284,285,288,289,327], and spontaneous gestures seem generally more used in primates living in open environments which facilitate the perception of visual signals [329–331]. Finally, the population characteristics, such as the wild or captive environment in which apes and monkeys are studied, may also have an effect on the laterality of manual gestures. Some authors suggested that manual laterality measured in captive primates may be the artefactual results of experimental conditions, particularly those implying the presence of human experimenters ([332–334] but see [188]). Concerning gestural laterality, the effect of captivity is not completely elucidated, particularly because of the lack of direct comparisons between wild and captive populations of primates, and because of the small numbers of studies addressing spontaneous, intraspecific gestures. It is to be noted, however, that some great ape studies show a higher right-hand preference for intraspecific gestures than for human-directed ones, in spontaneous or experimental contexts [107,287].

4.3.2. Effect of Gesture Characteristics

Thus, the preference of one hand to communicate also depends on the characteristics of the gesture itself. The gestural laterality measured in primates differs according to which gesture of the repertoire is studied (e.g., in chimpanzees and gorillas [282,285,289,319,335,336]. As evoked earlier, some authors propose that the most frequent gestures are more likely to be shaped by social pressures, explaining stronger hand preferences when producing them [285]. Moreover, the sensory modality in which the gestural signal is delivered (i.e., visual only, tactile, or audible) impacts its laterality, notably because visual and tactile gestures are more physically directed to the recipient than audible ones, hence are produced preferentially with the ipsilateral hand in relation with the position of the receiver (see in chimpanzees [285]).

4.3.3. Effect of the Interactional Context

The context in which gestures are produced, and particularly the emotional value of certain social situations, has been proven to affect gestural laterality in several primate species. Prieur et al. [285,289] demonstrated that the right hand preference of chimpanzees' and gorillas' gestures was stronger in contexts associated with negative emotional valence than in others. Recently, similar observations were made in red-capped mangabeys [280], in which brachio-manual gestures were more produced with the right hand than the left in aggression and submissive contexts compared to positive or neutral social situations (Figure 3). These results corroborate findings in humans, showing an activation of prefrontal regions of the left brain hemisphere in aggression contexts [164]. This right hand preference for aggressive gestures might be explained by "motivational hypotheses" in line with the "Valence theory" of emotional lateralization (see II.1.), which proposes that the left and right brain hemisphere are respectively specialized in approach- and withdrawal-motivated behaviors [139,156–158,162–164]. Indeed, although aggressive gestures might be underlined by negative emotions in the signaler (for instance, anger), they are also likely to imply a high motivation for approaching the interactant, and thereby to specifically involve left-hemispheric brain regions. In other vertebrate species, non-communicative aggressive behaviors have been found to be lateralized to the right and controlled by the left-hemisphere (e.g., in fishes, *Gambusia holbrooki*, *Xenotoca eiseni*, *Betta splendens* [337]; in green and brown anoles, *Anolis carolinesis* and *A. sagnei* [338]; in mammals such as the European fallow deer, *Dama dama* [339]; but see in domestic and Przewalski horses, *Equus caballus* and *E. przewalskii* [340,341]). Apart from this "motivational hypothesis", the fact that catarrhine primates preferentially gesture with the right hand in aggression situations may be explained by a lesser flexibility of communication in negative contexts, as evidenced for some vocalizations (e.g., alarm calls [342]). Aggressive gestures may be more lateralized than others consequently to a stronger effect of social influences through ontogeny (Section 2.6), and thus be less submitted to the influence of proximate factors. This may be the case of the threatening "hand-slapping" of olive baboons, which has been shown to be highly right-handed at the individual and population-level [275,276].

The emotional value of the interaction is not the only contextual factor which has been shown to affect gestural laterality. The hand used to communicate in primates may also depend on the relative position of the receiver and signaler [280,285,287,327]. One explanation for this is the directionality of gestures, which can result in the use of the ipsilateral hand to efficiently convey visual or tactile signals to a receiver. Moreover, as several primates favor one side or another to approach conspecifics, notably depending on dominance relationships (e.g., in red-capped and grey-cheeked mangabeys, *Cercocebus torquatus* and *Lophocebus albigena* [343]) or depending on the type of interactions (e.g., embracing and grooming in Colombian spider monkeys, *Ateles fusciceps rufiventris* [344]), it may be hypothesized that social laterality affects manual preferences in social interactions, including for gestural communication.
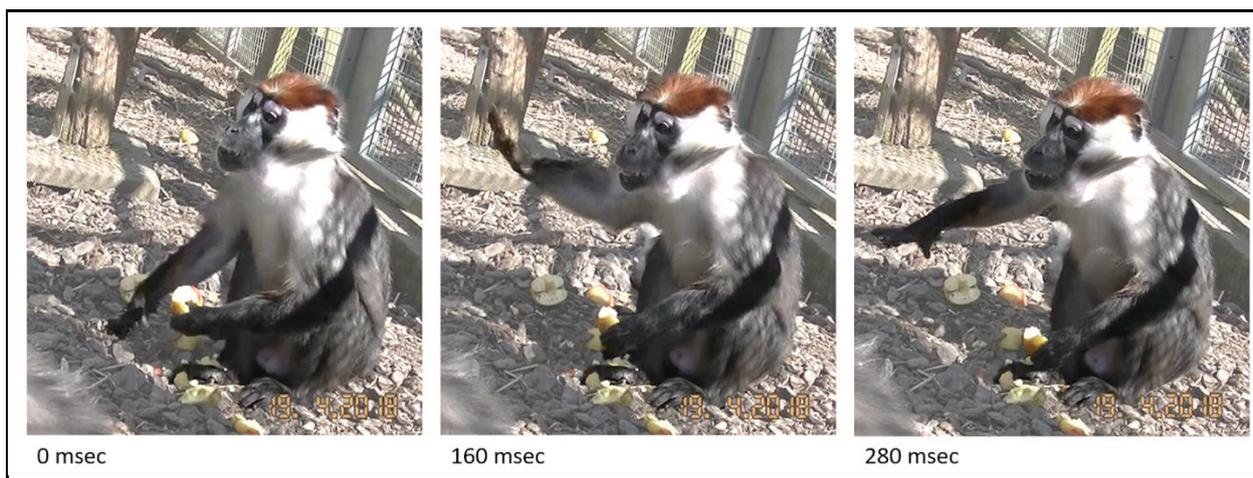
Figure 3. A male red-capped mangabey (*Cercocebus torquatus*) produces a rightward "throw arm" gesture, as part of a threatening display directed to a conspecific. Similarly to chimpanzees and gorillas, red-capped mangabeys gesture preferentially with the right hand in aggression contexts [280]. Photograph credit: Juliette Aychet.

4.3.4. Effect of Signaler and Receiver Characteristics

Primate gestural laterality indeed depends on the relationship between interacting individuals. In captive chimpanzees, gestures are more lateralized to the right hand when directed to dominant conspecifics, and this effect is lessened if the interactants are strongly affiliated [285]. These observations might be explained by the signaler's emotional state varying depending on the identity of the receiver, and particularly the level of psychosocial stress induced by competitive contexts. Such dominance effect has not been evidenced in captive gorillas [327], who exhibit lesser intragroup competition compared to chimpanzees [345–347]. Kinship between signaler and receiver seems to not affect the gestural laterality of gorillas and chimpanzees [285,289,348], however the possible effect of such factors has not been tested in other species.

In addition, demographic factors, i.e., the sex and age of the signaler, has been evidenced to affect gestural laterality in several primate species. Although no effect of sex has been found in chimpanzees and olive baboons' gestural laterality [275,276,291,348], male bonobos have been found to be more right-handed than females for gesture production [186]. Moreover, the converse sex effect has been evidenced in gorillas, in which females are more lateralized in favor of the right hand than are males, and in which males are more right-handed when they gesture toward females than toward male conspecifics [289]. Considering the social structure of these two species, we may hypothesize that these results are related to the dominance relationships of subjects (i.e., female dominance in bonobos and male dominance in gorillas [346,349]), yet the determinants of sex effect on primate gestural laterality is not clear. In humans, more left-handers are found amongst men than women regarding handedness in general, and some cognitive processes are lateralized differentially depending on the individual's sex [6,350–352], though no difference seems to be found for language-related functions and corresponding cerebral asymmetry [352,353]. Different hypotheses have been formulated concerning the effect of sex on human handedness or forelimb asymmetries for non-communicative actions in other mammals (e.g., cats and dogs, *Felis cactus* and *Canis familiaris* [354–356]). Notably, authors suggest a possible effect of sex hormones on cognitive lateralization [350,355], of genetic determinants located on the X chromosome [219,357,358] (but see [31]), and of gender-dependent differences in individual social experience through ontogeny, in the case of humans [359].

Finally, primate gestural laterality is affected by individuals' ages. In chimpanzees, gorillas, and olive baboons, the preference for right-hand gesturing is stronger in adults compared to juveniles [276,282,285,289,335]. This may be due to a maturation of the left

hemisphere specialization for intentional communication [276], or it may result from the subjects' individual experience, as adults' gestures are more likely to have been shaped by social experiences [360]. Further studies on the ontogeny of gestural communication would provide a better understanding of this phenomenon. Prieur et al. [285] also observed a senescence effect on chimpanzee gestural laterality, older individuals being less lateralized than young adults possibly because of physical limitations. Nevertheless, other studies have not highlighted any significant effect of age on the gestural laterality of captive chimpanzees and olive baboons [275,361]. On the whole, the extent to which sociodemographic factors affect primate gestural laterality is still poorly or not described in most species.

Multifactorial analyses have been applied to characterize the effect of all these parameters on the gestural laterality of captive chimpanzees and gorillas [285,289,327], and more recently in an exploratory study on captive red-capped mangabeys [280]. Studying primate gesturing with a multifactorial as well as comparative approaches represent promising perspectives for the understanding of the proximate and ultimate factors which shaped human gestural laterality [100,285,289]. In addition, further research efforts are needed with respect to the ontogeny of primate gestural communication and to the potential gestural laterality of non-hominid species, in order to better understand the evolutionary and developmental pathway of this trait.

5. Conclusions–The Way Forward

We aimed to emphasize here the importance of characterizing animal limb preferences to understand the development and evolution of human handedness, by distinguishing laterality for functionally different manual actions (i.e., object manipulation, actions directed to living targets, and non-manipulative, communicative gestures), which might be supported by different hemispheric specializations.

Future research may benefit from recent advances in neuroimaging methods [362], notably functional techniques permitting researchers to link lateralized behaviors to specific brain regions' activity. For instance, the use of functional Near-Infrared Spectroscopy (fNIRS) has been recently validated in non-human primates, allowing non-invasive recording of brain processing lateralization from a functional perspective [363].

Moreover, further developmental studies in different animal species may be needed to unravel the ontogeny of manual lateralities (for instance, regarding the development of gestural communication in non-human primates [267]). Improvements in MRI technology should help to determine whether contralateral hemispheric specialization of the brain is present at early developmental stages, its potential change across ontogeny, and whether it predicts limb preference at later stages [313].

Additionally, one of the major challenges for the understanding of human handedness origins is the improvement of comparative approaches, as still few studies directly involve several species [364]. Research on animal forelimb asymmetries often focuses on mammals (and particularly on the primate lineage), however comparisons of forelimb preferences across a wider range of vertebrate and invertebrate species may provide valuable insights into the evolutionary constraints that have shaped this trait [161]. Behavioral lateralization similarities in species which are phylogenetically distant may result from evolutionary convergence. Their characterization may thus permit us to make hypotheses on the ecological constraints which led to their emergence.

Finally, reliable comparisons of forelimb lateralizations in different species may only be made by homogenizing the task complexity in both experimental and observational studies. Human manual laterality has been argued to be unique because it is observed across different tasks in a large part of the population compared to other species, but one could argue that animals' forelimb asymmetries are rarely assessed for as complex tasks as the ones investigated in humans (e.g., writing or other complex tool uses). Quantitatively, would the right bias observed in humans still be as strong as the ones observed in other species when performing lower demanding tasks? Marchant et al. [365] described humans' manual preferences in diverse spontaneous actions, based on film archives of three tra-

ditional societies. They evidenced only a weak overall lateralization for manual actions (barely above 50% of right-hand use in the three study populations), but interestingly found a greater right-hand preference when specifically considering precision tool use (above 84% of right-hand use). The authors thus noted that "the disparity between the ethological and the typical psychological findings on handedness may thus be simply explained: questionnaire and performance testing paradigms focus only on a small and selected proportion of manual activities, those to do with tool use, and especially with skilled, fine-motor tool use. This gives an artefactual, biased picture of extreme lateralization." (p. 256). Task complexity has been hypothesized to affect manual laterality, individuals being more likely to be lateralized for actions with high level of manipulative requirements [111,161]. This has been evidenced in diverse mammal species (e.g., in human [365,366]; non-human primates [367–369]; marsupials [370]; or rodents: [371]), and may be true in other tetrapods, as authors observed stern clawed frog (*Wenopus tropicalis*) changing paw for food manipulation depending on the animacy of the target (Pouydebat et al., unpublished data), due to different levels of manipulative action complexity [372]. To adapt the experimental tasks and protocols in relation to the cognitive and functional capacities of the species (and even their ecology)—in order to propose similar tasks in terms of complexity—represents a real challenge for future studies on limb preference. Moreover, assessing human handedness based on ethological descriptions of spontaneous manual activities may provide more reliable research material to compare with animal observations.

Investigating animal forelimb laterality for diverse (clearly defined) tasks by adopting multi-disciplinary, developmental, and comparative approaches might represent promising perspectives for the understanding of handedness origins.

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