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Ph.D. Dissertation

Hemispheric Specialization Tied to Lateralized Motor Preference in Human and Non-Human Primates

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Our dragnet was filled with Midas abalone, harp shells, obelisk snails, and especially the finest hammer shells I had seen to that day. We also gathered in a few sea cucumbers, some pearl oysters, and a dozen small turtles that we saved for the ship's pantry.

But just when I least expected it, I laid my hands on a wonder, a natural deformity I'd have to call it, something very seldom encountered. Conseil had just made a cast of the dragnet, and his gear had come back up loaded with a variety of fairly ordinary seashells, when suddenly he saw me plunge my arms swiftly into the net, pull out a shelled animal, and give a conchological yell, in other words, the most piercing yell a human throat can produce.

"Eh? What happened to master?" Conseil asked, very startled. "Did master get bitten?"

"No, my boy, but I'd gladly have sacrificed a finger for such a find!"

"What find?"

"This shell," I said, displaying the subject of my triumph.

"But that's simply an olive shell of the 'tent olive' species, genus Oliva*, order Pectinibranchia, class Gastropoda, branch Mollusca--"*

"Yes, yes, Conseil! But instead of coiling from right to left, this olive shell rolls from left to right!"

"It can't be!" Conseil exclaimed.

"Yes, my boy, it's a left-handed shell!"

"A left-handed shell!" Conseil repeated, his heart pounding.

"Look at its spiral!"

"Oh, master can trust me on this," Conseil said, taking the valuable shell in trembling hands, "but never have I felt such excitement!"

And there was good reason to be excited! In fact, as naturalists have ventured to observe, "dextrality" is a well-known law of nature. In their rotational and orbital *movements, stars and their satellites go from right to left. Man uses his right hand more often than his left, and consequently his various instruments and equipment (staircases, locks, watch springs, etc.) are designed to be used in a right-to-left manner. Now then, nature has generally obeyed this law in coiling her shells. They're right-handed with only rare exceptions, and when by chance a shell's spiral is left-handed, collectors will pay its weight in gold for it.*

So Conseil and I were deep in the contemplation of our treasure, and I was solemnly promising myself to enrich the Paris Museum with it, when an ill-timed stone, hurled by one of the islanders, whizzed over and shattered the valuable object in Conseil's hands.

I gave a yell of despair! Conseil pounced on his rifle and aimed at a savage swinging a sling just ten meters away from him. I tried to stop him, but his shot went off and shattered a bracelet of amulets dangling from the islander's arm.

"Conseil!" I shouted. "Conseil!"

"Eh? What? Didn't master see that this man-eater initiated the attack?"

"A shell isn't worth a human life!" I told him.

"Oh, the rascal!" Conseil exclaimed. "I'd rather he cracked my shoulder!"

Jules Verne (1980)

Twenty Thousand Leagues Under the Sea

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Abstract

In literature there are large discrepancies about methods to assess cerebral lateralization in both human and nonhuman primate populations. This study aimed to allow valid comparisons across different primate species by employing a quantitative Multidimensional Method. A comprehensive range of interactions with both social and non-social targets were considered to verify which aspects might elicit the manifestation of lateralized behaviours underpinned by asymmetrical neuronal functions. Spontaneous activities were observed in two groups of zoo great apes, chimpanzees (*Pan troglodytes*) and gorillas (*Gorilla gorilla gorilla*), and a group of 3-4 year-old typical pre-school children. Results demonstrated a strong consistency in both human and non-human species for a right-hand/left hemisphere dominance during contact with inanimate targets (i.e. objects and environmental items), suggesting a evolutionary hemispheric specialization influenced by object animacy. Additionally, both great ape species significantly preferred to keep conspecifics closer than 3 metres to their left during manual activities, suggesting a right hemisphere specialization for emotion processing. Only the silverback gorilla (alpha male) manifested the opposite pattern, potentially related to his hierarchical role within the gorilla society. No side preference was found in typical children however, their young age may indicate that they are still undergoing hemispheric development for emotion processing. This study supports an evolutionary origin of hemispheric specialization underling manipulative and social asymmetric behaviours that occurred prior to the split of humans from great apes.

Keywords: chimpanzees, gorillas, children, cerebral lateralization, handedness

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Chapter 1

Human cerebral lateralization

Bilateral symmetry is widespread among the animal kingdom, except for sponges, comb jellies and cnidarians, and creatures displaying this trait have been classified under the phylum of Bilateria. The key feature of bilateral symmetry is the organization of the body with anterior/posterior (A/P), dorsal/ventral (D/V), and left/right (L/R) axes, which are otherwise described as frontal, transversal and sagittal planes, respectively (see figure 1).

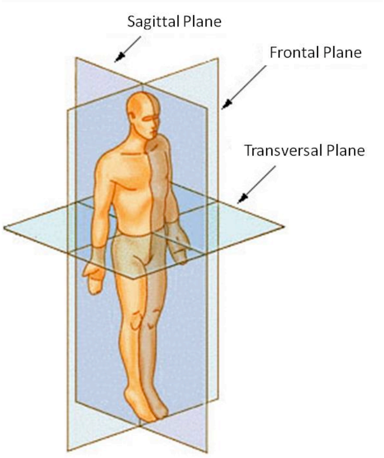


Figure 1. Body planes. Three axes characterize the bilateral asymmetry of the body (retrieved from http://athletics.wikia.com/).

The fact that bilateral symmetry is so widespread among the animal kingdom suggests that it should have been selected for its survival value. Indeed, the symmetry of an animal generally fits its life-style. According to Corballis (1989) it must have been evolved in association with linear locomotion, which can be performed at best only with symmetrically placed limbs (legs, arms, wings or flipper), and sensory perception, as a symmetrical sensory system allows to elaborate stimuli that can come from the right or the left side. Nevertheless, deviations from bilateral symmetry are very common in both vertebrates and invertebrates species. For example, humans and other mammals show internal organs that are asymmetrically distributed or do not manifest a symmetrical shape, such the heart, gut, liver, stomach and spleen, and the direction of these asymmetries is unvaried in all the individuals.

The most investigated manifestation of asymmetry is cerebral lateralization, which refers to the specialization of the two hemispheres in processing sensory information and controlling behavioural responses. This asymmetry is highly evident in humans, in which both hemispheres are specialized for the processing of different cognitive and behavioural functions. For this chapter and for the entire dissertation certain functions will be considered, such as the left hemisphere specialization for language abilities and for the control of manual behaviour, and the cerebral lateralization for the processing of emotions.

1.1 Cerebral lateralization for language

1.1.1 DISCONTINUITY AND CONTINUITY THEORIES

For long time language has been considered a characteristic that makes humans unique within the animal kingdom. The philosopher René Descartes was one of the major supporters of this assumption, which leads also to the idea that people are superior to any other living creature (as cited in Corballis, 1989, p. 492). Language not only refers to speech but also to the gestural communication that can occur either separately or in concomitance with vocal communication (Bear, Connors, & Paradiso, 2001). Although different forms of behavioural, gestural or vocal communication can be found in other animal species, such as fish, reptile, birds and other mammals, the peculiarity of human language is the generative grammar, which is the ability to make infinite possible combinations with language utterances. Thus, researchers supporting the *discontinuity theory* of the evolution of language stress that language emerged as a recent event after the divergence of our hominid ancestors from great apes, over 6 million years ago (MacWhinney, 2005). The linguist Noam Chomsky stressed the uniqueness of language in humans, which in his view would be not entirely acquired through experiences: Humans are born with an innate knowledge of language structural mechanisms (as cited in Corballis, 1989, p. 493). Therefore, according to the author, all the existing languages share the same grammatical principles and parameters.

On the other hand, researchers supporting the *continuity theory* claim that human language evolved from language-like precursors, in particular from non-human primates (King, 1996). Indeed, some species of apes and monkeys seem to communicate not only to report an emotional or arousal status, but also to exchange information with each other about the physical and social environment. Furthermore, continuity theorists argue that it is inappropriate to define language exclusively in human terms through the definition of syntax such as the production of sentences. Snowdon even argued that it might be more conceivable to treat syntax as a system that is rule-based and accounts for the ability to “generate predictable sequences of behaviour” (as cited in King, 1996, p. 194). In line with this definition, some non-human species, such as birds and non-human primates, have shown the ability to communicate using predictable sequences and semantic vocalizations (King, 1996).

1.1.2 EMPIRICAL EVIDENCE FOR LANGUAGE LATERALIZATION

The first discoveries about language lateralization go back to the second half of the 19th century, when the French neurologist Paul Pierre Broca studied the case of a patient (nicknamed Tan) who manifested serious deficits to produce articulated speech (as cited in Bears et al., 2001, p. 580). After a deep examination of the patient's brain, the neurologist discovered a lesion in the circumscribed region of the left frontal lobe, which was later named the Broca's area (see figure 2). This association between language disorders and lesions in the left hemisphere was also corroborated by another procedure, the Wada test, the "intracarotid sodium amobarbital procedure" (ISAP). This technique consisted in the anaesthetization of one hemisphere with a barbiturate and was first developed to assess asymmetrical cerebral language and memory representation (Bears et al., 2001).

During the same period of Broca's studies, the German psychiatrist Karl Wernicke identified another separate area for language processes in the superior surface of the temporal lobe of the left hemisphere (as cited in Bears et al., 2001, p. 580). Unlike the Broca's area, the Wernicke's area (see figure 2) was specialized in the comprehension of language.

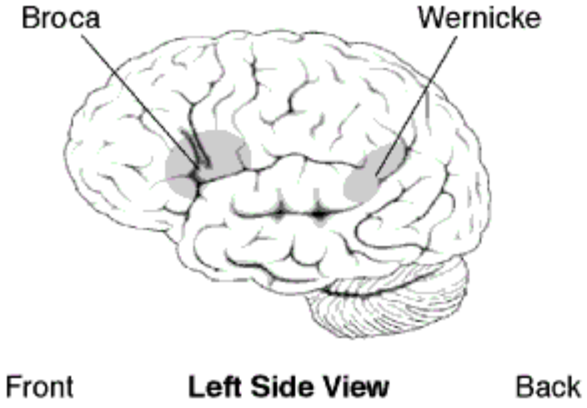


Figure 2. Human Broca and Wernicke's areas. Representation of the left hemisphere and the location of the Broca and Wernicke's areas, which are responsible for the production and the perception of language, respectively (retrived from http://www.psych.ndsu.nodak.edu/)

The neuropsychologist and neurobiologist Sperry provided another general idea of functional hemispheric specialization, particularly investigating the inter-hemispheric transmission of information, which is made possible by a commissure of 200 millions of axons that form the corpus callosum (as cited in Corballis, 1989, p. 494). The researcher was awarded Nobel Prize in Psychology and Medicine in 1981 for his studies on “split brain” patients, which had their corpus callosum surgically severed to prevent the diffusion of epileptic seizures. Patients were tested by presenting lateralized stimuli to their both visual fields and were asked to perform specific motor, linguistic or visual tasks. Although the normal activities performed by the split-brain subjects remained unvaried, patients were unable to describe verbally anything that appeared in their right hemi-visual field, suggesting that the left hemisphere, compared to the right, was more involved in the processing of basic speech production.

As Bishop reported (1990), some researchers developed two non-invasive perceptual techniques to infer the lateralization of language functions, the dichotic listening task and the split visual field task. The dichotic listening task (see figure 3) consisted in presenting a subject with two competing auditory messages simultaneously to both ears and this technique demonstrated that patients with lesions in the left-hemisphere manifested a better recall of dichotic stimuli to the right than to the left ear. However, patients with right hemisphere speech dominance manifested the opposite pattern, as although ears projected to both cerebral hemispheres, the auditory stimulus is better transferred through the ear controlateral to the hemisphere specialized for language (Kimura, 1961). Therefore, the perception of sounds in the left ear is worse that the right ear, as the stimuli have to cross the corpus callosum to reach the left hemisphere. On the other hand, inputs coming from the right ear follow the controlateral route and go directly to the left side of brain. The split visual field task is an analogues technique. Like the ears, both eyes project to both hemispheres and different studies demonstrated that the crossed pathway is more efficient than the ipsilateral route. Kimura (1966) found that the right visual field was better than the left visual field in detecting linguistic related material that subjects had to report through verbal communication.

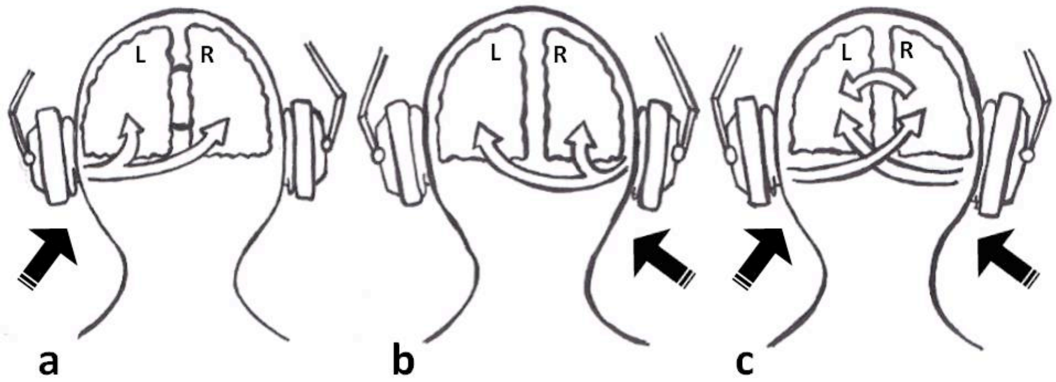


Figure 3. The dichotic listening task. This representation illustrates that each ears project to both hemispheres (a, b); when competing stimuli are presented to both ears, the contralateral pathway suppressed the ipsilateral one (c). Therefore, stimuli coming from the right ear and going directly to the left hemisphere are stronger than those coming from the left ear, which have to cross the corspus callosum (redrawn from Bishop, 1990).

Recent progresses in the technology have allowed neurologists and psychologists to detect more precisely the interested areas of cerebral lateralization for language functions. Indeed, neural imaging machineries, such as positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) can highly improve the identification of anatomical-functional correlations in sensory and motor area of language lateralization in the human brain (Knecht, et al., 2000; Pujol, Deus, Losilla, & Capdevila, 1999; Springer et al., 1999; Szaflarski et al., 2002; Tzourio, Crivello, Mellet, Nkanga-Ngila, & Mazoyer, 1998).

Genetic studies have provided further information about language lateralization. Gentilucci and Corballis (2006) reported the case of the English KE family, in which half of the members was affected from a disorder of speech and language acquisition. This syndrome seemed to be caused by a point mutation on the *FOXP2* gene on chromosome 7 (Lai, Fisher, Hurst, Vargha-Khadem, & Monaco, 2001). However, it is not yet clear whether the gene is involved in the development of morphosyntax or in the incorporation of vocal articulation. An fMRI study confirmed these genetic findings, as affected subjects of the KE family showed relative underactivation of the Broca’s area in the left-hemisphere, during a verbal experiment (Liégeois et al., 2003).

1.2 Handedness

1.2.1 MEASUREMENT AND DEFINITIONS

One of the most prominent manifestations of cerebral lateralization is human right-handedness. Indeed, the 90% of the entire population use predominantly the right hand for most daily unimanual activities, such as writing, throwing an object, opening a jar, using the scissors, etc (Annett, 2002; Perelle & Ehrman, 1994; Pontier & Raymond, 2004). The remaining 10% of the people either use prominently the left hand or do not manifest any consistent preference (Oldfield, 1971). Although ambidexterity (the indiscriminate use of either hands for a given task) is supposed to favour the individual when one hand is for example injured, handedness is largely widespread and this suggests that it should confer some advantages (Bishop, 1990). Otherwise handedness might be a non-adaptive by-product of some other adaptive human characteristic.

How to measure handedness

Fagot and Vauclair (1991) suggested that the selective value of handedness is task-dependent, as the preferential use of one hand is more advantageous and evident during the execution of highly cognitive demanding tasks. Indeed, the authors distinguished manual tasks in *low-level* and *high-level* activities, according to the difficulty and the familiarity in performing the manual task. *Low-level tasks* consist in grossly regulated, familiar, practiced, simple activities (e.g. simple food reaching), that do not require particular cognitive processes to be performed, thus the population is not expected to manifest a bias in the distribution of right- and left handed individuals. On the other hand, *high-level tasks* consist of novel, fine tuned, motor acts that require the individuals to involve both spatio-temporal abilities and very demanding cognitive processes, such as precise object manipulation during unnatural postures. In this condition, human population is expected to be distributed asymmetrically with respect to hand preference. Fagot and Vauclair's theory (1991) has been criticized for not considering gradations in the task, such as activities that require fine manipulation but are well familiar and stereotyped or activities that are very simple but have to be performed during an unstable posture. They did not even define how many trials are needed to delineate the degree of familiarity of a given task, making difficult the precise classification of high-level or low-level tasks (McGrew & Marchant, 1997).

The critiques moved against Fagot and Vauclair's theory (1991) raised one of the most puzzling arguments concerning whether hand preference should be treated as a dichotomized or continuous variable. McManus argued that individuals can be classified as right- or left-handers based on the hand they use to write (as cited in Bishop, 1990, p. 72). However, this kind of measure cannot account for countries where culture has forced left-writers to use preferentially their right hand. Moreover, many individuals use the non-writing hand for other tasks and MacManus justified this evidence arguing that a different cerebral mechanism is involved for writing execution and other activities (as cited in Bishop, 1990, p. 72). He further claimed that the tendency of left-hand writers to use the right hand for other activities is due to the fact that most of the tools have been designed for the exclusive use of the right hand.

According to Annett (2004) hand preference should be treated as a continuous variable and only a small group of the human population manifests an extreme right or left hand preference for daily activities. Indeed, most of individuals use also the non-dominant hand with different degree, according to the type of the task. Therefore, the author developed a subgroup classification of activities that were employed in the Annett Hand Preference Questionnaire (AHPQ) in order to determine degrees of right and left and hand preference. On the basis of the results accumulated by the questionnaire, the author distinguished the manual activities in primary (writing, throwing, tennis racquet, striking a match, hammering and using a toothbrush) and secondary activities (scissors, needle, sweeping, shovelling, dealing cards and unscrewing the lid of a jar), that differed from each other based on correlations between the activities, which are high for primary activities and moderate for secondary activities. In other words, primary activities were highly correlated with the use of the dominant hand, whereas secondary were more likely to induce individuals to use the non-dominant hand. The distinction of primary and secondary manual activities helped to trace a continuum of handedness, from strong right- to strong left-handedness, via true ambi-preference. Annett (2004) defined the gradual scale of handedness on 8 classes, where classes 1 and 8 referred to individual with an extreme preference for the right or the left hand, respectively, classes 2-5 to right writers with some left hand preference, and classes 6-7 to left writers with some right hand preference.

In accordance with Annett (2004), Salmaso and Longoni (1985) postulated that the strength of hand preference varies according with the type of the task. Thus, the frequency to use the dominant hand seems to be positively correlated with the experience of an individual to execute a given task.

It has been also argued that reports on the distribution of handedness in the human population have been mainly based on questionnaires investigating only precision tool-use, which might bias the actual percentage. Indeed, Marchant, McGrew and Eibl-Eibesfeldt (1995) coded a wide range of daily behavioural activities in three traditional societies and reported a strong right-hand preference only for tool-use manual activities, whereas a consistent mix-handedness was found for the non-objective-manipulatory and communicative manual activities in all three societies. These findings seem to suggest that handedness is strongly task related. In particular, human right-handedness seems to be correlated with tool-use activities.

Guilford and Fruchter pointed out that it is difficult to define which model for handedness assessment is the most reliable, as results on handedness reported in literature are mainly based on personal designed questionnaires and this variability does not allow for comparisons between the different works (as cited in Bishop, 1990, p. 72). Therefore, it seems difficult to clarify whether differences among studies are meaningful or are simply confounded by the methodological variation. For example, the assessment of handedness across different cultures can provide inconsistent results, as social pressure and religious influences can play a fundamental role in establishing individual handedness (Llaurens, Raymond, & Faurie, 2009). Raymond and Pontier (2004) reviewed 81 studies about the analysis of handedness across different cultures considering only hammering activity and found handedness variation in 14 countries. Even the hand used for writing varied across 17 different societies, as demonstrated through a survey delivered by Perelle and Ehrman (1994) and Peters, Reimers, and Manning (2006).

Definition of handedness

Although many researchers have attempted to define human handedness, there is still confusion about how to describe the different manifestations of hand lateralization and many authors have tried to clarify the terminology. One of the most accepted schemes about classification of hand preference proposed four terms:

- *Hand preference* is used to describe a hand bias manifested by an individual on a single task (MacNeilage, Studdert-Kennedy, & Lindblom, 1987);
- *hand specialization* is used to describe when the same hand performs a range of tasks;
- *task specialization* is used to describe a selected group of individuals that manifest the same bias in using one hand upon a particular task;
- *handedness* is used to describe a set of individuals that manifests the same hand lateralization across a battery of tasks. This is the case of human right-hand preference (Marchant & McGrew, 1998).

A different model distinguishes hand lateralization based not only on the frequency of use, but also on the ability to perform a particular task (McGrew & Marchant, 1997). Indeed, the preferential use of one hand determines only that one of the two hands is employed more frequently than the other one to perform most of the common tasks, whereas the degree of proficiency of hand use refers to the tendency of using the more skilled limb to execute, say, a range of complex tasks. If it is the proficiency that determines handedness, we should expect natural selection to have favoured the preferential use of the hand that provides the greater amount of success and that makes fewer errors.

Uomini (2009) reported that it might not be correct to speak about a dominant hand. Indeed, many daily activities performed by humans predict the involvement of both hands complementarily, which tend to play the same specific role across various tasks. The Complementary Role Differentiation (CRD) model predicts that one hand executes high frequency tasks, which involve finer temporal and spatial resolution, while the other one executes low frequency tasks, which involve grosser temporal and spatial resolution.

Therefore, it is more conceivable to say that both hands have different but equally important roles.

1.2.2 THE ORIGINS OF HANDEDNESS

For long time the anthropocentric view of handedness as a unique prerogative of humans has been largely widespread and for this reason the majority of the researches have been focused exclusively on human subjects. Indeed, the first studies on manual handedness did not consider the hypothesis that handedness might have evolved from an ancestral individual and even though the anatomical similarities between human and non-human primates were clearly evident, non-human animals were poorly considered in the observations.

Cultural and ontogenetic models

Collins claimed that human handedness emerged exclusively through cultural constrains that forced individuals to use preferentially one of the two hands (as cited in Hardyck & Petrinovich, 1977, p. 396). However, his theory seems not to justify how culture might have allowed the manifestation of left-handedness within the population, as it has long been oppressed by cultural persecutions. Moreover, if handedness mainly originated from cultural constrains, there would be high variability among different ethnic groups and historical periods. Right-handedness instead is widespread among many different human cultures (Bishop, 1990), especially within isolated communities and no data is available about populations that are predominantly ambidextrous or left-handed. Additionally, right-handedness is manifested also in actions that are not culturally sanctioned, such as tooth brushing or hammering. Thus, cultural pressure cannot lonely account for those people that are forced to use mostly the right hand but persevere in using the left hand for some activities (Teng, Lee, Yang, & Chang, 1976).

Language models

The analysis of both *in vivo* damaged and *post-mortem* brains report that the major pathways from the motor cortex to the musculature are crossed, so that the opposite hemisphere controls the two hands. According to Bishop (1990), Broca was one of the first researchers to realize the link between handedness and language. Since he noticed that the convolutions of the left cerebral hemisphere develop earlier that those of the right hemisphere, he suggested that this phenomenon might be responsible for a more precocious development of the motor control of the right hand, and for a left hemisphere control of the execution and coordination of articulation. Kimura (1973a,b) tried to shed light on this assumption by observing which hand right- and left-handers use to make gestures while they were speaking. The author found that right-handers tended to use predominantly the right hand to gesture while speaking, whereas left-handers did not manifest any significant bias. Further discoveries on brain-damaged patients showed that the frequency of atypical cerebral lateralization, such as the specialization for language functions in the right or in both hemispheres, was much higher in left-handers than right-handers (Bishop, 1990). Rasmussen and Milner (1977) reported also that an early left hemisphere lesion raised the probability that the patient had bilateral or right hemisphere language representation in association with left-handedness. Other researchers stressed that left-handers have reduced asymmetry rather than a reversal of asymmetry (Bishop, 1990).

Today, techniques including the functional Transcranial Doppler unltrasonography (fTCD), which works on the principles of fMRI, provide a more advanced support to investigate the association between cerebral language dominance and handedness in healthy subjects (Deppe et al., 2000). Knecht and colleagues (2000) compared brain activations during silent word generation in both left- and right-handers and found a greater left-hemisphere activation in 96% of the right-hand subjects tested. Interestingly, 76% of left-handers also showed greater left-hemisphere activation for the same task indicating that there is not a mirrored contralateral association for left-handed individuals. Further studies using fTDC supported these findings using a word generation task (Flöel, Buyx, Breitenstein, Lohmann, & Knecht, 2005; Knecth et al., 2000).

Differences in hand lateralization according to hemisphere specialization for language functions were also identified with behavioural neuropsychological methods: a left-hemisphere dominance in 80% of right-handers and in 70% of left-handers was reported using a dichotic listening task and a divided visual field task (Lavidor, Hayes, & Bailey, 2003). The authors found a significant relationship between the degree of handedness and the asymmetric accuracy when subjects were making lexical decisions based on stimuli presented either to the left or right side. These findings suggest the hypothesis of a continuous relationship between handedness and language lateralization.

Genetic models

The studies reported in literature that try to empirically demonstrate the genetic substrate of human handedness seem not to fit the simple Mendelian models that suggest a direct link between specific genes and the phenotypic expression of left and right hand preference. Therefore some researchers have proposed alternative genetic models in order to shed light on the origin of hand lateralization in human beings.

Annett (1978) proposed *the right shift theory,* according to which the genotype determines whether an individual is right-handed or rather does not manifest any preference. This assumption was conceived from non-human animals observations, in which the populations seem to manifest a normal distribution of right- and left-handers with a mean at zero. On the other hand, human hand preference manifests a near-normal distribution, but the mean is shifted towards the right-hand of the scale. According to Annett (1978), human distribution is like the non-human distribution, with a constant added, which is the right shift factor (see figure 4).

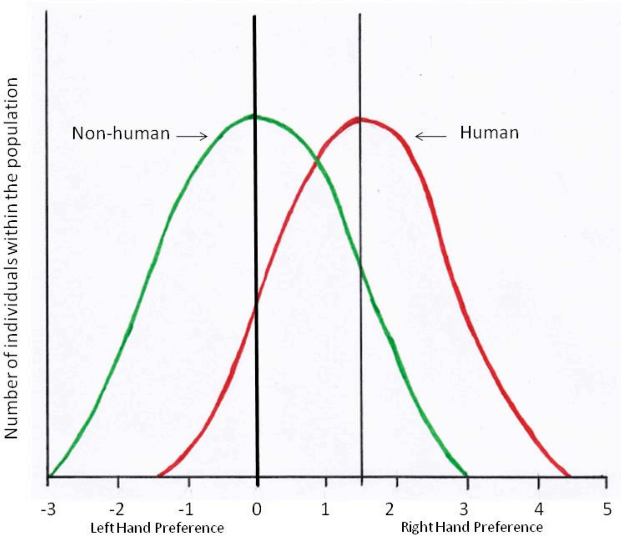


Figure 4. Human and non-human animal distribution of handedness. The chart depicts the theoretical distributions of the right- and left-handed individuals within human and non-human populations in accordance with Annett's (1975) model (redrawn from Bishop, 1990).

Annett and Kilshaw (1983) further assumed that handedness and language have the same genetic substrate. Indeed the right shift factor is characterized by two alleles (rs+ and rs-), which are responsible for the extent of which an individual manifest a cerebral lateralization for hand use and for language functions. In particular, the allele rs+ has an effect on the cerebral development in utero, by slowing the growth of the right hemisphere so that the left side of the brain is more likely to become dominant for cognitive and motor activities. Therefore, individuals homozygous or heterozygous for the allele rs+ possess the right shift factor and are more likely to manifest right-handedness, whereas homozygous for the allele rs- lack the right shift factor and their hand preference is totally shaped by the environmental forces. More specifically, this model is not based on the dominance effect of the allele rs+ but instead it is an additive model, where the effect of the heterozygous genotype rs+- expresses an intermediate phenotype between rs++ and rs--, with a greater chance of manifesting right handedness than rs--, but in part depending on the environmental influences (see figure 5).

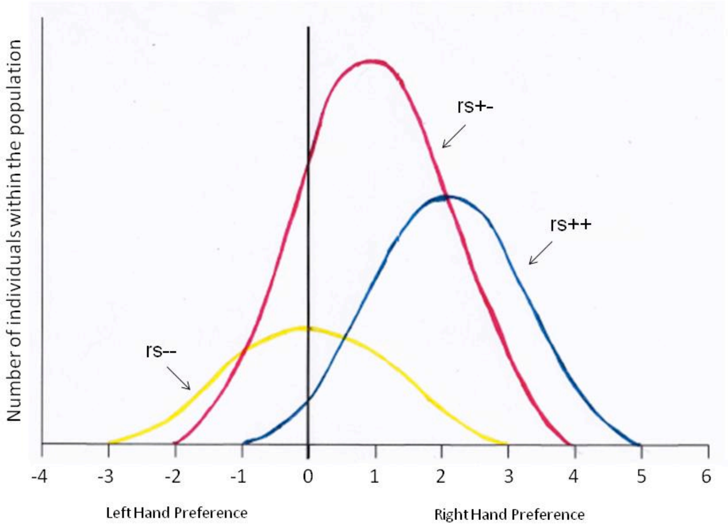


Figure 5. Distribution of human handedness according to the right shift theory. The chart depicts the postulated distributions of the right- and left-handed individuals within human populations for three genotypes, rs++, rs+-, and rs-- (redrawn from Bishop, 1990).

In Annett's genetic model (1978), handedness is treated as continuous variable, thus it is more flexible to fit several data sets. Furthermore, the right shift theory could represent a helpful tool to explain why cerebral lateralization in left-handers is not the mirror-image version of that of right-handers, as no specific factors are postulated for the determination of both left-handedness and hemisphere specialization for language.

A similar genetic model was proposed by McManus (1999), the *single gene model*, according to which human handedness is determined by two alleles at the same locus with an additive fashion, D (dextral) and C (chance). Homozygous for the allele D or C are right-handed or their hand preference is determined by chance, respectively. Heterozygous DC have a 75% of probability to manifest right-handedness. Moreover, the probability of left-hemisphere specialization for language is correlated to that of right-handedness manifestation. Although this model largely resembles Annett's right shift theory (2002), there are some subtle differences. First, the single gene model predicts the manifestation of two distinct phenotypes, right- and left-handedness, whereas Annett's model proposes that alleles determine right-handedness manifestation or no handedness at all. Second, the chance factor in McManus' (1999) model is related only to the CC genotype, whereas in Annett's right shift theory it affects all the three genotypes.

These genetic models seem to give good interpretation to the family data about heritability of handedness. For example, McManus (1991) and McKeever (2000) showed that right-handed parents are less likely to have left-handed children than partners with any other combination of handedness. Furthermore, left-handed parents have more probability to produce left-handed children. Additionally other authors found a strong maternal effect on offspring hand preference that would be consistent with a X-linked genetic determinism and a social influence determined by the generally closer contact between the mother and her child. Indeed, a higher prevalence of left-handed children was found when at least only the mother was left handed rather than when left-handedness was apparent only in the father (McManus, 1991; Spiegler & Yeni-Komshian, 1983). Nevertheless, these studies seem not to convince many scientists since they rely on small samples.

Evolutionary models

The hypotheses cited above about the origins of human handedness share the anthropocentric view that this trait emerged recently, after the split of humans from ape ancestors. However, recent evidence of lateralized motor actions, underpinned by contralateral neural regions in non-human animals (MacNeilage, Rogers, & Vallortigara, 2009; Rogers & Andrew, 2002; Vallortigara, Chiandetti, & Sovrano, 2011; Vallortigara & Rogers, 2005) led evolutionary theorists to explore a range of possible selective adaptive pressures for the emergence of right-handedness, challenging the long-lasting hypothesis that handedness, thus cerebral lateralization, is a unique prerogative of humans. Some speculated that right-handedness emerged as a result of gestural language (Corballis, 2002; Hopkins, et al., 2005b), tool use (Breuer, Ndoundou-Hockemba, & Fishlock, 2005; Greenfield, 1991), coordinated bimanual actions (Hopkins, Hook, Braccini, & Schapiro, 2003a) posture (MacNeilage et al., 1987) and bipedalism (Braccini, Lambeth, Schapiro, & Fitch, 2010; Westergaard, Kuhn, & Suomi, 1998).

For the remainder of this dissertation, the interest will be focussed on tool use and gestural communication, which are both based on the cerebral functional link between right-handedness and language skills. Although the two hypotheses seem to provide good theoretical and empirical support, the *causal* link between the emergence of right-handedness and language evolution is still hotly debated (Corballis, 2003; Vauclair, Meguerditchian, & Hopkins, 2005).

The Tool Theory

This is not the first time that tool-use has been implicated in the evolution of human language skills. In fact, some authors have suggested that object manipulation for actions related to tool-use, manufacture and even food preparation have common features to modern language and therefore serve as a likely precursor to language (Byrne & Byrne, 1993; Corballis, 2002; Greenfield, 1991; Mercader et al., 2007). Some scientists postulate that language evolved as an extension of right hand and left hemisphere ability to produce temporal sequences of motor activity derived from tool use (Bradshaw & Nettleton, 1982; Hewes, 1973; MacNeilage et al., 1987; Morgan & Corballis, 1978)

Initial supporters of the tool theory (Calvin, 1982; Steklis & Harnad, 1976) suggested that humans were unique for their bipedal posture, the ability to build and use a wide variety complex tool, the preferentially use of the right hand in complex motor skills, and language. The first manifestation of a greater involvement of upper limbs in tool-use occurred after the hominids acquired a bipedal gait, which freed the hands from the maintenance of posture. The most complex activities generally require the complementary involvement of both hands in which case the left-hand generally serves as a support mechanism (e.g. holds or steadies the object), while the right-hand performs the precision manipulations. These scientists suggested that the skilled motor actions performed by the right hand, underpinning the activities involving tool making and tool using, evolved in, and are dominated by, the left hemisphere.

Frost (1980) was one of the first scientists to infer the link between left-hemisphere specialization for motor skills and the development of language. He argued that speech, produced by the movements of the tongue, lips, and vocal chords, requires precisely timed and sequenced actions to manifest communication. He likened this process with that of the construction and use of tools, which involves skilled serial motor activities, such as the movements of arms, hands and fingers, hierarchically employed to reach a goal. Biederman (1987) supported this assumption and stressed that the ability to build and use tools is linked to language, as both activities can generate infinite complex structures that can be hierarchically arranged. In other words, humans can combine together different constructive elements in the same way they combine phonemes to form words and sentences. Indeed, language has a hierarchical structure, called grammar, which is based on several rules for combining words in a meaningful order (Greenfield, 1991). Tool-use has a similar hierarchical organization, in which simple hand movements are combined together in a specific order to reach a goal (e.g. figure 6). Given the structural relationship between language and tool-use, the combination of rules for the tool manufacturing was defined by Greenfield (1991) as *grammar action*. The similarity in skill sets begs the question if one led to the other.

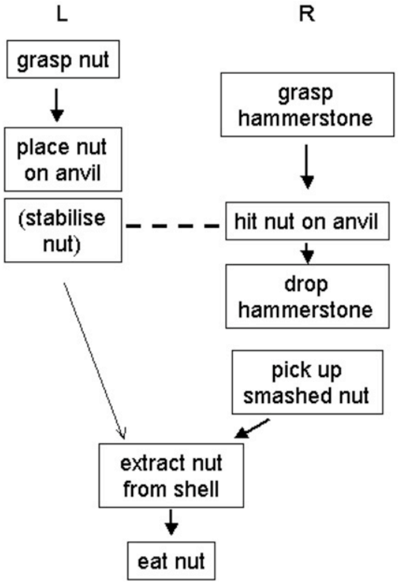


Figure 6. Sequences of manual activities during nut cracking. This example shows how simple unit of actions need to be hierarchically exploited to reach a goal during tool use, for both hands. L = left hand, R = right hand (adapted from Uomini, 2009).

With modern imaging techniques, scientists have been able to identify the regions of the brain that are active during handedness mentalizations. A recent study seems to demonstrate this assumption, as an overlap of activity between tasks related to language and tool use in the Brodmann area 44 (BA44, which is part of the Broca's area) was found in a group of healthy humans (Higuchi, Chaminade, Imamizu & Kawato, 2009). The researchers demonstrated that BA44 became activate during the execution or the imagination of sequential actions, suggesting that the same neural activities are used to process language and manual hierarchical actions. Furthermore, in primate imaging studies others have demonstrated that both action observation and tool use activated the arcuate sulcus in the inferior frontal cortex of monkeys, a region which is supposed to be the homologue of humans Broca's area (Nelissen, Luppino, Vanduffel, Rizzolati, & Orban, 2005; Petrides, Cadoret, & Mackey, 2005).

These findings seem to support the hypothesis that human language might have some functional link with the neural substrate for tool-use of primates (Greenfield, 1991), as both language and tool use underpin the same neural computations within the Broca's area. Furthermore, findings suggest that this overlap of activations for tool use within the language regions of the brain existed prior to our evolutionary split with extant primates. Therefore, one might hypothesize that the neural substrates tied to right-handed tool-use might have served as a pre-adaptation for the evolution of language in humans, thus creating a causal role between handedness and communication (Bradshaw & Nettleton, 1982).

The gestural-origins theory

According to *the gestural-origins theory* (Corballis, 2002; Hewes, 1973), human speech might have seen its precursor in the gestural communication of non-human primate that seemed to be able to communicate with a very simple grammar. Further in the evolution, other factors might have contributed in the increment of complexity of gestural communication, until it was substituted (although not completely, as humans still use gestures when they talk) by speech.

One of the most common features among primates is the hand, which is characterized by flexible fingers for a good grip on many kinds of object. The centres of the cerebral cortex control the cinematic movement of hands and thus the voluntary manipulation is higher than vocalizations, which instead are supposed to express an emotional status (Corballis, 2010; Gentilucci & Corballis, 2006). Most important, hands are also well adapted to create four-dimensional space-time representations of the four-dimensional environment, by creating images resembling objects or actions of the real world (e.g. forming the shape of a triangle, mimicking a fight by throwing a punch in the air).

Bipedalism might have encouraged the gestural communication, as hands were free from the maintenance of posture. Moreover, the increment of brain size led also to an improvement of the ability to mentally represent objects and the ability to learn from other conspecifics, favouring the passage from a primitive protolanguage (which was lacking of the generative ability) to a more modern language, increasing the ability to acquire more concepts and to arrange them hierarchically. This event was concomitant with the invention of stone manufactures and with the increment of tool use and object manipulation.

The passage from hand to mouth became possible also because a change in the vocal tract occurred as a consequence of the bipedalism, which induced the larynx to drop (see figure 7). This phenomenon allowed hominids and subsequently humans to produce particular sounds that other animals cannot perform. Moreover, Corballis (2002) pointed out that the combined mechanical articulation of lips, tongue, and the soft palate together with the larynx produce vocal words that could be considered as “sound gestures”, such as “visual gestures” are produced by the hands. The author suggested therefore that gestural sounds could have first emerged not as vocal words but as simple sounds such as tongue clacking or teeth chattering in chimpanzees. Hopkins (2010), for example, suggested that the foundation of speech might also be rooted in the lip-smacking expression of many non-human primate species, in which the sound made through breath releasing during lips protrusion developed then into more articulated words.

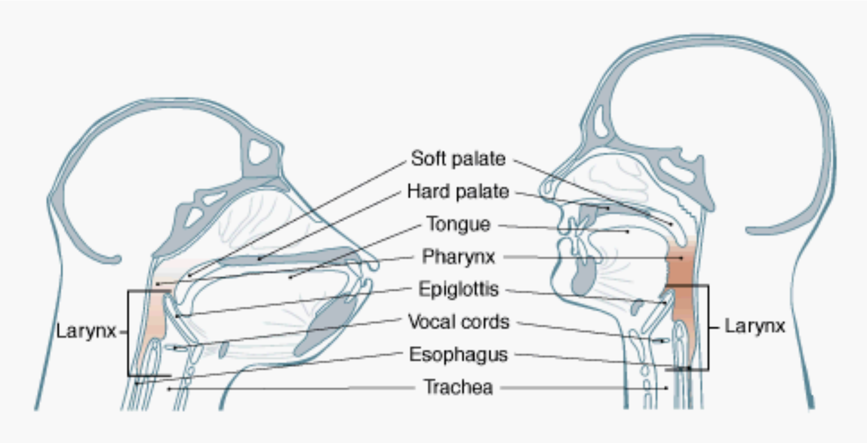


Figure 7. Descent of larynx. The larynx of a chimpanzees (left) is compared with the larynx of a human (right) (retrieved from http://pubpages.unh.edu/~jel/712/acquisition_ch9.htm).

Mouth movements associated with sounds gradually assumed dominance over hand movements, probably because they were more advantageous, and finally prevailed on the gestural communication, as we can see in the modern humans. In particular speech frees hand for other activities, especially for tool construction and might have led to the manifestation of a right-hand preference (Corballis, 2002).

The link between hand and language has been demonstrated by Gentilucci and colleagues (Bernardis & Gentilucci, 2006; Gentilucci, 2003; Gentilucci, Benuzzi, Gangitano, & Grimaldi, 2001), who found that the opening of the mouth during the pronunciation of a syllable changed in accordance with the size of the object they had to grasp (see figure 8). The same effect was shown when the speaker watched another person grasping different-sized objects. More advanced studies relying on neuro-imaging analysis, showed that Broca's area was activated during the representation of meaningful arm gestures (Buccino et al., 2001; Gallagher & Frith, 2004).

Figure 8. Grasping with mouth. The subject has to pronounce a syllable while grasping an object with the hand. SP = starting point (adapted from Gentilucci et al., 2001).

Manual communication thus might have preceded speech in evolution. According to the tool theory for the connection of right-handedness and left-hemisphere specialization for language, tool use might have played a causal role in the evolution of gestural communication as both relying on ordered-structured processes (Bradshaw & Nettleton, 1982; Gibson, 1993). The contralateral organization of the neural path underpinning hand praxis might have led the right hand to be more employed during skilled action, such as hierarchically arranging the simple movements of the hand and finger to construct communicative symbols. When speech finally occurred there were already pre-adapted motor skills in the left hemisphere and hence speech became lateralized as well.

1.2.3 ANCIENT HUMAN HANDEDNESS

One way to investigate the history of human handedness is to study ancient human fossils and tools, in order to verify whether our ancestral hominids already manifested lateralized manual behaviours. Indeed, as Cashmore, Uomini, and Chapelain (2008) pointed out, “the study of the evolution of handedness must necessarily start with [hominids] archaeological evidence” (p. 8).

An intense mineral formation on arm bones can positively reflect the mechanical loading on the arm and thus muscle strength (Steele, 2000). Based on this measures, some hominid species seemed to manifest right-handedness at the population level. As Cashmore and collaborators (2008) argued, skeleton of *Homo ergaster* (WT-15000) were found to have a greater development of clavicular area of attachment of the right deltoid muscle and a greater length of the right ulna compared to those of the left arm.

The fossilised cranial material can also provide information about the size, the structure, and the organization of the cortical surface of the hominid brain. These data could subsequently be used to assess hand preference on the basis of the assumption that handedness and language are linked to each other. Cranial endocasts from *Australopithecus* and *Homo* genders revealed common patterns to modern human with greater protrusions of the left-occipital and right-frontal hemispheres (Holloway, 1980). In particular, the left lobes were pronounced in the region of the Broca’s area, which suggested that individuals might have been right-handed.

Many authors suggested the possibility to predict hand preference from tool-making debris and from wear patterns on hand-held artefacts. For example, Toth (1985) noted that the orientation of cortex on flakes detached from a core reflected whether the knapper rotated the core clockwise or anti-clockwise. From two archaeological sites in Kenya and Spain, the researcher found that flakes suggested predominately a clockwise rotation of the stone, thus a right hand use for tool making.

Another indirect method to assess handedness in hominids is the observation of cave and rock art. Valladas and colleagues (2001) dated the oldest rock art as 30,000 years or more and one of the most widespread forms of prehistoric art was the representation of handprints or hand stencils on the surfaces of caves. Handprints consisted of covering the palm with a coloured substance and creating a positive print on a surface (e.g. figure 9a), whereas hand stencils were created by leaning the hand on a surface and colouring the outline of the hand with a substance that was either blown out from the mouth or applied manually with a brush (e.g. figure 9b). Hand stencils were more likely to be made with the non-dominant hand as the dominant-hand might have been used to perform the painting action (Cashmore et al., 2008).

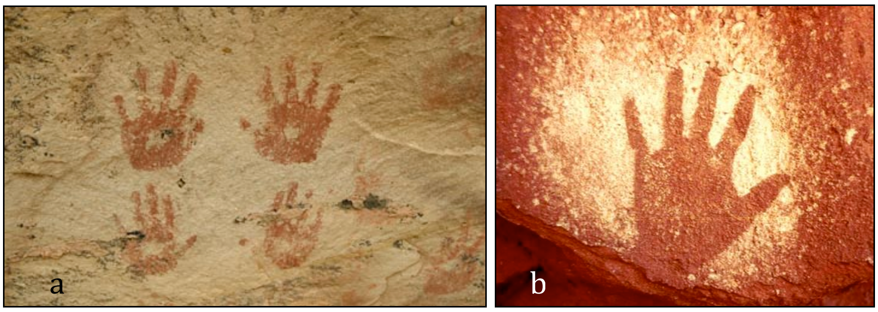


Figure 9. Handprints and hand stencils. a) Handprints from the archaic culture (photo by D. M. Chriss); b) an Anasazi hand stencil (photo by Gnesios).

However, Pager and colleagues pointed out that hand prints could have also be made with the non-dominant hand, thus they are not considered a reliable marker to assess hand preference in hominids (as cited in Cashmore et al., 2008, p. 16). The majority of hand stencils found in Europe, Australia, America, and Borneo show an overwhelming predominance of left-hands paints, suggesting that individuals preferred to use their right hand to apply the pigmented substance.

Although the fossil materials may help to make inferences on hominids' handedness, some skeletons may not present all bones of both hands, thus making difficult to verify differences between the two upper limbs. The analysis of stone tools can somehow be an easier method, as they have a better preservation than bones. However, their indirect link to hand-use makes them an ambiguous method to assess handedness. Also handprints and stencils can be misinterpreted, as it is difficult to identify whether a single individual or more made the pictures on a single wall or whether series of stencils were made in one bout or in separate occasions (Uomini, 2009).

Therefore, although the archaeological data could be considered a useful method to study the evolution of handedness, some evidences need to be treated cautiously. Thus, further researches on modern humans and on other living primates could help to fill some gaps related to the investigation of the origin and development of human handedness.

1.3 Cerebral lateralization for emotions

Although cerebral lateralization for language has been extensively investigated, human brain is specialized for other cognitive processes that are now acquiring more interest in the scientific literature. Indeed, left-hemisphere is specialized not only for language processing but also for other activities, such as focussing on relevant stimuli and in controlling behaviours that are acquired during learnt routines (MacNeilage et al., 2009). On the other hand, the right hemisphere is specialized in noticing details and responding to novel stimuli, in activating during emergency situations (MacNeilage et al., 2009), in controlling the endocrine functions, the heart rate, and the blood pressure, in recognizing faces and in the processing of emotions (especially strong and fearful ones) (Rogers, 2010). The latter skill has particularly provided interests in the scientific community, probably because humans live within a complex social system whose communication relay also on the emotive interactions between individuals.

For a social individual it is extremely important to understand the meaning of other people's behaviour, as a large amount of daily life is spent in observing and interpreting the actions of others (Barresi & Moore, 1996). Some researchers have reported that observing someone being touched elicits activity in the same area of the somatosensory cortex as being touched oneself (Blakemore, Bristow, Bird, Frith, & Ward, 2005; Keysers & Perrett, 2004). This process of perceiving the disposition and the intention of other individuals is known under the name of *social cognition* (see Santos et al., 2010), and it is highly related to the processing of emotions, as action observation can produce a strong emotional response and a consequential modification of the observer's behaviour. This ability to share other people's emotions facilitates social communication and social coherence, and might have contributed to the origin of the altruistic behaviour (de Vignemont & Singer, 2006).

1.3.1 THE RIGHT HEMISPHERE AND THE VALENCE HYPOTHESES

Although the majority of cognitive sciences seem to agree on the assumption that emotions are asymmetrically processed, controversy persists about which hemisphere is involved in this neurological system. Indeed, the oldest speculation about brain asymmetry states that the right hemisphere is uniquely specialized in the processing of all emotions, regardless of their positive and negative valence. This assumption is known as the *right hemisphere hypothesis* (Borod et al., 1998; Campbell, 1982). The first researcher that revealed the association between emotions and right-hemisphere was Mills, who observed a decrease of emotional expression in individuals with injuries on the right cerebral hemisphere (as cited in Demaree, Everhart, Youngstrom, & Harrison, 2005, p. 4).

The use of composite-face images represents a useful tool to assess lateralization of face and emotion processing. This method consists of presenting a subject with a picture created by matching one of the two hemi-faces, either the right or the left side, with its mirror-reversed part (i.e. the right side with its mirror-reversed right side and the left side with its mirror-reversed left image). The hemispheric lateralization is measured by asking the subject to judge which one of the two mirror-reversed images, right or left, is more expressive. This would help to infer the asymmetrical involvement of the hemispheres in facial expressions. Some studies used this method with adult subjects and reported that images composed of two left sides were more expressive than those composed of two right side (e.g. Campbell, 1978; Gilbert & Bakan, 2002; Lane, Kivley, Du Bois, Shamasundara, & Schwartz, 1995) (e.g. figure 10).

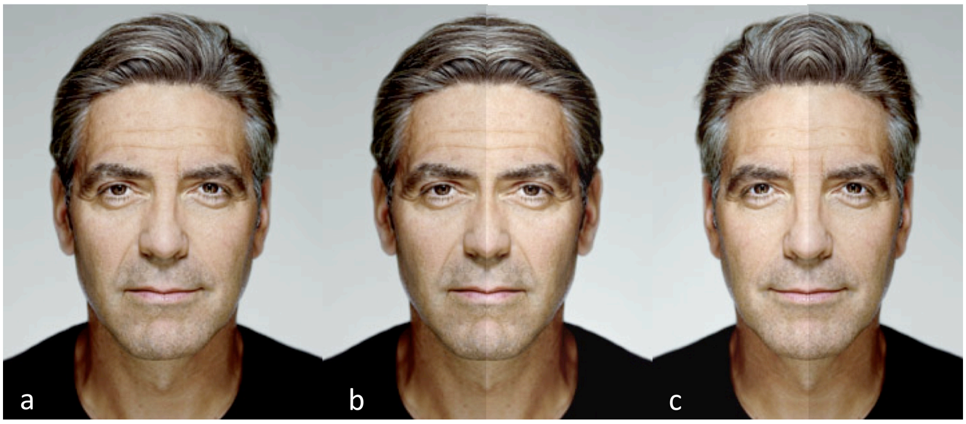


Figure 10. The composite-face task. The three pictures represent a simulation of a composite-face images. a) Original picture; b) composite-face image made with the two right sides of the face; c) composite-face image made with the two left sides of the face (remake from http://www.esquire.com/features/george-clooney-2-girls-1-cup-0408-3).

A further method uses chimeric faces, composed of two different half-faces, but presented to the subject as a complete face (e.g. figure 11). Aljuhanay, Milne, Burt and Pascalis (2010) reported that face identification was mostly based on the right side of the face (thus through the left visual field of the judger), suggesting a specialization of the right hemisphere not only for the processing of faces but also for the perception and the expression of emotions.

Figure 11. Chimeric faces. The faces were made with two sides of the same person but displaying different expressions (adapted from Bourne, 2008).

Humans generally have a stable pattern of cerebral lateralization for face processing. Indeed, consistent findings report that facial musculature is contralaterally innervated (Rinn, 1991) and that normal right-handed adults significantly display facial expression more intensely on the left than the right side of the face (Borod, Haywood, & Koff, 1997). Moreover, a range of perceptual and neuro-imaging techniques have accounted for a specialization of the right hemisphere in the perception of faces and facial expression in humans (Aljuhanay et al., 2010).

There is another branch of cognitive researchers claiming that emotions are differently processed in the two hemispheres, according to the type of emotion. Indeed, *the Valence hypothesis* bears that the right hemisphere is involved in the processing of negative emotions whereas the left-hemisphere in positive emotions (Davidson, 1995). This assumption first arose when Goldstein showed that patients with lesions to the left hemisphere were more likely to manifest depressing symptoms compared to the reversed hemispheric situation (as cited in Alves, Fukusima, & Aznar-Casanova, 2008, p. 63). The same pattern was found also by Sackeim and colleagues (1982) who also reported a pathological laughing condition in patients with damages to the right hemisphere and pathological crying condition in patients with damages to the left hemisphere. More advanced neuro-imaging techniques, as fMRI, Magneto-Encephalography (MEG), Electro-Encephalography (EEG), and Positron Emission Tomography (PET) analysis showed that amygdala is involved in the processing of negative emotions, as impairments of this structure reduce emotional responses and face recognition (Calder, Young, Rowland, Hodges, & Etcoff, 1996) or cause severe depression symptoms (Drevets, et al., 1992).

The valence hypothesis was recently associated with the *motivational approach-withdrawal hypothesis* (Demaree et al., 2005), which analyses the emotional system from an evolutionary prospect. Indeed, this model claims that individuals behave differently according to either positive or negative emotions with an approaching or withdrawing reaction, respectively. Thus, sadness, fear, and disgust are associated with withdrawal behaviours (right hemisphere), whereas happiness and surprise drive individuals to approach the environmental stimuli (left hemisphere).

Although the right hemisphere hypothesis and the valence hypothesis lead to different predictions for the perception of positive information, both would predict that the right hemisphere is superior to the left hemisphere in processing negative information (Root, Wong, & Kinsbourne, 2006). Moreover, Davidson (1992) also argued that the degree of left hemisphere implication in the processing of positive stimuli might depend on the subjective experience on positive emotions.

1.3.2 HANDEDNESS AND EMOTIONS

Recent interest has been driven also to the relationship between hemispheric specialization for emotion and handedness.

The observation of lateralized self-directed behaviours (SDBs), such as self-scratching or self-touching, seems to provide information about the asymmetrical processing of emotions of the brain, as they are supposed to reflect emotional involvement of the subject (Maestripieri, Schino, Aureli, & Troisi, 1992) with respect of the environmental factors, such as a particular social context or highly cognitive demanding tasks (Leavens, Aureli, & Hopkins, 2004). Dimond and Harries (1984) found a consistent higher preference for left-hand during self-touching behaviours, in particular directed to the chin. These findings supported the dominant role of the right hemisphere for the processing of emotions. Moreover, authors suggested that since emotions are expressed more intensely on the left side of the face (Borod et al., 1997), the left hand might be used as a pointer to increase this effect.

More recently Root et al. (2006) carried out an experiment in which subjects were asked to use their left and right hand to select as fast as possible between happy and sad faces alternatively. The researchers found that right-handers reacted faster in recognizing happy faces, whereas a shorter time of response was found when the left hand had to perceive sad faces, as compared to reversed assignment. These findings were in accordance with the valence hypothesis.

Although there is poor availability of studies investigating the relationship between hand and emotions, findings seem to suggest a direct link between hemisphere specialization for emotions and manual activity. Moreover, although it is still unclear which hemisphere underpins the processing of emotions, the manual preference tied to the expression of emotions seems not to be tied to the hand preference for tool-use. More investigation is needed to shed light on this issue.

In conclusion, although the hypotheses about cerebral lateralization for processing of emotions seem to be based on different assumptions, they can provide good support for many studies and account for different situational studies. Moreover, as Davidson (1992) suggested, the individual experience might influence the perception of different stimuli, thus the conceptual processing of positive and negative emotions in the hemispheres. A more plausible solution might be the investigation of cerebral lateralization in terms of evolution, in order to verify whether some typically predicted human aspects could be found in other species. Therefore, ascending the roots of evolution might help to clarify some still debated aspects of human cerebral organization. Our closest relatives, non-human primates, could further help the investigation of the evolution of cerebral lateralization and thus might help to shed light on some unclear questions.

Chapter 2

Cerebral lateralization in non-human primates

Over the past 30 years there was a widespread anthropocentric view that hemispheric specialization was unique to humans and that people had a special evolutionary status (MacNeilage et al., 2009). Therefore, lateralization was associated with human cognitive characteristics and abilities, such as tool-use, consciousness and language, while no other alternatives were considered plausible. However, lateralized behaviours have recently been documented in other vertebrates, such as fish, amphibian, reptiles, birds, mammals (Rogers & Andrew, 2002; Vallortigara & Rogers, 2005), and invertebrates (e.g. Frasnelli, Vallortigara, & Rogers, 2010). This evidence suggests that hemispheric specialization might have appeared earlier than human evolutionary split from our last common ancestor with the great apes as the result of an adaptive selection. Moreover, it has been postulated that cerebral lateralization confers some advantages. Indeed, Levy suggested that lateralization increases the neural capacities, by allowing the organisms to spare less neural tissue, as no duplication of functions occurs (as cited in Ghirlanda & Vallortigara, 2004, p.2). This is important for complex functions such as language processing, which requires extensive neural circuitry (Corballis, 2002). Moreover, cerebral lateralization enables the two hemispheres to process separate and parallel functions, as demonstrated in domestic chicks, which can simultaneously check for a predator with one eye, while the other one spots seeds spread on a pebble floor (Rogers, 2000a). Andrew (1991) and Vallortigara (2000) have also argued that lateralization would prevent the simultaneous initiation of incompatible responses, particularly in species with laterally placed eyes that can scan independently. For examples, frogs can select between pray objects seen in both lateral visual fields and in this context intra-hemispheric communication plays a relevant role in reducing potential competition or response emission (Ingle, 1973).

During the last decades, the number of studies concerning cerebral lateralization in non-human animals has conspicuously increased. In particular the interest has been largely focused on non-human primates, as they are considered humans closest relatives and especially because they can provide a good support for the investigation of the emergence of handedness and language.

2.1 Non-human primates as an ideal model

The first studies on cerebral lateralization in non-human primates are dated before the second half of the 20th century and were mainly based on invasive observations on split-brained rhesus macaques, reporting anatomical and functional similarities with humans (Hamilton & Vermiere, 1988). These methods provided interesting discoveries about primate cerebral functions, especially because similar results could have not been achieved with humans subject. However, there are important differences between macaques and humans brain that do not allow making convincing inferences on the evolution of human cerebral lateralization. Therefore, researchers attempted to investigate lateralization in humans' closest relatives, great apes, which show more complex cerebral functions compared to the other non-human primates and are phylogenetically and anatomically very similar to humans.

2.1.1 GREAT APES

The cluster of Great apes includes four species: chimpanzees and bonobos (genus *Pan*), gorillas (genus *Gorilla*), and orang-utans (genus *Pongo*). They are genetically very close to humans, particularly chimpanzees and bonobo, whom divergence from human DNA has been estimated at around 5% (Britten, 2002).

Compared to other non-human animals and non-human primate species, great apes have more complex cerebral convolutions and an augmented cerebellum, which contribute to cognitive processes such as planning complex motor patterns, visuo-spatial problems solving, and procedural learning. Furthermore, their brain size is disproportionately larger than the body, probably because they need “extra” neurons for the elaboration of all cognitive functions (Gibson, Rimbaugh, & Beran, 2001). Like humans, the great bundle of nerves that underlies the hemispheric inter-communication allows the individuals to enhance the ability of problem solving through the specialization of different areas, so that parallel-processing activities can be performed (Gibson, 1990). Also large brain size has contributed in increasing the cerebral cortical connectivity that might have favoured the brain lateralization in humans (Hopkins & Rilling, 2000).

The size of the brain is mainly correlated with the life history and it is probably an effect of large body. Indeed, a great cognitive demand might be related to the necessity of assuming a consistent amount of food in order to nourish a large body size. Moreover, since food is not always easily available or is hard to retrieve, tool-use, cooperative hunting, referential pointing and iconic gestures can be elicited to improve the foraging. Furthermore, locomotion requires good spatial orientation, thus extreme cognitive challenge, especially during arboreal movements, in which individuals have to found the right branches to sustain their heavy bodies (Russon, 1998). Finally, complex social relationships require great flexibility to interact with different individuals and competitions for food can represent an important ground for the evaluation of social cognitive abilities (van Schaik et al., 2003).

Many studies on lateralization have taken great interest in the observation of great apes not only because they have very developed brains, but also because they are anatomically very similar to humans (Byrne, Corp, & Byrne, 2001). Indeed, the hands of great apes are very similar to humans' ones, with the opposable thumb that allows a solid grip and fine manipulation of objects (see figure 12).

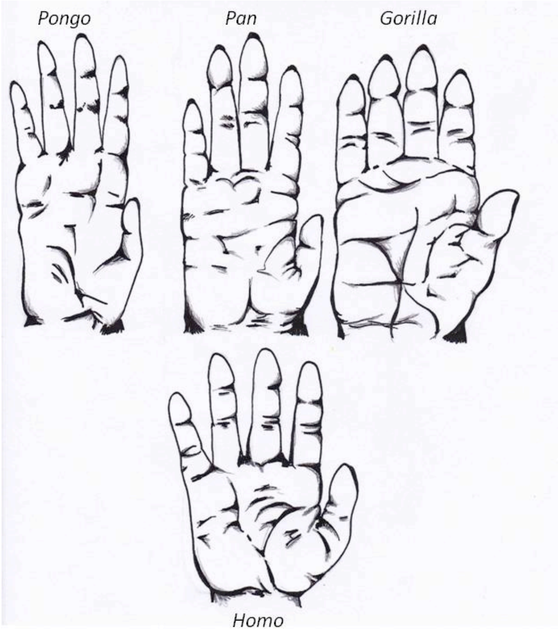


Figure 12. Representations of the hands of genus *Pongo*, *Pan*, *Gorilla*, and *Homo*.

Moreover, great apes and humans share similar cerebral anatomical asymmetries, such as a longer Sylvian fissure in the left hemisphere than the right (Gannon, Holloway, Broadfield, & Braun, 1998) and the protrusion of the right frontal lobe (Cain & Wada, 1979; Zilles, et al., 1996). In particular, the anatomical asymmetries of non-human primates tend to be similar to right-handed humans, though handedness lateralization is stronger in humans.

This evidence led many researchers to further investigate great apes cognition and in particular to deepen the issue about the origins of left-hemisphere specialization for language and the related handedness in humans.

2.2 Language lateralization

2.2.1 GREAT APES COMMUNICATION

There is clear evidence that many species of non-human primates, in particular great apes, show efficient communicative social skills akin to those of humans based on visual and tactile stimulation, such as facial expression, eye gaze, referential glancing, manual gestures and tactile signals (e.g. huddling, grooming) (Dunbar, 2010; Preuschoft, 1992; Tanner & Byrne, 1996), which seem to challenge the hypothesis that human language evolved from monkeys vocalizations. The long debate probably started when Sue Savage-Rumbaugh taught to Kanzi, a bonobo male, 256 symbols that were displayed on a board and each of them referred to a particular object, person, or action (as cited in Corballis, 2002, p. 45). These lexigrams, as they were called, were not figurative representations of the objects, but clueless abstract symbols. Kanzi not only learnt the meaning of all the lexigrams, but could also spontaneously combine few of them together in order to form specific requests. Interestingly, the small sequences of symbols seemed to follow the rules of a very basic grammar, such as that of a 2 year-old child.

The communicative ability of Kanzi has been defined as *protolanguage*, which is a primitive syntax in which few enunciates can be combine together in order to vehicle a simple request or a description of the environment (Corballis, 2002). Thus, protolanguage is suggested to represent a necessary intermediary stage in the evolution of language (Smith, 2008). Though very simple, the construction of concepts requires the subject to form mental representations of the surrounding environment and the ability to combine them with logical meaning. Indeed, Tomasello (1996) demonstrated that a group of captive chimpanzees successfully choose the right tool to reach a piece of food, without relying on previous experiences or on conspecific imitation, suggesting that chimpanzees can form mental representations. Protolanguage might be limited to species that have to interact with many stimuli, such as objects and social interactions, where animals might need a more structural form of communication to describe the complex environment (Corballis, 2002), rather than simple arousal vocalizations. Therefore, Povinelli argued that although chimpanzees seem to have mental representations of the environment that can be combined together with very basic grammar rules, they have not developed human-like communication because inanimate and social environment are not as much intricate as that of humans to require a complex grammar (as cited in Corballis, 2002, p. 54). Moreover, a more complex communicative system would require the development of particular cognitive abilities, thus a consistent expenditure of energy.

According to scientists supporting a continuity theory of language, human speech might have originated from a simple grammar system in non-human primates, at least apes, that gradually became more complex with the increasing of complexity of environmental and social stimuli. Since neurophysiological evidence suggests that nonhuman primates have little if any cortical control over vocalization (which is critical to speech), there seems to be more support for the hypothesis that the common ancestor of humans and chimpanzees was much better pre-adapted to develop a voluntary communicatory system based on visible gestures rather than sounds (Corballis, 2002).

2.2.2 LANGUAGE LATERALIZATION IN GREAT APES

It has been speculated that the neural structures underlying manual movements in great apes, perhaps also including tool use and gestural communication (Wheaton, Nolte, Bohlhalter, Fridman, & Hallet, 2005), are homologous with the lateralized language areas in the human brain (Hopkins, Russell, & Cantalupo, 2007; Kelly et al., 2002). Indeed, a consistent number of studies found an overlap of brain regions underpinning language and manual tool-use. In particular, non-human primates, especially great apes, have been shown to possess lateralized language areas, which are very similar to those of humans, suggesting an evolutionary continuity between human speech and ape primitive communication.

Recent neuro-imaging studies have indicated that all four species of great apes display homologous human Broca's (i.e. Brodmann area 44) (Cantalupo & Hopkins, 2001; Cantalupo, Pilcher, & Hopkins, 2003) and Wernicke's (i.e. Brodmann's area 45) (Spocter et al., 2010) areas that are asymmetrically larger in the left hemisphere (see figure 13). Moreover, Higuchi et al. (2009) found that the homologous Broca's and Wernicke's areas were active in the ape brain during tool use, suggesting that there is an overlap of neural activation for both language perception and tool-use in humans within Broca's area. Additionally, Pollick and de Waal (2007) reported that this area is activated during both the production and perception of gestures but not vocalizations.

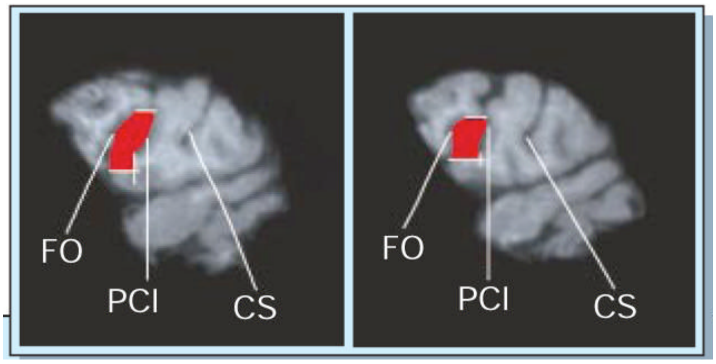


Figure 13. Broadmann's area 44 is asymmetrical in great apes. A representation of the Broadmann area 44 (in red) in the left hemisphere (left) and in the right hemisphere (right) of a chimpanzee's brain. FO = fronto-orbital sulcus, PCI = precentral-inferior sulcus, CS = central sulcus (adapted from Cantalupo & Hopkins, 2001).

More recently a group of researchers reported variation in the position of the chimpanzees cerebral areas homologous to the Broca's area of humans (Schenker et al., 2010). Specifically, findings revealed that the inter-individual variation of the chimpanzees' cerebral area responsible for language functions was comparable to that of humans, but any significant population-level asymmetry for any measure of this area was not apparent. These findings suggested that the expansion of the Broca's area might be occurred during human evolution as an adaptation of our species for language abilities.

Further neuro-imaging and post mortem studies on chimpanzees reported a leftward asymmetry in the planum temporale surface area (PT) (a flat bank of tissue that lies in the superior temporal lobe) (Good et al., 2001; Watkins et al., 2001), which is particularly greater in right-handers than left-handers (Foundas, Leonard, & Hanna-Pladdy, 2002). Furthermore, the evidence that this area overlaps with Wernicke's area (Eckert, Leonard, Possing, & Binder, 2006), suggested that PT asymmetry might be considered an anatomical marker of cerebral lateralization for language (Dorsaint-Pierre et al., 2006). Similar results were obtained in all species of great apes (Cantalupo et al., 2003; Gannon et al., 1998), where a significant leftward asymmetry was found for all four species. Hopkins and Nir (2009) further examined the effect of handedness on the PT area asymmetries in chimpanzees for both communicative and non-communicative manual activities with a magnetic resonance study and reported a greater leftward asymmetry in the grey matter volume of the PT only for communicative gestures, particularly in right-handers, whereas non-communicative gestures were associated neither with asymmetries of the surface area nor with asymmetries in the grey matter volumes of the PT. However other studies did not find a correlation between the PT area and communicative gestures, but instead reported an association between this area and non-communicative gestures. These findings suggest that both communicative and non-communicative gestures might be associated with asymmetries in the homologous language areas of humans in the left hemisphere, however involving different areas. Although there are clear differences in the motor functions of tool-use and manual gesture, these behaviours might reflect similar cognitive mechanisms, suggesting that left-hemisphere specialization for language might not be unique to humans, but occurred before we split from apes. Moreover, tool use may have served as pre-adaptation for the emergence of motor functions associated with language. However, more researches are needed to further corroborate existing behavioural and structural evidence.

2.3 Handedness in great apes

Although there is growing body of evidence showing a predominant hand preference in great apes, most of the findings concerns chimpanzee subjects. Hand preference has been studied also in other great apes, such as orang-utans (*Pongo* sp.) (e.g. Olson, Ellis, & Nadler, 1990) and bonobos (*Pan paniscus*) (e.g. Hopkins, Bennett, Bales, Lee, & Ward, 1993; Hopkins & de Waal, 1995), however few studies reached the authors' criteria for inclusion, mainly because of sample size and methodological issues. In particular, studies investigating handedness in orang-utans have not received enough interest in this context probably due to their solitary social system, which is completely different from that of humans. Bonobos, on the other hand, are now gaining more attention, since they are very close to chimpanzees and thus to humans. However, the poor availability of subjects in zoo settings might have discouraged scientists to study this species. Specifically, this dissertation will consider studies on handedness tied to cerebral lateralization in chimpanzees (*Pan troglodytes*) and gorillas (*Gorilla* sp.), which, among the great apes, are the species most involved in the investigation of the evolution of human lateralization.

2.3.1 CHIMPANZEES HANDEDNESS

Most of the works on handedness reported in literature are focused on chimpanzees (*Pan troglodytes*), probably because they represent the closest cousins of humans. According to McGrew and Marchant (1997), there are more studies on chimpanzees than other great apes and these are second in number only to rhesus macaques. Hopkins (2006) suggested that the genus *Pan* among the great apes is more likely to manifest handedness at the population-level compared to genus *Gorilla* and *Pongo*. Indeed, unlike the other apes, chimpanzees are highly gregarious individuals, with complex social dynamics that require high cognitive specializations. Moreover, although they are considered highly specialized frugivores, they also supplement their mainly vegetarian diet with insects, birds, birds' eggs, honey, soil, and small to medium-sized mammals (including other primates) (Boesch & Boesch, 1989). This variegated diet is sometimes difficult to retrieve, thus chimpanzees might have evolved highly complex cognitive abilities, such as the employment of tools. Indeed, chimpanzees have been largely studied for the investigation of several cognitive skills, especially for their ability to build and use tools of different materials, such as sticks, stones, leaves, etc. (Boesch & Boesch, 1990). This ability, in fact, could be considered a precursor of to the capacity of humans to make very complex artefacts. Moreover, tool-use would represent an interesting ground for the investigation of handedness and, consequently, the tool-origin theory of hand lateralization. Chimpanzees have been found to be lateralized at the individual-level for different type of tool-use, such as ant fishing (McGrew & Marchant, 1999; Lonsdorf & Hopkins, 2005), wadge dipping (using a "sponge" to drink water from the tree holes) (Boesch, 1991), and nut-cracking (using a stone to open nuts) (Boesch, 1991; Humle & Matsuzawa, 2009; Sugiyama, Fushimi, Sakura, & Matsuzawa, 1993).

To date, investigations of handedness in chimpanzees have focused on manipulative motor behaviours in both wild and captive subjects and have shown inconsistent patterns of population-level handedness according to species, sample size and complexity of manual tasks (Hopkins et al., 2007; McGrew & Marchant, 1997; Papademetriou, Sheu, & Michel, 2005). However, it should be noted that methodologies between laboratories differed significantly, confounding interpretations of results and comparisons between laboratories.

2.3.2 GORILLAS HANDEDNESS

Historically, gorillas were considered the ape species with a most human-like right-hand, mainly on the basis of Shafer's study, which reported a right bias for different tasks in most of 47 zoo gorillas (as cited in Aruguete, Ely, & King, 1992, p. 185). However, more recent investigations seem to refute this assumption, as inconsistent findings about gorilla handedness have been reported in the literature. Indeed, it is still unclear whether gorillas manifest handedness at the population-level. One of the main causes is related to the poor availability of subjects, both in captivity and in the wild, which makes difficult to run population-level statistical analyses. In 1993, Hopkins and Morris reviewed 17 studies on gorillas and found that only half of them considered groups composed of more than 6 subjects. McGrew and Marchant (1992) faced similar review problems, as only 11 out of 21 studies involved 6 or more subjects. Furthermore, when they applied more strict statistical criteria for the analysis of data in a more recent review (McGrew & Marchant, 1997), the number of studies considered reliable decreases to six. Some authors (e.g. Tutin, 1996) also noted that few studies have been focused on wild gorillas, especially on western lowland species (*Gorilla gorilla gorilla*), perhaps due to the difficulty to habituate the subjects to human presence and to the poor visibility of subjects in the dense forest.

The low number of studies does not allow scientists to make statistical comparisons and this is also compounded by discrepancies in task consideration across studies. Different simple reaching and complex bimanual activities have been considered in different studies and, regardless of the difficulty of the task, there seems to be a general manifestation of individual-level preference (Annett & Annett, 1991; Byrne & Byrne, 1991; Fagot & Vauclair, 1988), whose direction, however, varies across the different tasks, although the strength of hand preference is not correlated to task difficulty.

Compared to chimpanzees, gorillas remain relatively understudied. However, the interest for this species in the investigation of handedness is slowly increasing, as more observations are needed to shed light on the handedness of gorillas, in order to add more information on great apes' handedness.

2.3.3 HANDEDNESS ASSESSMENT

One of the main issue that still does not allow to make inferences about the evolution of hand preference in apes and thus in humans, is whether great apes manifest population-level handedness. According to some authors, great apes might manifest handedness at the population-level, but only if specific factors are respected. This section will describe the factors.

Captivity vs Wild

One of the main differences concerning the manifestation of population-level hand preference in great apes is related to wild and captive environmental settings. Indeed, population-level right-handedness has been reported in captive chimpanzees for several measures, including simple reaching (Colell, Segarra, & Sabater-Pi, 1995a; Hopkins, Russell, Hook, Braccini, & Schapiro, 2005c), bimanual feeding (Hopkins, 1994), coordinated bimanual actions (Colell, Segarra, & Sabater-Pi, 1995b; Hopkins, Wesley, Izard, Hook, & Schapiro, 2004), throwing (Hopkins, Russell, Cantalupo, Freeman, & Schapiro, 2005a), and manual gestures (Hopkins et al., 2005a). On the other hand, population-level hand preference is quite rare in the wild (Byrne & Byrne, 1991; Corp & Byrne, 2004) and most of the studies reported weak laterality with most of the individuals being ambipreferent. Indeed, McGrew and Marchant (1997) have failed to find population-level handedness in two studies of spontaneous hand use in wild chimpanzees and other great apes. Some have argued that laterality observed in captive animal might be an artefact because of exposure to humans and human behaviours (McGrew & Marchant, 1997; Palmer, 2002). Indeed, McGrew and Marchant (1997) argued that there are several factors related to captive environment that could influence the laterality of animals, such as disturbed sociality, contact with right-handed keepers, asymmetrical cages, stimuli availability, action repetition, unnatural and complex tasks, etc. The authors stressed the importance of testing subjects in naturalistic settings, which are more likely to provide reliable data than captive settings. Moreover, hand preference in captive non-human primates could be biased by particular testing circumstances. For example, Hopkins and Leavens (1998) reported that some studies have demonstrated that food-positioning influences hand preference of non-human primates in simple reaching, as subjects tend to use the hand that is closest to the object. However, recent findings showed a significant population-level preference in using the right hand to grab the food in both biased (food positioned in the right or left side of the subject) and unbiased (food positioned in front of the subject) circumstances (Hopkins & Fernàndez-Carriba, 2000) suggesting that chimpanzees are lateralized regardless of the food-positioning.

Task complexity

Some primatologists argued that hand preference, in particular at the population-level, cannot be found in spontaneous activities, but there are specific factors that seem to elicit it. Some researchers claimed that human daily manual activities do not generally elicit handedness at the population-level (Marchant et al., 1995). Similarly, non-human primates could not manifest population-level asymmetry if tested only considering simple manual activities, such as tripedal reaching. In order to verify whether non-human primates could display human-like handedness it would be necessary to test them during particular conditions that require high cognitive-demanding skills.

According to the *theory of task complexity*, the more the task requires high cognitive skills to solve it, the more (the population-level) handedness will be likely to occur (see Cashmore et al., 2008). Task complexity can be related to different aspects of the task, especially those that are cognitively demanding, such as novelty, bimanual coordination, sequences of action, precision, and manipulation. Very recently, a group of researchers (Meguerditchian, Calcutt, Lonsdorf, Ross, & Hopkins, 2010) reported no population-level handedness for simple unimanual actions in gorillas, but found a significant right-handedness at the population-level during bimanual coordinated activities, which consisted in holding the food with one hand, while the other one manipulated it.

It was further argued that the manipulation and the employment of tools is more likely to elicit handedness in great apes (Boesh, 1991). However, the majority of the studies in the wild reported individual-level hand preference, with almost exclusive use of one hand (McGrew & Marchant, 1997). Data on tool-use in gorillas is very limited (e.g. Boysen, Kuhlmeier, Halliday, & Halliday, 1999) and there is only one study that reported tool employment in wild populations (Breuer et al., 2005).

Bimanual manipulation

A precise bimanual manipulation on one object is thought to be the best task to require and evoke manual laterality (Byrne et al., 2001; Hopkins, 2006; Rogers & Kaplan, 1995). Indeed, during bimanual tasks, hands are engaged in a coordinated activity and play complementary but equally efficient roles. One of the most considered bimanual tasks reported in literature is the *tube task*. This activity consists in a PVC tube smeared with peanut butter internally that the subject has to retrieve with the index finger while the other hand holds the object (Hopkins, 1995) (e.g. figure 14). This task has been employed for many studies, not only for chimpanzees, but also for gorillas (Hopkins, Stoinski, Lukas, Ross, & Wesley, 2003b), orang-utans (Hopkins et al., 2003b), bonobos (Chapelain, Hogervorst, Mbonzo, & Hopkins, 2011) and for other non-human primate species (for a review see Chapelain & Hogervorst, 2009). The tube task has been considered a sensitive measure of hand preference, as it has revealed a marked population-level laterality in different species of non-human primates (Meunier & Vauclair, 2007; Vauclair et al., 2005; Westergaard & Suomi, 1996).

Figure 14. Tube task demonstration. A chimpanzee subject is trying to reach the peanut butter with the index finger, by performing a coordinated bimanual task (adapted from Hopkins et al., 2004).

Most studies that found population-level handedness were carried out in captivity and, particularly, when subjects had to perform the tube task. Moreover, Palmer (2002) pointed out that most of the results reporting handedness for the tube task have come from a specific laboratory (i.e. Yerkes Research Centre, Atlanta, GA), where experimental animals live in a captive environment and have many opportunities to interact with humans. Llorente, Mosquera, and Fabré (2009), though, observed chimpanzees hosted in a semi-naturalistic environment and found a trend for right-handedness during the tube task, which was more prominent than that one manifested during simple reaching activities. Similar findings were reported outside the Yerkes Research Cent, such as the University of Texas M.D. Anderson Cancer Centre from 116 chimpanzees (Hopkins et al., 2003a) and at the Alamogordo Primate Facility in New Mexico, where a population-level right handedness was found (Hopkins et al., 2004). Additionally, MRI scans of asymmetrical cerebral structures of 66 chimpanzees and behavioural observations of manual activities (Hopkins & Cantalupo, 2004) revealed that handedness was associated with neuro-anatomical asymmetries only when the subject was performing the tube task and not for simple manual activities, such as feeding and object reaching.

In the wild, chimpanzees have been reported to being strongly lateralized for bimanual manipulation of food (Corp & Byrne, 2004). Also gorillas manifested individual-level lateralization for the bimanual sequential manipulation of plants with defences (Byrne & Byrne, 1991). In particular, for one category of plants, gorillas manifested population-level handedness in using the right hand to manipulate the plant, while the left was employed to hold the food. Interestingly, a group of researchers found population-level right-handedness in a group of 35 gorillas for coordinated bimanual tasks (i.e. food processing), and the degree of preference within the population (5:1 vs 2:1 in chimpanzees) exceeded any other known reports of hand use in primates, suggesting that lateralization for bimanual feeding is robust in captive gorillas (Meguerditchian et al., 2010). The authors suggested that strong degree of right-handedness observed in the sample may reflect an inherent adaptation for hemispheric specialization for bimanual actions, given the importance of hierarchical, bimanual motor actions in the feeding ecology of gorillas (Byrne & Byrne, 1993).

Posture

Manual laterality is strictly related to posture, as generally a limb used to provide postural support could not perform other activities. McGrew and Marchant (1997) also pointed out that an ideal study of hand laterality in non-human primates should simultaneously record what the “other” hand is doing while the focal one is performing any kind of manual activity. Furthermore, all forms of postures should be recorded, as the behaviours of both hands can vary according to whether the subject is in a seated, bipedal, quadrupedal or climbing position.

MacNeilage and collaborators (1987) postulated an evolutionary theory for the origin of handedness that is known as the Postural Origin Theory (P.O.T.). This model proposes that human handedness would have evolved from an ancestral arboreal primate, which used the right hand in positional and locomotor behaviours and the left hand for visually guided reaching and grasping. Once primate had assumed a terrestrial bipedal locomotion, the opportunity for manipulation increased and the right hand, which was pre-adapted for grip activities, became dominant for all hand use. Thus, according to this theory, arboreal species are more likely to use their left hand for manipulation and reaching behaviours and the right hand for ballistic grasping. On the other hand, terrestrial species are supposed to use more frequently the right-hand for manipulative tasks, as it was released from its function of postural support for vertical climbing.

Hopkins and collaborators (2003b) revealed a phylogenetic discontinuity among great apes for the tube task in hand preference, with chimpanzees and gorillas being significantly more right-handed than orang-utans, which conversely manifested a population-level left-handedness. These findings seem to be in line with the P.O.T, as orang-utans are more likely to manifest left-handedness, as they are a more arboreal species, compared to chimpanzees and gorillas, which manifest more terrestrial habits.

The postural origin theory led researchers to suppose that a bipedal posture might elicit the strength of handedness and in particular the manifestation of right hand use in non-human primates and thus many attempted to verify this hypothesis. However, a part from humans, terrestrial primates do occasionally walk bipedally and generally for short displacements, thus it is difficult to assess handedness in this condition. Nevertheless, Braccini and colleagues (2010) were able to induce bipedal tube task in semi-captive chimpanzees by hanging the PVC tube on the head of the subject and far from anything that could help the postural support by using one hand (figure 15c). They also compared the results with other conditions, in which subjects were asked to assume more stable postures, such as a seated (figure 15a) or a bipedal posture with one hand that maintained the position (figure 15b). Results showed an increased in the strength of hand lateralization when the subjects had to manipulate the object bipedally and without any support. However this preference was not significant for any particular direction. The authors offered the hypothesis that more unstable posture might enhance pre-existing lateral biases of great apes and possibly of other non-human primates.

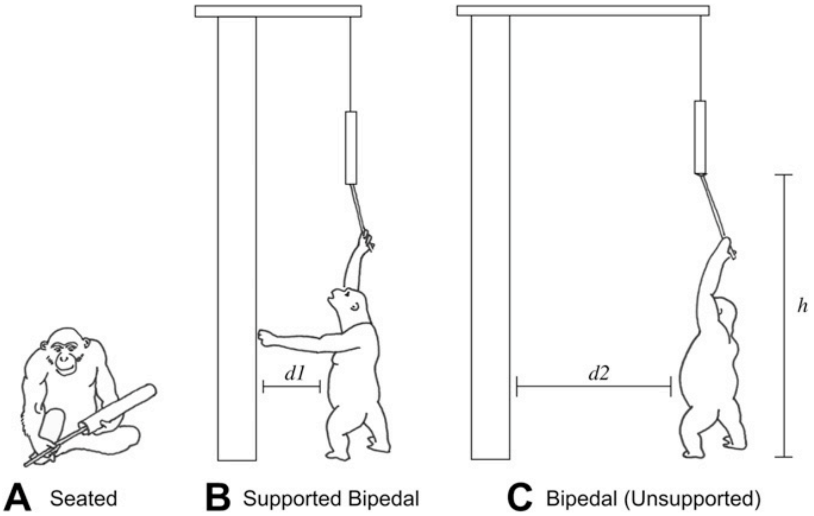


Figure 15 Tube task in different postural conditions in chimpanzees. The subject manipulates the object from a) a seated posture, b) a bipedal posture with one hand as a support, and c) bipedal posture without any manual support (adapted from Braccini et al., 2010).

It seems difficult to find an absolute method to assess handedness in non-human primates and comparisons between wild and captive studies are quite difficult to obtain, due to considerable differences in the setting, the type of measures, the sample, and other variables. However scepticism over these findings has largely been dispelled, as newly obtained data in support of a right hand bias continues to mount from an increasing number of great ape species for a range of manual actions (e.g. Hopkins et al, 2004; Llorente et al., 2009; Llorente et al., 2011; Meguerditchian et al., 2010) across captive and wild settings (Llorente et al., 2011; Lonsdorf & Hopkins, 2005).

2.3.4 HANDEDNESS AND LANGUAGE IN GREAT APES

The causal relationship between language and handedness has been investigated principally in non-human primates, particularly focussing on asymmetrical gestural communication. Indeed, researchers attempted to demonstrate if gestural communication of our closest relatives might elicit a predominant use of the right hand, which may be used as a marker for left-hemisphere specialization for language functions. A group-level right-handedness was reported for gestural communication in great apes, such as bonobos (Hopkins & De Waal, 1995) and 227 captive chimpanzees (Hopkins et al., 2005b). Interestingly, authors found that chimpanzees were more strongly right-handed for communicative than non-communicative gestures, such as tool-use, object reaching, and coordinated bimanual actions. However, these studies investigated gestures directed toward human experimenters and, according to some researchers (e.g. Tomasello, 1996) results could have been biased by the particular environment conditions. Therefore Hopkins and Wesley (2002) replicated the latter study and found significant population-level right-handedness for manipulating activities and gestures across different experimenter positions. Moreover, Meguerditchian, Vauclair, and Hopkins (2009) reported a predominant right-handedness in species-typical gestures directed to both humans and chimpanzees.

These findings further corroborate the hypothesis that communicative gestures may be the result of different underlying neural generators including those employed during object manipulation. However, it could also be argued that handedness tied to both communicative gestures and object interactions are highly right-lateralized behaviours because they both exploit the left hemisphere's functional capabilities to produce hierarchical temporal sequences of events to reach a goal state. In great apes, communicative gestures may represent an evolutionary step towards language skills, extending the left hemisphere's specialized processing derived from tool use. This line of reasoning would suggest that this step occurred prior to our evolutionary split from great apes and may be unique to humans and great apes. Based on the review above, great ape handedness appears to be present for interactions with objects and during communicative gesture, expressing a similar pattern of handedness with humans and reinforcing the ape model for the evolution of language. More findings would provide more support to the hypothesis that human language might have evolved through an evolutionary process from non-human primates' manual gestures (see Corballis, 2002).

2.4 Cerebral lateralization for emotions

In the last few decades, it has been put forward the hypothesis that brain lateralization might have first evolved for perceptual processes (Rogers, 2002a; Rogers & Andrew, 2002; Vallortigara, 2000; Vallortigara & Rogers, 2005). Indeed, many species of vertebrates manifest lateralized motor behaviours that are not related to paws or hands. For example, some studies demonstrated a left or right preference, at least at the individual-level, during detour tasks or when approaching/withdrawing a prey, predator or conspecifics (for a review see Rogers, 2002b; Vallortigara & Rogers, 2005; Vallortigara, Rogers, & Bisazza, 1999). Additionally, lateralized behaviours are apparent in animals without limbs, such as fish (e.g. Bisazza, Facchin, & Vallortigara, 2000). From this considerations emerged the idea that lateralization for motor functions might have been shaped by pre-existing perceptual brain asymmetries (Chapelain & Blois-Heulin, 2009). In particular, it has been argued that the perception of the environmental stimuli could be affected by the emotional state of the perceiver.

2.4.1 FACIAL EXPRESSIONS

To date, most of the studies investigating lateralized emotional perception in non-human primates have mainly involved facial expressions. One of the first studies investigated facial asymmetry for the expression of emotions in rhesus macaques and reported that individuals began to move the left side of the mouth earlier than the right side when displaying grimace (figure 16) and the expression was maintained longer in the left than the right side (Hauser, 1993). Additionally, the author found that the left side of the face was more expressive than the right one. This finding is consistent with more recent studies in other non-human primates (marmosets: Hook-Costigan & Rogers, 1998; baboons: Wallez & Vauclair, 2011) and in humans (Borod, 1993; Davidson, 1995; Gazzaniga & Charlotte, 1990; Sackeim et al., 1982), indicating a degree of overlap between cognitive function related to the processing and the displaying of emotions through facial expressions, in both human and non-human primates.

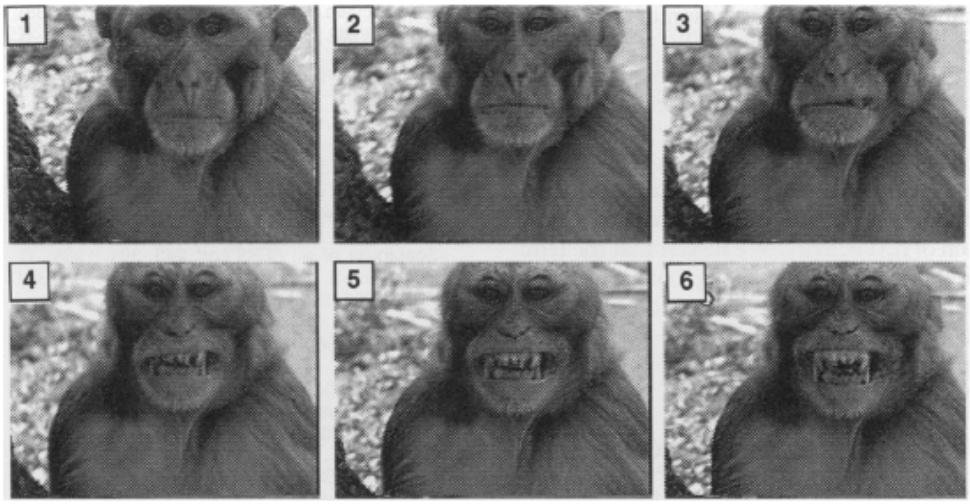


Figure 16. A frame-by-frame representation of a macaque facial expression during fear-grimace. The frames 3 and 4 clearly show that the left side of the mouth starts moving earlier than the right side (adapted from Hauser, 1993).

Some studies on the assessment of lateralized facial expressions in non-human primates also involved great apes. For example, Fernández-Carriba, Loeches, Morcillo, and Hopkins (2002) calculated the widening of the two hemi-mouth lengths during facial expressions in a group of chimpanzees, which was considered a quantitative measure (see Hook-Costigan & Rogers, 1998). Moreover, authors used a more qualitative measure, in which some human subjects were asked to judge chimeric pictures of chimpanzee's facial expressions, in order to verify which side of the hemi-face manifested a more intense expression. Findings revealed asymmetry in chimpanzees' facial expressions, with a more involvement of the left side of face (right hemisphere) in the expression of emotions from both the quantitative and qualitative measures.

2.4.2 SELF-DIRECTED BEHAVIOURS

Great apes' asymmetrical self-directed behaviours (SDBs), e.g. self-scratching and self-touching, were also proposed as a marker of the lateralized cerebral elaboration and expression of emotions, as they seem to be elicited by social stressful conditions (Leavens, Aureli, Hopkins, & Hyatt, 2001; Rogers & Kaplan, 1995). Dimond and Harries (1984) reported a left-hand face self-touching preference in chimpanzees, orang-utans, and gorillas. Leavens and colleagues (2001) further investigated asymmetrical SDBs in chimpanzees during high and low cognitive-demanding tasks reporting a significant right-hand bias in conditions of high task difficulty, whereas no lateralization during low task difficulty conditions was apparent. Few years later, some researchers tried to replicate this latter experiment, distinguishing different type of SDBs, such as rubbing and scratching (Hopkins et al., 2006). Additionally they also specified to which side of the body the manual actions were more directed. Results showed a population-level right-hand preference for self-rubbing significantly more toward the right (ipsilateral) side of the body. Furthermore, although no handedness was revealed for self-scratching, a significant population-level preference was detected for scratching the left side of the body. The authors offered the hypothesis that the right hemisphere may modulate cutaneous sensations differently across the right and the left side of the body, in which the ipsilateral descending inhibition is responsible for pain and itch, whereas the controlateral for the expression of a negative arousal state.

2.4.3 SOCIAL LATERALITY

According to Bard and collaborators (2004), “Emotion need to be studied as it occurs in the natural life of primates [...], with an ethological approach” (p. 352). Indeed, emotion processing seem not to represent a cognitive ability already set at the beginning of life, but it is strongly dependent on the environment. Therefore, some researchers were interested in investigating also whether non-human primates manifested lateralized behaviours during social interactions. For example, Casperd and Dunbar (1996) observed visual orientation to an opponent in gelada baboons (*Theropithecus gelada*) during agonistic context and found that both opponents showed a significant preference during orientation with respect to the interacting individuals, which suggested a right-hemisphere specialization for the processing of emotion-involving activities.

More recently, Baraud, Buytet, Bec, and Blois-Heulin (2009) have shown that the position of the members relative to a focal individual can influence the social visual laterality of mangabeys. The authors found that subjects were approached significantly more from their left side. Moreover, when surrounded by many members, subjects tended to keep them on the right side of their frontal visual field. In particular, approach side and relative position differed according to the social rank, as high-ranked mangabeys were approached significantly more from their left than right side. These findings suggested that different social interactions could enhance lateralized behaviours that can be affected by the type of conspecifics. In particular, the arousal status might be influenced by the social rank of the approaching conspecific and consequently influence the lateralized positioning of the individuals with respect to the recipient.

All these experiments suggest a more involvement of the right hemisphere in the processing and expression of emotions than the left hemisphere, during social interactions or situations that involve the subject to attend complex tasks that might elicit a stressful state. Therefore, the right hemisphere hypothesis related to the elaboration of emotions seems to be supported, at least for the processing of negative emotions. Findings in non-human primates, thus, seem to be consistent with the majority of studies carried out in humans investigating cerebral lateralization for the processing of emotions, suggesting that the right sided hemisphere dominance might be the product of an evolutionary process, that human must have inherited before their split from great apes. Although poor information is still available about great apes hemispheric emotional processing, during these last decades lateralized perception has gained more interest in literature. Moreover, more observations are needed about different perceptual abilities to better clarify whether the right hemisphere is solely involved in the processing of emotions or rather a bilateral hemispheric involvement based on the valence of emotions is apparent in non-human primates.

Chapter 3

Development of cerebral lateralization

Many scientists have attempted to shed light on the evolution of cerebral asymmetry and have tried to understand why human brain is so clearly cognitively lateralized. As Haeckel pointed out, “ontogeny recapitulates phylogeny” (as cited in MacNeilage, 1998, p. 504), therefore one good way to clarify the issue might be to investigate whether infants and children manifest cerebral lateralized functions.

Since the first investigations on human handedness, it was widely accepted that the infant brain does not manifest cerebral lateralization until approximately the age of 2 years (Krashen, 1981). Indeed, brain asymmetry has been thought to be linked with the degree of behavioural complexity, thus only mature humans could manifest lateralization. In the literature there are two main approaches related to this issue. According to some scientists, all cognitive functions, including speech, develop initially in parallel in both hemispheres, so that infants do not manifest any cerebral lateralization. Therefore, both hemispheres are equally likely to acquire speech and other functions. Some clinical studies seem to confirm this hypothesis, such as Rasmussen and Milner (1977), who showed that children with a left-hemisphere lesion could still acquire a relatively good proficiency in language skills. Corballis and Morgan (1978) argued that a gradual lateralization of functions occurs during ontogenesis, becoming fully established by adolescence (Miller & Turner, 1973). According to these assertions, the manifestation and the degree of cerebral lateralization strongly depend on environmental factors. Other authors, on the other hand, argue that cerebral lateralization is already apparent in newborn children, thus morphological and behavioural asymmetries are present at the beginning (Grabowska, Herman, Nowicka, Szatkowska, & Szelag, 1994). Specifically, lateralized functions are supposed to gradually develop from an already genetically established asymmetrical configuration. Indeed, some of the asymmetries apparent in infants can become more pronounced during child growth and new asymmetrical structures or behaviours can eventually appear *de novo* during child development (Segalowitz & Berge, 1995). The ontogenesis of lateralization is described in terms of degree, as asymmetrical functions could become more prominent, although the direction of lateralization is already established at the birth. This idea seems to be much supported by perceptual, anatomical and behavioural findings, which show that lateralized cerebral functions are apparent much earlier in child development.

3.1 Development of language lateralization

For long time many have thought that the infant and child brain is not lateralized for language processes simply because they cannot yet speak or manifest simple communicative skills (Krashen, 1981). Certainly, infants do not show any evidence of an elaborate linguistic system, however they use some forms of communication that could be antecedent to adult speech.

Vocal babbling is known to include a wide range of speech sounds and seems not to develop by imitation, as it occurs also in deaf infants (Oller & Eilers, 1998). It is also not correlated with the expression of an emotional state, since emotional vocalizations are quite distinct and have not been shown to be related to ongoing speech (Myers, 1976). The fact that babbling is widespread in infants might have some adaptive utility, such as representing an immature and early form of communication that later develops into speech.

Along with babbling, infants show another form communication, which is pointing. This gesture has been generally classified as a referential behaviour, as it creates a referential triangle including the signaller, the recipient, and the distant object that relates the two individuals (Butterworth, 2003). Moreover, pointing is believed to represent a fundamental step for human speech acquisition in infants, because the word pronounced by the mature speaker to utter the name of the entity indicated and the entity itself is underpinned by an auditory-visual learning association (Butterworth, 2003). For this reason, psychologists claim that pointing, like speech, should be considered a human adaptation for reference (see Leavens, Hopkins, & Bard, 2005). Cochet and Vauclair (2010) observed pointing in 1-3 years old toddlers and found a significant right-hand preference, which strength did not increase with age. The same pattern was previously found by Bates, O'Connell, Vaid, Sledge, and Oakes (1986) in 13-28 months old infants. These findings seem to suggest that an early hemispheric dominance for linguistic functions is apparent in infants, thus supporting the hypothesis of an already precocious presence of cerebral lateralization at the early stage of human development.

The first studies on cerebral lateralization for language functions in infants and children were mainly derived from asymmetrical perceptual manifestations. Indeed, 2-month-old infants showed a better performance in perceiving speech sounds with the right ear/left hemisphere than the left ear/right hemisphere, suggesting an early specialization of the left-hemisphere for language perception and processing (Best, 1988). Moreover, 3½-month-old infants showed different patterns of ear asymmetries for vowel versus consonant discrimination, with the right ear being more specialized in perceiving consonants and the left ear more specialized in perceiving vowels (Best, Hoffman, & Glanville, 1982). Since consonants involve rapidly changing acoustic properties and vowels are associated with much more slowly changing (Cowell, 2010), the left hemisphere might be more responsive to rapidly changing acoustic stimuli than the right hemisphere. This would explain why infants, children, and adults generally manifest a better performance in perceiving speech with the right ear/left hemisphere and musical notes with the left ear/right hemisphere.

Best et al. (1982) reported a progressive development in asymmetrical functions, by assessing speech and music perception in 2-, 3-, and 4-month-old infants through a dichotic listening technique. The results of this study showed a consistent left ear/right hemisphere advantage for music perception in all the three categories of age. Moreover, a right ear/left hemisphere advantage for speech was found in all groups except for 2-month-old infants. Such a change in cortical maturity between 2 and 3 months of age seems to confirm previous findings about development and maturation of cortical influences towards behaviour around the same age (Best et al., 1982). However, these inferences do not necessarily imply that cerebral lateralization for language develops from a non-lateralized substrate. Alternatively, asymmetrical cognitive functions might mature during infancy and childhood at different rates, but from a neural substrate that is cognitively lateralized from the birth (Best, 1988)

Aside from dichotic listening tasks, there are other techniques that have been used to assess language lateralization in infants and children. For example, MacKain, Studdert-Kennedy, Spieker, and Stern (1983) employed a preferential looking paradigm to test 5- to 6-month-old infants. In this experiment, subjects were asked to watch two side-by-side videos, each simultaneously displaying a woman pronouncing nonsense words, while a speaker positioned between the two monitors emitted a sound that matched one of the two videos. The looking time revealed a preference for the video that matched audio presentation, but only when the correct video was in the right-side of the monitor. These findings suggest a selective left-hemisphere activation for the common articulatory pattern underlying both auditory and visual sensory modalities for speech perception.

There is also evidence of anatomical asymmetries for language functions in the cerebral hemispheres of infants and foetuses. One of the most well-known asymmetries reported in foetal (Chi, Dooling, & Gilles, 1977; Hering-Hanit, Achiron, Lipitz, & Achiron, 2001; Kivilevitch, Achiron, & Zalel, 2010) and infant brains (Hiscock & Kinsbourne, 1995) was the presence of a laterally larger surface area of the planum temporale in the left-hemisphere compared to the right hemisphere, similar to that found in adults (Galaburda, LeMay, Kemper, & geschwind., 1978). This region incorporates Wernicke's area, which is responsible for language comprehension (Bear et al., 2001). Other researchers showed that the Sylvian fissure appears more marked in the left than in the right hemisphere, as observed in adults (Witelson, 1995), and that the anterior region in the cortical surface of Broca's area is larger in the left hemisphere, compared with the right hemisphere in both adults and infants (Falzi, Perrone & Vignolo, 1982).

More recently, neuro-imaging studies have provided clearer information about hemisphere specialization for language processing. Dehaene-Lambertz, et al. (2006) found left hemispheric lateralization of language function in 0–3 months-old infants through an fMRI experiment, suggesting that the neural substrates supporting language might be already apparent from birth. These findings are in line with the genetic theories regarding the emergence of language lateralization (Annett, 2002; Annett and Kilshaw, 1983; McManus and Bryden, 1992), since environmental factors are not supposed to account for the development of language at a very early age. However, an fMRI study found greater right-hemisphere and inferior frontal gyrus activations in children during a verbal fluency task and this trend of brain activation pattern was more prominent than in adult subjects (Gaillard et al., 2003), suggesting that a shift of hemispheric specialization for language functions from the right to the left side might occur before adulthood. In other words, there seems to be a stabilization and increment of cerebral lateralization degree along with the maturation of linguistic skills. Indeed, Schlaggar et al. (2002) reported that there is still an increment of the linguistic performance of the left frontal regions even across 9- to 25- years-old subjects. Additionally, authors found a decrease in the activations of the medial brain regions in the right dorso-lateral frontal cortex in 12-15 years old subjects, suggesting that a developmental stabilization of cerebral lateralization still takes place after childhood. Therefore, it might be argued that a delay in the maturation of cerebral lateralization of functions might be related to a delayed linguistic and cognitive expressions in infants or vice versa.

Results in literature seem to report some inconsistencies about *when* hemisphere specialization for language functions emerges in human development. However, whether we accept the hypothesis that cerebral lateralization is already settled at the moment of birth or not, one cannot deny that asymmetrical neurological functions, in particular those related to language, undergo developmental change throughout infancy and childhood at many levels (Workman, Chilvers, Yeomans, & Taylor, 2006). Specifically, cerebral lateralization seems to be related with the ability of infants and children to perceive and process linguistic patterns of speech. Therefore the degree of cerebral lateralization for language seems to become stronger with the maturation of language skills

3.2 Development of handedness

It has been argued that there is no asymmetric behaviour more difficult to assess than the manual activity of infants (see Hiscock & Kinsbourne, 1995). Currently, the perception is that handedness becomes stable in early childhood, but there is varying evidence regarding how early it can be reliably identified in younger children and possibly even in infants and foetuses. This section will review the main findings concerning the study of hand preference in infants and children.

It is claimed that manual laterality fluctuates during infancy and part of the childhood, as the proportion of right-handers among the population is always lower than that of adults (Hiscock, & Kinsbourne, 1995). Additionally, there are some periods in which left-handedness is even predominant in children who will eventually manifest right-handedness. Therefore, dominant handedness in humans generally tends to become evident in school-aged children.

Best (1988) reported that handedness seems to become more consistent already in infants of over 6 months of age. The researcher showed that infants older than 7 months manifested a clear right-hand preference in reaching for a toy placed in the midline of the subjects, compared to 3- to 6-month-old infants, who tended to use either hand with equal frequency. This result mainly suggests that although parents may exert subtle influences toward right-hand use in their children (e.g. routinely placing eating or writing utensils near their children's right hand), there seems to be a neurological or genetic substrate for the preferential use of one hand in infants, that develops in consistency throughout infancy. Also Mebert found a preference in using more frequently the same hand, either the left or the right, to perform a bimanual manipulation in infants (as cited in Bishop, 1990, p. 59). Nevertheless, it is worth noting that not all studies were able to replicate these experiments, reporting no evidence of handedness at early ages. Bishop (1990), for instance, reported that manipulation of objects tend to be performed first with the non-dominant hand, then bilateral, then with the dominant hand alone, once again bilateral, then with one hand, then increasingly with the dominant hand. Moreover children at the age of 1 year and 6 months still manifest a marked bilaterality, and the use of the dominant hand becomes stable at age of 2 years.

Although unstable hand preference might be found at toddler age (Bryden, Pryde, & Roy, 2000; Hempel, 1993; Manoel & Connolly, 1995), this instability tends to decrease with pre-school age, in particular for the right hand (Bishop, 1990; Cornish & McManus, 1996; De Agostini, Pareé, Goudot, & Dellatolas, 1992; Michel, Sheu, & Brumley, 2002). A longitudinal study, in fact, revealed that 1- to 2-year-old toddlers preferred to use their right hand for more complex manipulative tasks, such as grasping and inserting pegs, whereas no hand preference was apparent when performing more simple tasks, such as manipulating a block (Geerts, Einspieler, Dibiasi, Garzarolli, & Bos, 2003). Therefore Provins (1967) suggested that handedness becomes more marked when a precise manipulation is required, thus during fine coordination of muscle activity. In particular, according to the author, hand preference is supposed to develop along with child increasing of practice in performing more skilled tasks and it is also correlated with an increment of the degree of neuro-motor maturation. Therefore, we might expect that child handedness should appear earlier during the performance of daily activities, such as combing, tooth brushing, in which the child has acquired more practice during his/her development, while activities rarely seen in childhood, such as dealing cards, should not enhance the manifestation of hand preference. However, this hypothesis seems not to find support in adult handedness, in which a great degree of hand lateralization during less practiced activities that yet require a fine manipulation is apparent (Provins, 1967). Additionally, a cross-cultural study on assessment of handedness during toy tower building in children coming from Papua, New Guinea and from England reported a more stable hand preference in Oceanian children, who have poor familiarity with building toys, compared to European ones (Connolly & Bishop, 1992).

More developmental investigations reported a differential usage of hands in infants under the age of 6 months. Indeed, Cobb, Goodwin, and Saelens (1966) showed that the right hand of newborns and young infants is more active than the left hand, especially for performing a fist, although these findings have been claimed to not actually account for any postural or cognitive lateralization. Caplan and Kinsboune (1976) assessed handedness in 21 babies aged from 1 to 4 months on grasping a rattle and found that the right hand held the object longer than the left hand.

Many other researchers reported voluntary grasping around 5 months of age and both cross-sectional (Cornwell, Harris, & Fitzgerald, 1991; Fagard & Lockman, 2005; Fagard & Marks, 2000) and longitudinal studies (Corbetta & Thelen, 2002; Coryell, 1985; McCormick & Maurer, 1988) showed some traces of hand preference. Although handedness seems to fluctuate during the first months of life for object grasping activities, Fagard (1998) reported that at this age there are more right-handed than left-handed individuals. He also found that the number of ambipreferent subjects tends to decrease with growth.

According to some studies, there is evidence of handedness already in uterus (Hepper, Wells, & Lynch, 2005). The earliest account comes from Hepper, Shahidullah, and White (1991), in which a 90% of 15-week-old foeti showed a right bias in thumb sucking (e.g. figure 17), while the remaining 10% used the left thumb, and a longitudinal study demonstrated that this asymmetry correlated with handedness at 10-12 years of age (Hepper et al., 2005). Other researchers reported a preference in moving more the right than the left hand in foeti of 10 weeks of gestation (Hepper, McCartney, & Shannon, 1998), which was later confirmed by a four dimensional ultrasound analysis (Kurjak et al., 2002).

Figure 17. Prenatal thumb sucking. The image depicts an ultrasound scan of a 18-week-old foetus (retrieved from http://www.zawaj.com/are-ultrasound-scans-allowed-in-islam/fetus-sucking-thumb/)

A preference in turning the head more toward the right than the left was found in foeti at 38 weeks of gestation (Ververs, de Vries, van Ceijn, & Hopkins, 1994), which seems to correlate with the postnatal asymmetric tonic neck reflex (ATNR) attitude, a head right- or leftward movement, while ipsilateral limbs extend and controlateral limbs flex (Gesell, 1938) (see figure 18). This asymmetrical behaviour represents the first lateralized behaviour reported in newborns. Hopkins, Lems, Janssen, and Butterworth (1987) demonstrated that this bias is manifested already from the first hours after birth in orienting and maintaining the head to the right side (Rönnqvist & Hopkins, 1998), suggesting it should not be attributed to the effect of handling by nurses.

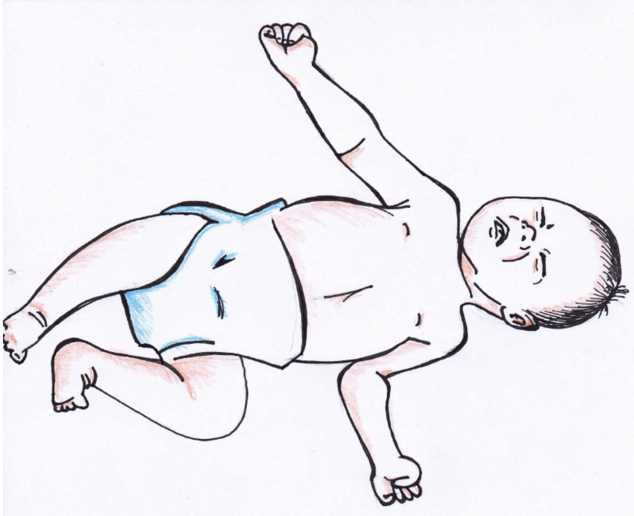


Figure 18. Asymmetric tonic reflex. The picture depicts a newborn with head turned to the right side, while contralateral limbs are flexed.

Kinsbourne (1972) claimed that ATNR in infants might reflect a different activation of the hemispheres with the left side of the brain being more highly activated than the right. However, more recent findings reported that postnatal ATNR (2-4 days after birth) was correlated with the hand used for thumb sucking in foetus, suggesting that prenatal handedness might be related with postnatal lateralized motor behaviours (Hepper et al., 1991). A right-hand bias in making contact with the mouth was found by Hopkins and collaborators (1987) in 10 out of 12 newborns and this behaviour was claimed to be intentional, as the mouth opened before the hand reach it (see Bishop, 1990).

There seems to be agreement among researchers that hand preference develops from infancy to childhood and keeps strengthen until adulthood. Indeed, although there is evidence of signs of hand preference quite early, handedness seems to be unstable during the first months of life and tends to develop slowly (Corbetta & Thelen, 2002; Cornwell et al., 1991; Fagard, 1998). According to Fagard and Marks (2000), handedness becomes steadily observable in the first bimanual skills at around one year of age. Moreover, although some aspects of handedness might become stabilized after the age of three years (Annett, 1970; Ingram, 1975), the degree of hand preference, either toward the right or the left, keeps increasing during early childhood (McManus et al., 1988). Although it is still unclear whether handedness appears in early development or later in childhood, it seems to be accepted by most of the authors that although handedness undergoes development, it appears to become stable after infancy but before school age, especially when children start manifesting bimanual complex manipulation of objects.

3.3 Development of cerebral lateralization for emotions

Based on the evidence that infant emotional and neurological development is not fully mature, it has been argued that the cerebral structure underpinning asymmetries emotional expressions may not follow adult patterns (Best & Queen, 1989). A left-hemiface/right hemisphere bias for emotional expression has been found in 6-8 years of age and in adults (Rubin & Rubin, 1980), whereas 2- to 3-year-old children have been reported to be right-hemiface/left hemisphere biased, as reported by Best and Queen (1989). Other studies have shown a reversal of hemiface intensity in 6- to 13-month-old subjects, compared to adults (Best & Queen, 1989; Rothbart, Taylor, & Tucker, 1989), where a more intense oral expression on the right then the left side of the face was found in infants. Therefore, these findings suggest a development early in life of the asymmetrical processing of emotional expression that may even manifest a shift in hemispheric dominance from infancy to adulthood. Indeed, some findings have more recently confirmed that the development of left hemi-spatial/right hemisphere preference for attending emotional expression in the perception of chimeric faces seems not to be appear before 4-5 years old. However, it is worth to highlight that few studies are reported in literature about the development of lateralization of emotions and most of them are based on the perception of facial expressions.

A recent study investigated oral asymmetry for positive and negative emotions during facial expressions in 12-24 month-olds, showing that the left side of mouth opened wider than the right one during negative emotions, while no oral asymmetry was found for positive emotional expressions (Schuetze & Reid, 2005). Additionally, this preference tended to strengthen with development, as 24-month-olds manifested a stronger asymmetry than the younger participants. These findings, thus, seem to support a right hemisphere specialization for the processing of emotions, in particular for negative ones, which is supposed to increase with age (Safer, 1981). Indeed, it has been suggested that lateralisation for the perception and expression of happiness might begin later in the child development, whereas the expression of a negative emotional state may appear earlier, as reported by Schuetze and Reid (2005). This kind of development in the asymmetrical expression of emotions might be related to an evolutionary adaptation of a self-preservation mechanism. Additionally, Schuetze and Reid's findings (2005) seem to be in line with those found in adults, in which an asymmetric facial expression for negative emotions but not for positive was apparent (see Borod, 1993). Other authors, who also reported a significant increase in the degree of lateralisation for negative affect between 18 and 24 months of age, suggested that the discrepancy of cerebral lateralization for emotional expression between infants and adults might be linked to a maturation of several neuropsychological systems for more complex emotions that occur during this period of life (Thompson, 1994). These findings suggest that an asymmetrical processing of emotions seem to be apparent in infants during the production of facial expressions, but only for negative emotions, whereas positive emotions are expressed later in life. This different development of emotion elaboration might be related to an adaptive system, which aim is to conserve the integrity of the individuals during the early period of life.

In general there seems to be quite confusion about whether infants and children manifest a cerebral asymmetry for the processing and the expression of emotions and this inconsistency might be due to the low number of studies in the literature. There is however agreement among researchers that infant neurological asymmetries are not fully mature, but rather undergo development (Best & Queen, 1989). Two possible developmental strategies have been postulated: The brain asymmetry of a child develops in order to adequately process emotion before the understanding of emotion can be achieved; alternatively, the development of the ability to understand how to display emotions might influence autonomic nervous system regulation (Bard et al., 2004) and thus gradually shape the specialization of the hemispheres for the processing of emotions (see Watling & Bourne, 2007). Indeed, socialization and cultural experiences seem to exert a strong influence on the neural substrates for the cognitive processes related to the perception and the elaboration of emotions (Bard et al., 2004). Nevertheless, the point at which the development of lateralization for emotions becomes stable is still unclear.

Chapter 4

Aims and objectives

It is clear from a review of the literature that there are large discrepancies in the way we collect data on cerebral lateralization in both human and nonhuman primate populations that cause confounds for direct comparisons both within and between species. Therefore, the principal aim of this study is to assess cerebral lateralization in human and non-human primate groups employing a non-traditional and newly developed methodology. The Multidimensional Method (MDM) (Forrester, 2008) systematically captures, codes and analyzes spontaneous behaviours for the purpose of allowing valid comparisons across the different species. Thus, a comprehensive range of interactions with both social and non-social targets were considered in a quantitative manner, to verify which aspects might elicit the manifestation of lateralized behaviours underpinned by asymmetrical neuronal functions. Specifically, two conditions were investigated. First, based on the hypothesis that right-handed actions for tool-use are underpinned by left-hemisphere specialized areas for orchestrating hierarchical sequences of events to reach a goal state (which may have paved the way for the evolution of language skills) (Calvin, 1982; Frost, 1980; Greenfield, 1991; Steklis & Harnad, 1976), I aimed to test whether the target animacy (animate and inanimate objects) of the manual actions could be enough to bias the preferential use of hand, thus either supporting or contradicting the theory that interactions with inanimate objects have been a critical predecessor to the evolution of language. Second, since the social environment is likely to influence the lateralized behaviour of gregarious species (Baraud et al., 2009; Vallortigara & Rogers, 2005) and since the left side of the body/right-hemisphere is supposed to be more involved during arousing situations (Borod et al., 1998; Campbell, 1982), this study considered the positioning behaviour with respect to conspecifics in order to verify whether it might show lateralization, thus shedding light on the asymmetrical involvement of hemispheres for the processing of emotions of human and non-human primate species.

Great apes represent a relevant functional model to study the evolution of human cerebral lateralization not only because of their phylogenetic proximity to humans, but also because they display clear anatomical human-like features (Byrne et al., 2001; Hobaiter & Byrne, 2011; Savage-Rumbaugh, McDonald, Sevcik, Hopkins, & Rubert, 1986; Videan & McGrew, 2002). Therefore, a group of zoo chimpanzees (*Pan troglodytes*) and semi-free ranging western lowland gorillas (*Gorilla gorilla gorilla*) were considered for this study. Furthermore, great apes seem to share more cognitive abilities to human infants than adults (Weiss & Santos, 2006). In particular, infants do not have a fully functioning linguistic system, which might be comparable with that of great apes. Moreover, the similarity of environment between semi-free ranging apes and pre-school children, make the comparison of both manipulative and social cognitive abilities more reliable, compared to a comparative study between apes and adult humans. Thus, a group of pre-school children was also involved in the project.

Chapter 5

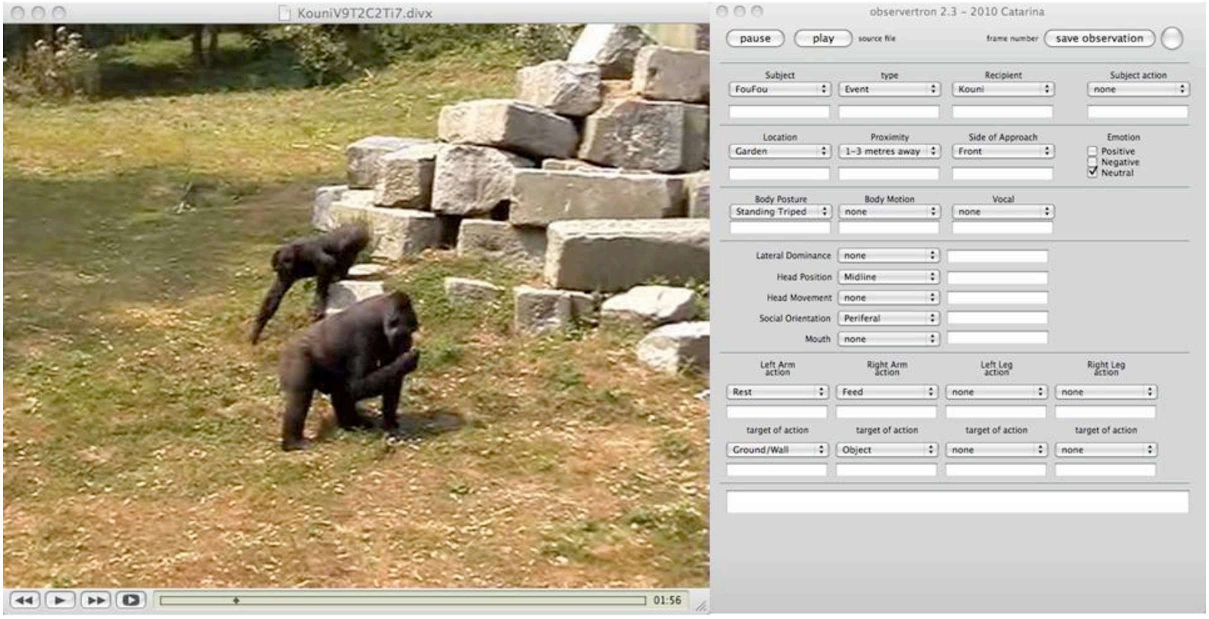
General methodologies

5.1 General methodologies about non-human primates studies

For long time, many scientists investigating animal behaviour and cognition have claimed that laboratory researches can provide more reliable data, than studies carried out in the field, as based on quantitative methodologies (Altmann, 1974). Indeed, quantitative researchers focus on numbers and frequencies rather than on meaning and experience, providing information that is statistically easy to analyse and fairly reliable. On the other hand, qualitative methodologies are based only on descriptive observations of animal behaviours. As Altmann (1974) suggested, laboratory and field studies both focus on plausible variable for the investigation of animal behaviour, but they cannot lonely provide a complete reliable interpretation of the findings. Indeed, one of the main aims that a scientific study should considered is to minimize the number of plausible alternative hypotheses that are consistent with the data (Altmann, 1974). The author argued that studies with captive animals provide data that allow to control many variables (internal validity) but ignore whether the artificial world may distort the results, or whether these animals could solve the task in a more natural condition. On the other hand, wild individuals provide more reliable information about the ecological and adaptive meaning of data (external validity) but do not allow researchers to manipulate experiments and exclude important variable that might influence the results. Therefore, there seems to be imbalance between the laboratory and the field methodologies and the increasing interest to preserve the ecological and ethical integrity of animals had led some scientists to solve this inconsistency, by using the methodologies employed in field studies to design laboratory experiments or to use manipulated tasks usually employed in laboratory experiments for field contexts (Altmann, 1974). However, only recent advanced technology allows applying quantitative methods to non-invasive studies. For example, it is becoming increasingly popular to categorize and quantify observed animal behaviours in a naturalistic setting –both in the wild and in captivity. This approach has yielded many interesting results that can now be compared with studies of human behaviours and cognitive processing. Therefore, the need for invasive investigation of brain regions within a laboratory setting, particularly for cerebral asymmetry, has decreased, as plausible inferences about cognitive processes can be made by observing the animal behaviour. This does not mean that brain functional investigations should not be employed, but there is growing interest in considering the natural context of non-human species, in order to have a better prospective of the ecological and evolutionary validity of results.

5.2 Quantitative ethological data capture: A Multidimensional Method

A Multidimensional Method (MDM), i.e. OBSERVERTRON®, has been considered a good technique for variable categorization, coding and analyses, in order to facilitate direct comparisons between the different subjects categorizations (Forrester 2008; Forrester, Leavens, Quaresmini, & Vallortigara, 2011). The primary aim of the MDM is to extract synchronous and sequential patterns from a distributed database of lateralized activities within a natural social context. The MDM is a non-invasive, quantitative approach to the investigation of animal communication. One of the advantages of this method is that video streams are viewed in synchrony and coded offline to establish the direction and timing of physical actions and creating an ‘action database’. Indeed the MDM programme is put side by side to the interested video that run with Quick Time Player 7.0 (see figure 19) and both programmes work only on a Macintosh devices.



Subject: FouFou
type: Event
Recipient: Kouni
Subject action: none
Location: Garden
Proximity: 1–3 metres away
Side of Approach: Front
Emotion: ☐ Positive ☐ Negative ☑ Neutral
Body Posture: Standing Triped
Body Motion: none
Vocal: none
Lateral Dominance: none
Head Position: Midline
Head Movement: none
Social Orientation: Periferal
Mouth: none
Left Arm action: Rest
Right Arm action: Feed
Left Leg action: none
Right Leg action: none
target of action: Ground/Wall
target of action: Object
target of action: none
target of action: none

Figure 19. A view of a gorilla video next to OBSERVERTRON®. All the menus of the MDM device include several behavioural categories that can be chosen according to the actions manifested by the focal subject in a specific frame.

Moreover, the flexible nature of the observation makes this a valuable tool for capturing and analysing a large breadth of lateralized and non-lateralized behaviours across a broad range of animal species. Specifically, the programme consists in various menus, each containing all the lateralized behavioural categories manifested by the subjects during their activities. The degree of utilization of this MDM varies according to the type of the subject that the experiment need to observe and to the behaviours on which the study is focused for the analysis.

Below is listed the description and the content of every menu. All the behavioural categories reported in the programme refer uniquely to the focal subject (Tables 1 and 2).

Table 1.

Multidimensional Method Coding Scheme (part I)

Variables	Description	List of behavioural categories
Subject	The name of the focal subject	(Changes according to the species)
Type	Bouts or event	Bout, event
Recipient	The name of the individual that interacts with the focal subject	(Changes according to the species)
Subject action	Refears to when the focal subject approaches or withdraws another subject or when the focal subject is approached or withdrawed by another member	Passive approach, active approach, passive withdraw, active withdraw, none, not visible
Location	The side of the environment were the focal subject is observed	(Changes according to the species)
Proximity	The distance between the focal subject and a conspecific	Touching, within 1 metre, 1-3 metres away, >3 metres away, none, not visible
Side of approach	Refears to the side of the focal subject showed toward the approached/withdrawed conspecific or the side of the focal subject showed toward a conspecific that approaches/withdraws tha focal subject	Left, right, front, rear, none, not visible
Emotion	The type of the social interaction	Positive, negative, neutral
Body posture	The posture assumed by the focal subject	Lean forward, lean back, lean left, lean right, lying on stomach, lying on back, sitting, standing quadrupedal, standing tripedal, stranding bipedal, bow, squatting, brachial, leaper vertical, leaper horizontal, swinging, other, none, not visible
Body motion	The direction of the body movement of the focal subject	Lean forward, lean back, lean left, lean right, none, not visible
Vocal	The type of vocalization performed by the focal subject	Vocal, bilabial, fibulation, other, none
Lateral dominance	Refers to the position of the hands when are both maintaing posture, as paralled positioned or one more ahead than the other one	Left, right, both, none, not visible
Head position	The position of the head with respect to the body midline	Midline, left, right, bowed, other, none, not visible
Head movement	The direction of the head movement with respect to the body midline	Upward, downward, leftward, rightward, other, none, not visible
Social orientation	The orientation of the sight with respect to a conspecific	Facing, adverted, periferal, glance, stare, other, none, not visible
Mouth	The movement of the mouth	Open teeth, open no teeth, closed lips relaxed, closed lips pursed, groom, lip hang, bite, kiss, other, none, not visible

The MDM allows choosing only one behavioural category for each variable per frame.

Table 2.

Multidimensional Method Coding Scheme (part II)

Left arm action	The action performed by the left arm and hand	Rest, feed, turn, clung, start walking, start climbing, start jumping, swing, roll/tumble, groom, tool use, raise up, lower down, move horizontally, wave/shake, clap, snap, stretch/reach, kick, grab, pull, move, hold, carry, jump, stomp, throw, hit/slap, touch/stroke, push/shove, manipulate, drumming/tapping, beating, embrace, punch/poke/prod, pick up, drop/release, retract, other, none, not visible
Right arm action	The action performed by the right arm and hand	(Same as left arm action)
Left leg action	The action performed by the left leg and foot	(Same as left arm action)
Right leg action	The action performed by the right leg and foot	(Same as left arm action)
Target action	Refears to the type of the target toward wich the arm or leg action is directed and makes contact	Social partner, ground/wall, object, self, none, not visible

The MDM allows choosing only one behavioural category for each variable per frame.

Although the MDM allows for the coding of many different variables, only the ones that are directly related to the purpose of each single experiment have been considered.

The programme works in such a way that each time a pre-selected behaviour is manifested by the focal subject, the experimenter presses “pause” key and chooses from the interested variable/menus the behavioural categories displayed in that specific frame. Every time the “pause” key is pressed, the previous menu setting does not change. This makes coding easy and fast especially when small changes of behaviours occur between two close events. Each single “action database” is saved and then automatically sent to a database called “Sequel Pro”. Afterwards, the entire data coding is copied on an Excel file for the construction of the tables and graphs and for the statistical analysis.

Chapter 6

Experiments on lateralized behaviours in non-human primates

Handedness based on object animacy

6.1 Experiment 1: Chimpanzees

6.1.1 INTRODUCTION

Among the different theories about the origin of handedness, there is the hypothesis about the correlation between hand preference and the left-hemisphere specialization for language regions (Annett & Kilshaw, 1983). Indeed, within the 90% of right-handers (Annett, 2002) approximately 95% of individuals have language-processing regions situated in the left hemisphere of the brain (Foundas, Leonard, & Heilman, 1995; Pujol et al., 1999). Within an evolutionary context, it has been suggested that right-handedness emerged as a result of speech (Annett, 2002), gestural language (Corballis, 2002; Hopkins et al., 2005b), tool use (Breuer et al., 2005; Greenfield 1991), coordinated bimanual actions (Hopkins et al., 2003a; Wundrum, 1986) posture (MacNeilage et al., 1987) and bipedalism (Braccini et al., 2010; Westergaard et al., 1998).

Today, research demonstrates that lateralized motor actions, underpinned by contralateral neural regions, occur across a wide range of vertebrates (MacNeilage et al., 2009; Rogers & Andrew, 2002; Vallortigara et al., 2011; Vallortigara & Rogers, 2005) and invertebrates (Frasnelli et al., 2010) suggesting that these lateralized capabilities may predate our split from extant great apes. Therefore, great apes represent a relevant functional model to study the evolution of human cerebral lateralization not only because of their phylogenetic proximity to humans, but also because they display clear anatomical human-like features (Byrne et al., 2001; Hobaiter & Byrne, 2011; Savage-Rumbaugh et al., 1986; Videan & McGrew, 2002). Moreover, recent neuro-imaging studies have indicated that all four species of great apes display homologous human Broca's (Cantalupo et al., 2003) and Wernicke's (Spocter et al., 2010) areas that are asymmetrically larger in the left hemisphere and that were active during tool use (Higuchi et al., 2009), further suggesting that modern human language emerged as an exaption of neural organization that also predates our evolutionary divergence from great apes.

Handedness has been extensively explored in great apes, but not in a systematic way that is useful to make direct comparisons between human and non-human primate. Furthermore, there are still inconsistencies among studies concerning whether great apes exhibit handedness at the population-level. It has been suggested that simple spontaneous activities are not likely to elicit handedness in great apes, as well as in humans (Marchant et al., 1995), and complex coordinated bimanual tasks could be considered as a good candidate (Byrne et al., 2001; Hopkins, 2006; Rogers & Kaplan, 1995). However, McGrew and Marchant (1997) strongly criticized the administration to non-human primates of human-designed tools, such as the tube task (Hopkins, 1995), which are not representative of a natural condition and seem not to provide reliable inferences about the evolutionary adaptation of handedness. Moreover, although humans demonstrate a reliable right-hand dominance for object manipulation, this measure is not representative of the spectrum of routine activities of modern humans, ancestral humans, or extant apes.

Zoo chimpanzees can provide a more comprehensive picture of handedness as their behaviours are expected to be close to a naturalistic context. Furthermore, it was considered whether during spontaneous manual activities the distinction of targets with a more functional purpose (e.g., tool use) and targets with a more emotive valence (e.g. self-scratching, manual gesturing) might offer a broader evaluation of manual preference, in order to elucidate the evolutionary corelationship between hemispheric specialization and handedness in humans.

6.1.2 MATERIALS AND METHODS

Subjects and housing

This experiment involved a group of captive chimpanzees (*Pan troglodytes*) (n = 9), including 2 adult males, 5 adult females and 2 juveniles. The individuals in this group were institutionalized animals with a variety of rearing histories (Table 3). At the time of data collection there was no clear alpha male.

Table 3

Chimpanzees Demographic Information

Subject	Sex	Data of acquisition	Birth type	Birthdate - Age	Kinship
Camilla	F	21 April 1998	Captive Born	21 April 1998 - 10Y	Davidino's sister
Davidino	M	2 March 2000	Captive Born	2 March 2000 - 8Y	Camilla's brother
Giorgina	F	5 December 2002	Captive Born	5 December 2002 - 6Y	Luisa's daughter
Giudy	F	1 January 1976	Unknown, probably wild born	~1972 - ~36Y	Valentina's mother
Jacky	M	21 September 1992	Unknown	~1989 - ~19Y	-
Luisa	F	1 January 1977	Unknown, probably wild born	~1973 - ~35Y	Giorgina's mother
Mary	F	22 February 1992	Unknown	~1990 - ~18Y	-
Samy	F	1 January 1976	Unknown, probably wild born	~1972 - ~36Y	-
Valentina	F	28 February 2006	Captive Born	28 February 2006 - 2Y	Judy's daughter

The age of the subjects has been calculated approximately on the basis of the period of observation.

Y = years old

This colony was hosted at “Parco Natura Viva – Garda Zoolical Park”, in Verona (Italy). Specifically, the chimpanzees’ enclosure was located in the Safari area of the park. Indeed, “Parco Natura Viva” was characterized by a walking area and a safari area, the latter accessible only by cars. The enclosure of the chimpanzees was split into different segments, comprised of a round indoor room linked to an outdoor sector through an inner corridor made from iron mesh and accessible through three sash doors. The sash doors were mechanically controlled by the keepers. The outdoor environment was an island (2113 m^2) furnished with two vertical wood towers, (linked to one another with ropes), a small branch, and two accessible caves (see figure 20). A water dyke, which was 9-metre large, surrounded the island, in order to prevent the chimpanzees from escaping the outdoor enclosure. Visitors could observe the subjects only in their outdoor enclosure.

Figure 20. A view of the chimpanzees' enclosure at Parco Natura Viva (Italy). The outdoor enclosure is characterized by an island, where two wood towers and ropes allow vertical locomotion. There are also two caves where subjects can hide. The wooden fortification on the left separates the indoor from the outdoor enclosure, which are linked to each other by three small doors. The island is surrounded by water to prevent subjects to escape.

Chimpanzees spent the night in the indoor enclosure where they were provided with fruit and vegetables in the evening. During the daylight and weather permitting, chimpanzees were locked outdoor until the late afternoon. Every day a different enrichment was provided in order to facilitate the transition of the chimpanzees between the indoor and outdoor enclosures. Furthermore, enrichment activities have been shown to and in order to increase the manifestation of natural behaviours for the improvement of the animal welfare (Carlstead & Shepherdson, 2000).

Procedure and data coding

In order to ensure reliable identification of the non-human primates subjects, and allow for the groups to adapt to the presence of the experimenter and experimental equipment, a familiarization period was necessary. Once reliable identification was achieved, a continuous focal sampling method was initiated where each recording session lasted 10 minutes, considering 9 sessions for each focal sampling, equating to 90 minutes per subject. The sessions of registration were carried out during the summer of 2008 and were counterbalanced over day (e.g. Altman 1974), in order to ensure the subjects to be observed during different situations. Indeed each focal subject was observed not within an isolated context, but in its daily social environment. In particular I considered sessions that included both routine activities and the circumstances in which subjects were more active, such as food distribution and enrichment time for non-human primate species, and free play or activities that involved manipulation for the group of children. The video registrations were carried out in outdoors enclosure The view of the video camera was wide enough to include not only the focal subject but also the social context within which the focal individual was behaving. Video footage was captured using a Sony digital video camera, which was subsequently streamed and saved on a Macintosh computer (iMac) for off-line coding and analysis.

The data coding was carried out manually by inserting the same behavioural categories displayed on OBSERVERTRON® on an Excel file. This process differed from OBSERVERTRON® only because the latter was more automated and faster. Furthermore, the data coding was focussed on lateralized unimanual actions directed towards an external target. Therefore, in cases where one hand reached towards a target object but the other hand was used for postural support or a separate manual activity, the action was excluded from analyses. In addition, I coded the animacy of the target object, distinguishing between animate targets, which involved interactions with social partner or the self, and inanimate targets, which involved interactions with objects or anything not alive belonging to the environment. Frequencies of inanimate targets included also locomotion: The event in which hand started walking or climbing was considered. Therefore, the variables considered for this experiment were the following: *Subject*, *Left Arm Action*, *Right Arm Action*, *Target Animacy* (for both arms/hands) (see Tables 1 and 2).

Statistical analyses

To analyse the data set a 2 (left hand, right hand) x 2 (animate target, inanimate target) repeated measures analysis of variance (ANOVA) was used, with paired-sample t-tests for post-hoc analyses. Binomial test was used to assess handedness at the individual level, for both animate and inanimate targets. All subject data was based on 90 minutes of observation time. To normalize the weighting that each subject contributed to the data set, proportions for each subject of each response type in relation to the total number of actions for that subject were calculated.

6.1.3 RESULTS

Table 4 indicates the frequencies of both left and right unimanual actions towards animate and inanimate target objects.

Table 4

Chimpanzees Scoring on Unimanual Handedness Based on Target Animacy

Subject	Left Inanimate	Right Inanimate	z-score	Left Animate	Right Animate	z-score	Total	Observation (min)
Camilla	33	50	1,76	16	6	-1,92	105	90
Davidino	42	43	0,00	9	5	-0,80	99	90
Giorgina	26	28	0,14	4	7	0,60	65	90
Giudy	18	36	2,31*	15	20	0,68	89	90
Jacky	19	33	1,80	13	24	1,64	89	90
Luisa	4	12	1,75	3	6	0,67	25	90
Mary	35	45	1,01	10	8	-0,24	98	90
Samy	35	53	1,81	10	4	-1,34	102	90
Valentina	32	33	0,00	7	7	0,27	79	90

The table reports only unimanual events during interactions with inanimate and animate targets

* Significant lateral asymmetry (p < .05)

The 2 (left hand, right hand) x 2 (inanimate target, animate target) ANOVA (frequency and proportion) revealed significant interactions of lateralized unimanual action and target animacy (frequency: F(1,8) = 8.813, p = .018; proportion: F(1,8) = 11.902, p = .009) (see figure 21).

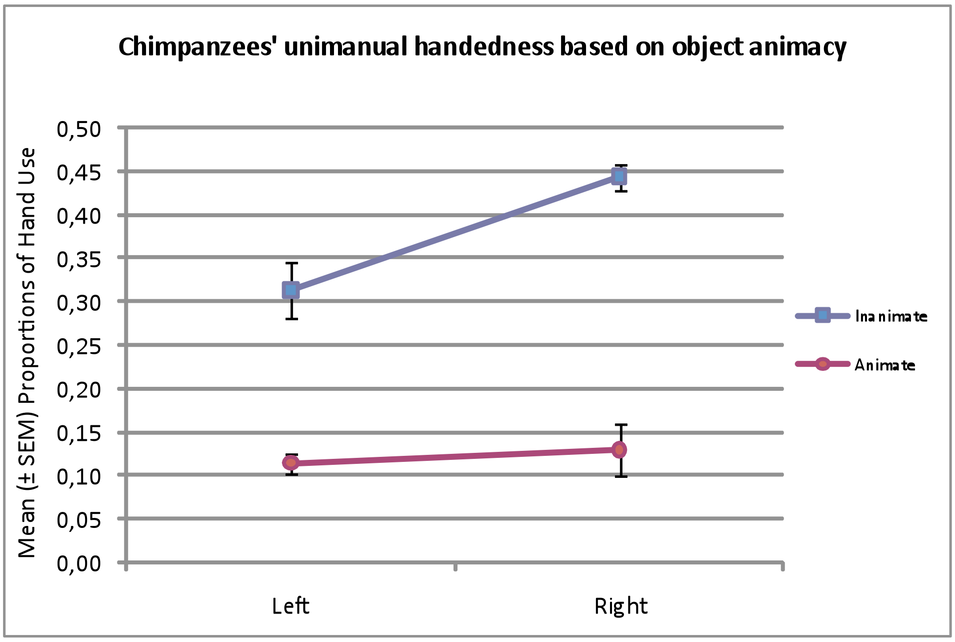


Figure 21. The chart depicts mean values of proportions relative to unimanual activities of left and right hand during contact with inanimate (blue line) and animate (red line) targets.

Main effects of target type (inanimate, animate) demonstrated higher overall amount of actions towards inanimate targets versus actions directed towards animate targets (frequency: F(1,8) = 28.19, p = .001; proportion: F(1,8) = 46.60, p < .001). Main effects of hand (left, right) were also identified (frequency: F(1,8) = 10.25, p = .013; proportion: F(1,8) = 8.306, p = .020) indicating a higher frequency of right handed actions compared to left handed actions. Post-hoc analyses were conducted using paired-sample t-tests to test the dominance of right-handed actions (frequency: M = 37, SE = 4.19; proportion: M = .444, SE = .015) compared with left hand actions (frequency: M = 27.11, SE = 3.89; proportion: M = .313, SE = .033) for inanimate targets only, (frequency: t(8) = -4.080, p = .004; proportion: t(8) = -3.817, p = .005), revealing a significant preference in using more frequently the right than the left hand. Right-handed actions (frequency: M = 9.67, SE = 2.39; proportion: M = .129, SE = .030) were also compared with left-handed actions (frequency: M = 9.67, SE = 1.51; proportion: M = .114, SE = .012) for animate targets only (frequency: t(8) = .000, p = 1.000; proportion: t(8) = -.566, p = .587) which demonstrated no such significant difference.

6.1.4 DISCUSSION

Experiment 1 revealed a significant interaction between handedness and target animacy, where the right hand was more influenced by the animacy of the target than the left hand. Moreover, chimpanzees showed to use both hands with equal frequency for actions directed towards animate targets. This pattern was also demonstrated by Aruguete and colleagues (1992), but was not discussed in light of underlying neural generators.

With respect to the previous literature, it is not surprising that there is evidence of a right hand bias for manual actions in a group of captive apes. What is interesting is that the right hand bias was only significant for actions directed towards inanimate target objects regardless of task type, complexity or social context. This implies a dominance for left hemisphere processing of external inanimate stimuli. This finding is not in conflict with either the human and ape handedness data, but the interpretation of the current results may reflect a causal relationship between tool use and the evolution of language-like skills. Indeed interactions with inanimate objects may require and underpin a sequence of hierarchical actions to create a valid goal state, which might be comparable to a simple or proto-syntax, similar to that which underpinned an early human proto-language. Therefore interactions with objects (and ultimately tool-use) may have extended the left hemisphere's temporal-sequential processing abilities (originally selected for external stimuli) to a language-based syntax (internal stimuli).

The mixed-handed finding for self-directed behaviours and conspecific-directed manual actions is not inconsistent with previous studies of great ape handedness (e.g. Aruguete et al., 1992). This interaction demonstrates a greater involvement of the right hemisphere/left hand compared with actions to inanimate objects. However, if animate objects require an increase in right hemisphere processing compared with inanimate objects, or if inanimate objects require an increase left hemisphere processing compared with animate objects is yet to be determined.

I postulate that the left hemisphere has a preference for either manipulating and/or predicting manipulations required by the engagement with the object. However, it is difficult to distinguish whether the neural process linked to hand employment is biased by the animacy of the target or by the predicted tasks afforded by the external stimuli. It may be more likely that an inanimate object requires manipulation to reach a goal state compared with an animate object. For example, tools require manipulation in order to achieve a goal. On the other hand, emotive tactile interactions with conspecifics and the self may require perseverative actions to fulfil a social requirement, but no immediate goal state (e.g. grooming).

It is difficult to draw a definitive causal relationship between hemispheric specialization for language and handedness based on a simplistic coding of unimanual actions directed towards animate and inanimate target objects. Nevertheless, one could debate claims that only particular tasks with varying complexities, particularly bimanual tasks (e.g. Hopkins & Rabinowitz, 1997), are necessary to influence the manifestation of preferential hand use in non-human primates. In fact, this study brings into questions whether it is the task or the animacy of the object that influences handedness.

6.2 Experiment 2: Gorillas

6.2.1 INTRODUCTION

The Experiment 2 was the exact replication of Experiment 1, but in this case a group of zoo gorillas was considered. Indeed, compared to chimpanzees, there are less studies investigating handedness in gorillas and there seems to be still inconsistency about whether they manifest population-level hand preference. Moreover, the fact that tool-use has been rarely reported in gorillas (Breuer et al., 2005) might have probably discouraged researchers to investigate handedness in this species. Fortunately behavioural psychologists are giving progressively more attention to the study of handedness in gorillas, especially since Byrne and Byrne (1991) demonstrated that gorillas manifested an intense frequency of bimanual food elaboration and that this activity seems to elicit right hand preference at population-level (Meguerditchian et al., 2010). Moreover, a recent publication documented the first observation of tool use in a wild western adult female of gorilla, which used a branch as a walking stick in order to test water deepness and to aid in her attempt to cross a pool of water (Breuer et al., 2005). This evidence suggests that gorillas could represent a good candidate with chimpanzees to test the development of human handedness tied to hemispheric specialization in non-human primates. Moreover, since gorillas are terrestrial creatures, rather than arboreal creatures, they may rely more on visual signals and therefore may be an even better model for the study of the evolution of human handedness, compared to chimpanzees.

6.2.2 MATERIALS AND METHODS

Subjects and housing

This experiment consisted of a group of semi free-ranging western lowland gorillas (*Gorilla gorilla gorilla*) (n=12), which included one silverback, seven adult females, and four juveniles (Table 5).

Table 5

Gorillas Demographic Information

Name	Sex	Rank	Birth type	Birthdate - Age	Kinship
Dishi	M	Juvenile	Captive born	31 March 2004 - 2Y	Kishi's son
Djala	M	Silverback	Wild born	1982 - 22Y	-
Emmie	F	Lowest	Captive born	13 October 1995 - 11Y	-
Foufou	F	High (similar to Mumba)	Captive born	11 November 1996 - 8Y	Mumba, Kibi, and Kishi's half sister
Jaja	M	Juvenile	Captive born	30 October 2003 - 1Y	Mumba's son
Kibi	F	Middle	Captive born	25 May 1996 - 10Y	Mumba, Foufou, and Kishi's half
Kishi	F	High (not highest)	Captive born	04 December 1992 - 14Y	Mumba, Foufou, and Kibi's half
Kouni	M	Juvenile	Captive born	16 February 2005 - 1Y	Kibi's son
Mumba	F	High	Captive born	28 July 1991 - 15Y	Kishi, Foufou, and Kibi's half sister
Tamarilla	F	Low (2nd to bottom)	Captive born	30 July 1990 - 14Y	Tamky's sister
Tamky	F	High (above Kishi	Captive born	09 October 1993 - 13Y	Tamarilla's sister
Yene	F	Juvenile	Captive born	15 January 2005 - 1Y	Foufou's daughter

The age of the subjects has been calculated approximately on the basis of the period of observation.

Y = years old

The individuals formed a biological family group, which means that the alpha male was the father of all juveniles. Furthermore, every subject was peer-raised, that is grew up under the care of their conspecifics. These characteristics made this group of gorillas an unique and interesting experimental sample for the aim of this dissertation, as their behaviours and social dynamics were more similar to wild individuals than captive ones. The gorillas were part of the John Aspinall Foundation®, a charity association actively involved with several projects that incorporated a diverse range of conservation activities of endangered species, both in captivity and in the wild.

The group was hosted at Port Lympne Wild Animal Park, which was nestled in the Kent countryside (U.K.), in an enclosure called, "Palace of the Apes", the world's largest gorillarium (see figure 22). The gorillas' enclosure was placed in the "Primate trail", where many endangered species of non-human primates were hosted. Three main sections characterized the area dedicated to gorillas. There was a large outdoor section, the garden, provided with naturalistic items, such as trees, grass, logs, and small hillocks made out of stones (see figure 22a). Furthermore, there were also iron boxes filled with honey or jam, that gorillas could gather by dipping a stick through small holes. These devices represented a structural enrichment to elicit tool use and manipulation in the individuals. The garden enclosure had viewing windows at ground level and unimpeded visual access via a raised walkway that followed the top of the garden wall.

The outdoor enclosure was connected to another smaller outdoor section, which was characterized by a big iron mesh cage with windows for visitors and it was divided in a lower and an upper side (figures 22b). These two levels were connected to each other with iron ladders, hanging tyres, and ropes. The upper side of the enclosure was also provided with big nests made out of iron mesh, in which gorillas could rest or sleep. The floor was made out of cement and covered with hay, which was used not only for playing activities, but also to make nests more comfortable for resting. Finally, the upper level of this enclosure allowed the access to an inner indoor enclosure, in which there were 14 bedrooms where gorillas could sleep during the night.

Figure 22. Two views of the gorillas' enclosure at Port Lympne Park (U.K.). a) The garden enclosure is characterized by green field and rocks to mimic a natural environment and is connected by little doors to a smaller outdoor enclosure (on the right) and to the indoor enclosure (on the left); b) the smaller outdoor enclosure covered by a mesh cage and filled with ropes, tiers and metal ladders to get across the upper and the lower level. The floor is entirely covered by hay.

Sash doors connected all the sections of the whole enclosure and were kept always open so that the individuals could freely move from one side to another. Every day keepers provided the gorillas with fruit and vegetables that were dropped from the roof of the indoor enclosure into the deep straw. This allowed the individuals to spend much of their day foraging through the straw in search of tasty morsels, much as they would do in the wild. Visitors could observe the gorillas through all the sections of the entire enclosure, except for the indoor side, which was accessible only by the staff of the zoo.

Procedure and data coding

The same procedure of the Experiment 1 was applied for Experiment 2. Video registrations were taken during two sessions: 4 subjects (Djala, Foufou, Jaja, and Tamarilla) were observed during the summer of 2004, whereas the rest of 8 subjects (Dishi, Emmie, Kibi, Kishi, Kouni, Mumba, Tamki, and Yene) were observed during the summer of 2006.

For this study two synchronized digital video cameras were used (Panasonic NVGS11B), in order to capture both the focal individual in full frame and a wide-angle to encompass the subject, conspecifics, and surroundings. Synchronization was established using a flash bulb. Cameras were tripod mounted and followed gorilla activity using zoom, tilt, and swivel to optimize view. Synchronized video streams were compressed into a single file (15 frames per second) viewed in a top/bottom format for subsequent coding.

Coding categorization was based on the same MDM method of Experiment 1, but with the employment of OBSERVERTRON® and the analysis of data considered the same variable of Experiment 1. Thus, unimanual actions directed upon animate and inanimate target were registered.

Statistical analyses

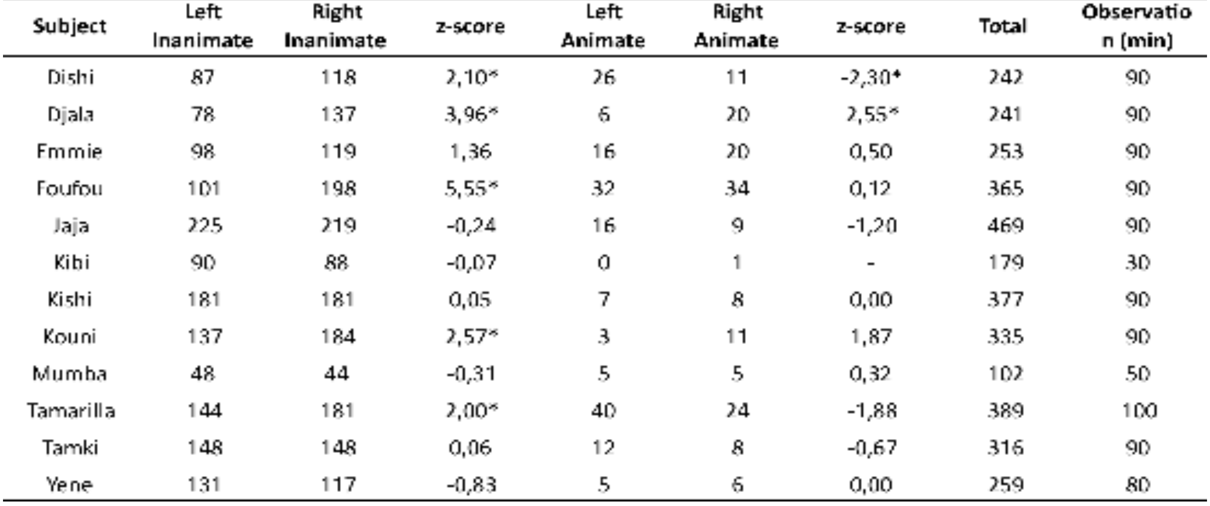
To analyse the data set a 2 (left hand, right hand) x 2 (animate target, inanimate target) repeated measures analysis of variance (ANOVA) was used, with paired-sample t-tests for post-hoc analyses. Binomial test was used to assess handedness at the individual level, for both animate and inanimate target. Subjects were not observed for the same amount of time, e.g. 90 minutes of observation time. To normalize the weighting that each subject contributed to the data set, proportions for each subject of each response type in relation to the total number of actions for that subject were calculated, as I did in Experiment 1.

6.2.3 RESULTS

Table 6 indicates the frequencies of both left and right unimanual actions towards animate and inanimate target objects.

Table 6

Gorillas Scoring on Unimanual Handedness Based on Target Animacy



Subject	Left Inanimate	Right Inanimate	z-score	Left Animate	Right Animate	z-score	Total	Observation (min)
Dishi	87	118	2,10*	26	11	-2,30*	242	90
Djala	78	137	3,96*	6	20	2,55*	241	90
Emmie	98	119	1,36	16	20	0,50	253	90
Foufou	101	198	5,55*	32	34	0,12	365	90
Jaja	225	219	-0,24	16	9	-1,20	469	90
Kibi	90	88	-0,07	0	1	-	179	30
Kishi	181	181	0,05	7	8	0,00	377	90
Kouni	137	184	2,57*	3	11	1,87	335	90
Mumba	48	44	-0,31	5	5	0,32	102	50
Tamarilla	144	181	2,00*	40	24	-1,88	389	100
Tamki	148	148	0,06	12	8	-0,67	316	90
Yene	131	117	-0,83	5	6	0,00	259	80

The table reports only unimanual events during interactions with inanimate and animate targets

* Significant lateral asymmetry ($p < .05$)

The 2 (left hand, right hand) x 2 (inanimate target, animate target) ANOVA (frequency and proportion) revealed significant interactions of lateralized unimanual action and target animacy (frequency: $F(1,11) = 6.033$, $p = .032$; proportion: $F(1,11) = 5.597$, $p = 0.037$) (see figure 23).

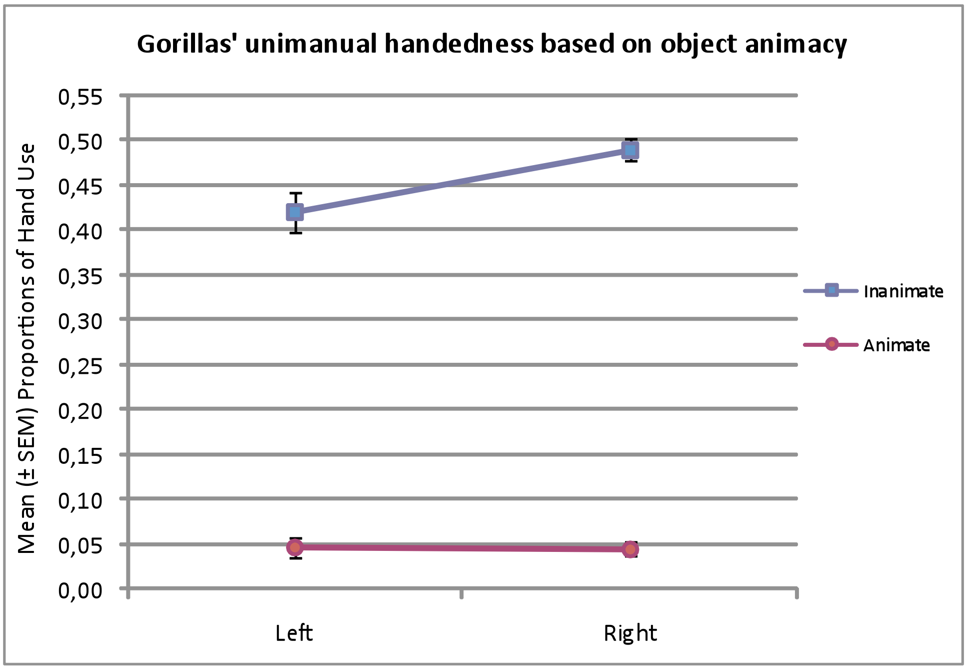


Figure 23. The chart depicts mean values of proportions relative to unimanual activities of left and right hand during contact with inanimate (blue line) and animate (red line) targets.

Main effects of target type (inanimate, animate) demonstrated higher overall amount of actions towards inanimate targets versus actions directed towards animate targets (frequency: $F(1,11) = 84.330$, $p < .001$; proportion: $F(1,11) = 594.156$, $p < .001$). The effects of hand (left, right) were not significant (frequency: $F(1,11) = 4.131$, $p = .067$; proportion: $F(1,10) = 3.952$, $p = .072$), indicating only a trend for higher frequency of right handed actions compared to left handed actions. Post-hoc analyses were conducted using paired-sample t-tests to test the dominance of right-handed actions (frequency: M = 144.5, SE = 14.59, proportion: M = .049, SE = .012) compared with left hand actions (frequency: M = 122.33, SE = 14.10; proportion: M = .042, SE = .023) for inanimate targets only, (frequency: $t(11) = -2.303$, $p = .042$; proportion: $t(11) = -2.243$, $p = .046$), revealing a significant preference in using more frequently the right than the left hand. Right-handed actions (frequency: M = 13.08, SE = 2.74; proportion: M = .45, SE = .008) were also compared with left-handed actions (frequency: M = 14, SE = 3.64; proportion: M = .046, SE = .011) for animate targets only, (frequency: t(11) = .368, p = .720; proportion: t(11) = .146, p = .887) which demonstrated no such significant difference.

6.2.4 DISCUSSION

Gorilla handedness interacted with the animacy of a target object such that the subjects of the group of gorillas were equally likely to use the left and right hands for actions upon animate targets, but biased upon using the right hand for actions toward inanimate objects. In addition, a non-significant trend for right-handedness was found; however, post-hoc analyses revealed that right- hand dominance appeared to manifest only for actions upon inanimate targets.

The results of this study reflect a consistency of pattern with chimpanzees handedness based on target animacy. Indeed, both species revealed a right-hand/left-hemisphere dominance for actions toward inanimate objects, bolstering theories proposing that object manipulation skills were a critical precursor to the emergence of human language skills potentially based on a shared, simple, and syntactic structure (Greenfield, 1991; Hopkins et al., 2007). Moreover, as previously reported in chimpanzees, gorillas manifest an equal use of hands during interactions with the self and the conspecifics. Thus these findings seem to be in line with the right hemisphere hypothesis (Borod et al., 1998; Campbell, 1982), as during actions that presuppose a more emotive involvement the right hemisphere is more cognitively engaged, compared to actions that are supposed to have a more ordered-structure and less emotive purpose.

Furthermore the results of this study seem to corroborate the hypothesis that inanimate targets would be reached toward for a functional purpose with a relatively reduced emotive perhaps more analytical element (e.g., manipulation, tool use, and food preparation), whereas animate targets may be reached toward for either a functional (e.g., climbing) and/or emotive

Lateralization for emotion processing

6.3 Experiment 3: Chimpanzees

6.3.1 INTRODUCTION

To date, few studies have investigated the influence of arousal emotive status on lateralized behaviours of non-human primates and most of them have focussed on visual and acoustic perceptions, using stimuli based on facial expressions or dichotic sounds (e.g. Hauser, 1993; Hook-Costigan & Rogers, 1998; Chapelain & Blois-Heulin, 2008). Moreover, great apes were poorly considered in these types of investigations, with the exception of some studies that focussed on asymmetrical facial expressions (Fernández-Carriba et al., 2002) and on the lateralization of self-directed manual behaviours during stressful arousing contexts (Leavens et al., 2001). Most of the findings reported in literature seem to support a dominance of the right hemisphere for the processing of emotive stimuli. However, all these studies were carried out by observing individuals within an isolated situation and by using artificial stimuli, such as human-design tasks or pictures.

Recently, Baraud and colleagues (2009) investigated the influence of lateralized positioning between group members in two zoo species of mangabeys, revealing a group-level significant preference in being approached from the left visual field and a bias in keeping conspecific in the right visual field during approaching behaviour, regardless of the type of interaction. The findings suggested that approaching an individual on its left side might facilitate the perception of its arousal status (since the left side of the face is more expressive). However the authors seemed not to give a good interpretation for the evidence of keeping conspecifics significantly more in the right visual field, thus the pattern seems to support neither the right hemisphere nor the valence hypothesis. Therefore, although this study seemed initially to investigate whether social interactions might elicit lateralized behaviours in non-human primates, it basically further supported the hypothesis that the left side of the face is more expressive.

Similarly, the current experiment aimed to assess cerebral lateralization for the processing of emotions in a group of zoo chimpanzees, during their daily activities, by investigating lateralized behaviours during social interactions. In particular, I observed whether subjects manifested a side preference in keeping their conspecifics that were in close visual proximity, while they were performing any kind of manual action. However, any information about the side of the approached individual was not collected, as this preference varies according to the behavioural strategy of the approaching individual and, thus, seems not to provide information about the cerebral lateralization of the recipient. Unlike Baraud et al. (2009), it was not considered the right/left visual field, as this measure might be more acceptable in animals with laterally placed eyes and small binocular overlap (Robins, Lippolis, Bisazza, Vallortigara, & Rogers, 1998). Instead, the analysis has been addressed to the body hemifield that the focal subject showed to conspecifics, because although the body is still in one position, head can turn toward different kind of stimuli (that could be not necessarily related to the social environment). Furthermore, the influence of social stimuli is more likely to influence the motor responses of the whole body, such as the hand and foot movements for turning or attacking reactions (Robins et al., 1998).

6.3.2 MATERIALS AND METHODS

Subjects and housing

Like in the Experiment 1, subjects were 9 chimpanzees (*Pan troglodytes*) hosted by "Parco Natura Viva – Garda Zoological Park", including 2 adult males, 5 adult females and 2 juveniles.

Procedure and data coding

This experiment was based on the same procedure employed for Experiment 1, as the same videos were considered. Moreover, the same MDM method to code lateralized behaviours during social interactions was employed. In particular, I collected information on lateralized behaviours by observing the side positioning of the focal subject with respect of one or more conspecifics, every time he/she was performing manual activities (e.g. object manipulation, self touching, etc). The reason manual activities were consider as a reference point for social laterality relies on the necessity to collect events with a recurring and rational scan. Moreover, since manual activities generally require investment of concentration and energy by the performer, less attention can be addressed to the surrounding environment and a strategic position might facilitate the individual to be as more reactive as possible to the social dynamics. The side of the body that the focal subject exposed toward the interacting member was distinguished as transversal (front or rear) or lateral (left or right) (Baraud et al, 2009) and was detected as *social laterality*. Moreover, it was considered only the choice of the focal subject to position itself with respect to other members. Therefore, any event related to when a conspecific approached the focal subject was not considered. Furthermore, the distance between the focal subject and the conspecific(s) was coded and I considered only the events in which the subject and the recipient were less than 3 metres of distance, in order to have a clearer information of the side of positioning. The MDM method allowed to code not more than 2 conspecifics at the same time, therefore when there were more than 3 conspecifics within 3 metres away of the focal subject, I noted information only about the 2 closest conspecifics. Therefore, the variables considered for this study were the following: *Subject*, *Recipient*, *Subject Action*, *Proximity*, and *Side of Approach* (see Tables 1 and 2).

Statistical analyses

To analyse the data set a paired-sample t-tests was used to assess differences between frontal and rear sides and between left and right sides. Moreover, a Friedman test was employed to estimate differences between front, rear, right, and left behavioural categories. Binomial test was used to assess side preference at the individual level, for both transversal and lateral condition. All subject data were based on 90 minutes of observation time and analyses were all based on frequencies. To normalize the weighting that each subject contributed to the data set, proportions for each subject of each response type in relation to the total number of actions for that subject were calculated.

6.3.3 RESULTS

Table 7 indicates the frequencies of transversal (front and rear) and lateral (left and right) side preference during social laterality.

Table 7

Chimpanzees Scoring on Transversal and Lateral Side Preference during social laterality

	Tranversality			Laterality				
Subject	**Front**	**Rear**	**z-score**	**Left**	**Right**	**z-score**	**Total**	**Observation (min)**
Camilla	117	9	-9,53*	3	16	2,75*	145	90
Davidino	42	12	-3,95*	27	7	-3,26*	88	90
Giorgina	56	3	-6,77*	56	23	-3,60*	138	90
Giudy	25	5	-3,47*	5	7	0,29	42	90
Jacky	80	3	-8,34*	36	14	-2,97*	133	90
Luisa	22	0	-4,48*	22	1	-4,17*	45	90
Mary	98	14	-7,84*	33	19	-1,80	164	90
Samy	28	5	-3,83*	58	10	-5,70*	101	90
Valentina	130	12	-9,82*	21	30	1,12	193	90

Side of the focal subject showed to conspecific positioned within 3 meters away are reported in the table.

* Significant transversal or lateral asymmetry ($p < .05$)

Analyses with paired t-test were conducted to test the transversal condition, in order to verify the dominance of front side preference (frequency: $M = 66.44$, $SE = 13.77$; proportion: $M = .536$, $SE = .048$) compared with rear side preference (frequency: $M = 7$, $SE = 1.63$; proportion: $M = .068$, $SE = .015$) (frequency: $t(8) = 4.625$, $p = .002$; proportion: $t(8) = 9.843$, $p < .001$), demonstrating a significant preference for keeping one or more conspecifics frontally (see figure 24).

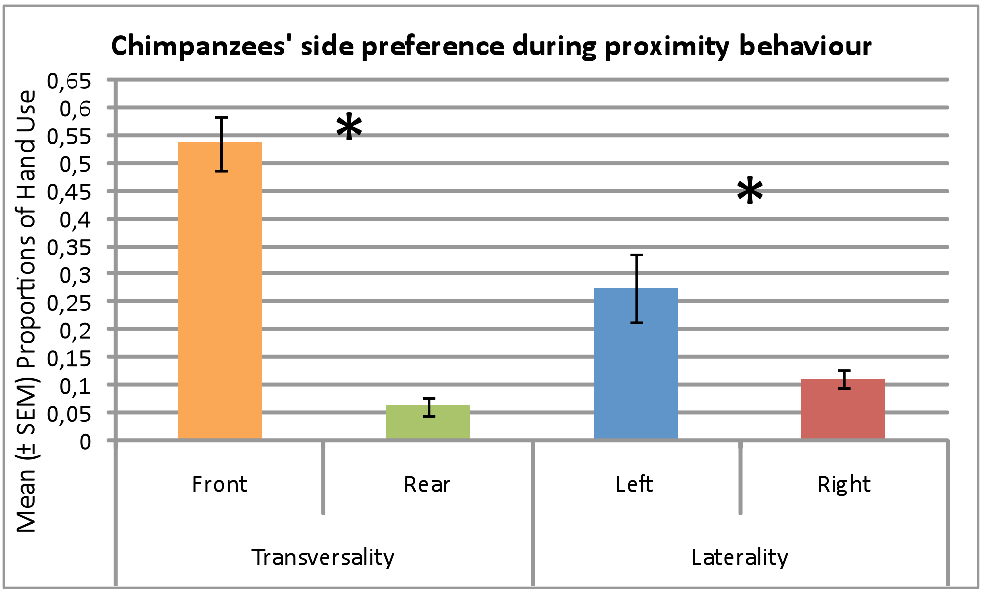


Figure 24. The chart depicts mean values of proportions relative to transversal (front and rear) and lateral (left and right) side preference during social laterality.

The lateral condition was also analysed with a t-test, by comparing the dominance of right side preference (frequency: M = 14, SE = 3.002; proportion: M = .11, SE = .01) with left side preference (frequency: M = 29, SE = 6.46; proportion: M = .275, SE = .062) (frequency: t(8) = 2.243, p = .055; proportion: t(8) = 2.339, p = .048), which also demonstrated a significant preference for the left side (see figure 24). Friedman test revealed significant differences between behavioural categories (frequency: $\chi^2 = 18.172$, $p < .001$; proportion: $\chi^2 = 18.172$, $p < .001$).

6.3.4 DISCUSSION

The group of chimpanzees manifested an overall significant preference in keeping the closest conspecifics (less than 3 metres) in their frontal side, compared to when they kept them behind, while they were performing manual activities. Additionally, when chimpanzees had their conspecifics either to their left or their right side of the body, they significantly preferred to keep them significantly more to their left than the right side. This choice was totally under the control of the focal subject, as any potential approaching event performed by conspecifics was discarded from the analysis. Moreover it was considered only when the focal subject positioned itself with respect to the other group members.

The fact that chimpanzees overall prefer to keep their conspecifics frontally might be tied to the conformation of the visual field. Indeed, non-human primates, as humans, are characterized by frontally located eyes for a stereoscopic vision. According to Conroy (1990), primates evolved to meet the needs of living an arboreal life, thus it is extremely important to perceive the intricate three-dimensional world, in order to move through the environment. On the other hand, avian and low vertebrates have laterally placed eye, which in some species can scan independently and attend different stimuli simultaneously presented in the lateral fields of both eyes (Ingle, 1973; Rogers, 2000a). Therefore, they are more likely to manifest a lateralized approaching behaviour, compared to primates that might need to attend stimuli frontally, in order to have a better resolution and perception of the stimulus. A further hypothesis suggests that a frontal approach is more advantageous in primates, and perhaps particularly in great apes, as it allows the recipients to pay more attention both to the facial expressions, which represent an important means to convey social information, and to the entire body, in order to anticipate the recipient's behavioural reactions (see Baraud et al., 2009). Therefore, one might infer that keeping conspecifics in the front side would make individuals less vulnerable to eventual aggressions especially during the performance of manual activities, such as tool-use, feeding, self-grooming.

The current study revealed also a significant preference during lateral condition as chimpanzees preferred to keep the conspecifics on the left side of the body and this evidence seems to support the right hemisphere hypothesis (Borod et al., 1998; Campbell, 1982). Indeed, according to this theory the right hemisphere is dominant in the processing of all type of emotions. Therefore, chimpanzees might prefer to keep their conspecifics on the side that is more sensitive to the social environment, which is strictly related to emotion processing (Santos et al., 2010). Moreover, since the right hemisphere is supposed to activate also during emergency situations (MacNeilage et al., 2009), I postulate that chimpanzees might prefer to expose the side that is more involved in novel and unexpected situations and that controls more quickly the behavioural response initiation. In particular, keeping conspecifics in the left side may enable animals to concentrate on two tasks simultaneously, such as foraging and predator vigilance (Rogers, Zucca, & Vallortigara, 2004). Furthermore, in line with what Baraud and collaborators (2009) postulated, this position might likely favour subjects to show their left side of the face to other group members, which, according to human (Borod et al., 1997; Campbell, 1986) and non-human primate studies (Hauser, 1993; Hook-Costigan & Rogers, 1998; Fernández-Carriba et al., 2002), express more intensely the subject's emotional status, thus facilitating social interactions. Additionally, keeping conspecifics on the left side allows to expose more the left visual field than the right one. This also would implicate a right hemisphere dominance, which is supposed to be specialized for face recognition, specifically (Gross & Sergent, 1992).

The finding about lateral social laterality is not in line with the study of Baraud and collaborators (2009), as they found a preference in keeping conspecifics in their right visual field. Moreover, they did not find any significant lateralization when considered the enlarged and rear visual field, thus when the head was moving.

The results of this study seem to suggest that social interactions enhances lateralized behaviours in chimpanzees. Indeed, subjects seem to manifest asymmetrical positioning when performing manual activities, with respect to the nearest conspecifics and this preference could be related to a right hemisphere specialization for the perception of emotional stimuli and for the control of behavioural responses during unexpected situations.

6.4 Experiment 4: Gorillas

6.4.1 INTRODUCTION

This experiment is the exact replication of Experiment 4, but a group of western lowland gorillas was involved, in order to test whether there is consistency in great apes for the manifestation of lateralized behaviours during social interactions.

5.4.2 MATERIALS AND METHODS

Subjects and housing

Like the Experiment 2, subjects were 12 western lowland gorillas (*Gorilla gorilla gorilla*) living in a peer-raised, semi free-ranging, biological family group at Port Lympne Wild Animal Park, UK.

Procedure and data coding

The same procedure of the Experiment 2 was applied for the current experiment.

Coding categorization was based on the same MDM method of Experiment 2 and the analysis of data considered the same variables used in the Experiment 3. Therefore, I collected information about the side of the body that the focal subject preferred to expose to other group members, while he/she was performing manual activities.

Statistical analyses

To analyse the data set a paired-sample t-tests was used to assess differences between frontal and rear sides and between left and right sides. Moreover, a Friedman test was employed to estimate differences between front, rear, right, and left behavioural categories. Binomial test was used to assess side preference at the individual level, for both transversal and lateral condition. Subjects were not observed for the same amount of time, e.g. 90 minutes of observation time. To normalize the weighting that each subject contributed to the data set, proportions for each subject of each response type in relation to the total number of actions for that subject were calculated, as I did in the previous experiments.

6.4.3 RESULTS

Table 8 indicates the frequencies of transversal (front and rear) and lateral (left and right) side preference during social laterality.

Table 8

Gorillas Scoring on Transversal and Lateral Side Preference during social laterality

	Tranversality			**Laterality**				
Subject	**Front**	**Rear**	**z-score**	**Left**	**Right**	**z-score**	**Total**	**Observation (min)**
Dishi	159	72	-5,66*	137	52	-6,11*	420	90
Djala	125	36	-6,93*	28	49	2,28*	238	90
Emmie	105	5	-9,44*	45	23	-2,55*	178	90
Foufou	212	261	2,20*	110	70	-2,90*	653	90
Jaja	115	15	-8,68*	54	22	-3,55*	206	90
Kibi	28	24	-0,42	30	15	-2,08*	97	30
Kishi	84	3	-8,58*	62	32	-2,99*	181	90
Kouni	96	64	-2,45*	76	70	-0,41	306	90
Mumba	27	4	-3,95*	19	16	-0,34	66	50
Tamarilla	31	9	-3,32*	34	45	1,12	119	100
Tamki	91	27	-5,80*	46	25	-2,37*	189	90
Yene	70	50	-1,73	101	62	-2,98*	283	80

Side of the focal subject showed to conspecific positioned within 3 meters away are reported in the table.

* Significant transversal or lateral asymmetry (p < .05)

Analyses with paired t-test were conducted to test the transversal condition, in order to verify the dominance of front side preference (frequency: M = 95.25, SE = 54.90, proportion: M = .403, SE = .119) compared with rear side preference (frequency: M = 47.50, SE = 71.21; proportion: M = .146, SE = .108) (frequency: t(11) = 3.568, p = .004; proportion: t(11) = 4.497, p = .001), demonstrating a significant preference for keeping a conspecific frontally (see figure 25).

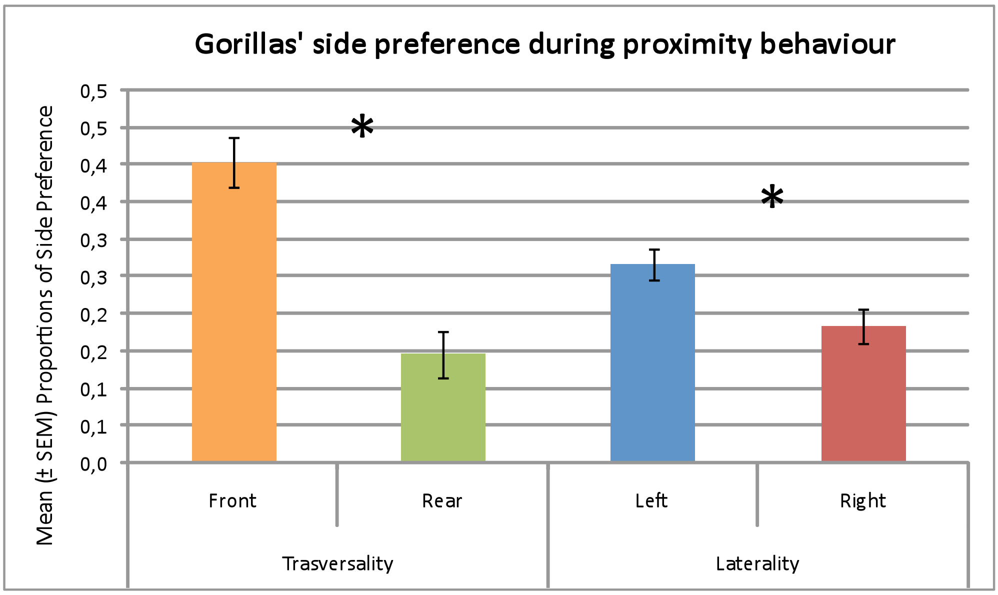


Figure 25. The chart depicts mean values of proportions relative to transversal (front and rear) and lateral (left and right) side preference during social laterality.

The lateral condition was also analysed with a t-test, by comparing the dominance of right side preference (frequency: M = 40.08, SE = 20.53; proportion: M = .183, SE = .077) with left side preference (frequency: M = 61.83, SE = 37.01; proportion: M = .266, SE = .069) (frequency: t(11) = 2.735, p = .019; proportion: t(11) = 2.973, p = .013), which also demonstrated a significant preference for the left side (figure 25). Friedman test revealed significant differences between behavioural categories (frequency: $\chi^2 = 18.2$, $p < .001$; proportion: $\chi^2 = 18.2$, $p < .001$). At the individual level, 9 out of 12 showed a significant bias: 8 for the left and one (Djala, alpha male) for the right side.

6.4.4 DISCUSSION

This study revealed an overall significant preference in semi-captive gorillas in keeping conspecifics on the front side while they were performing different kind of manual activities. Moreover, the analysis of the lateral condition revealed a significant preference in keeping conspecific more frequently in the left side, compared to the right side. This group of gorillas differed from that of chimpanzees, as the former was a biological family group and have a clear alpha male, whereas the latter was a manufactured group and did not have an alpha male at the time of data collection. During the data analysis it became clear that at the individual-level one individual manifested a reverse pattern to the rest of the family group, which was identified as the alpha male (Djala). This finding suggests that the alpha male may exhibit a different pattern during social laterality, because of his hierarchical role within the group.

The findings of this experiment are in line with chimpanzees side preference during social interactions. Indeed, both species of great apes manifested a significant preference in keeping conspecific in the front side and this preference might be tied to the advantage of having a better perception of others' behaviours during the performance of manual activities. Moreover, gorillas acted as chimpanzees when they had to keep group members laterally, as they manifested a significant left bias. Once again, the right hemisphere dominance for emotion processing (Borod et al., 1998; Campbell, 1982) and activation during unexpected event (MacNeilage et al., 2009) seems to be supported. Thus, the left side of the body would react faster during behavioural responses, such as making the first walking step to run away from a dangerous event coming from the right side by turning leftward or, conversely, in protecting the body and the face from an expected attack, thus working as a shield.

The evidence about keeping conspecifics more on the right side for the gorilla male suggests that, given that gorillas society is based on a single-male dominance over a multi-female group (Doran & McNeilage, 1997), alpha males might have evolved different social behavioural strategies compared to females, both for competing and reproductive reasons. In particular, this finding might support the *motivational approach-withdrawal hypothesis* (Demaree et al., 2005), which claims that the right hemisphere is dominant in controlling withdrawal behavioural responses, while the left hemisphere is dominant in controlling approaching behavioural responses. Therefore, male gorillas might tend to show their right side, as they represent the dominant individuals within the group and are should more prone to approach the other group members, especially females for copulation. Furthermore, human studies have demonstrated that individuals with greater relative right hemisphere activation are less likely to make recommendations of risky behaviour and are less likely to report preferences for engaging in risky behaviours (Drake & Ulrich, 1992). Therefore, alpha males should be more risky, in order to defend the colony from foreign attackers and to approach females for reproduction.

Therefore, there seems to be consistency among great apes in manifesting specific transversal and lateralized behavioural responses during social interactions. These behaviours might have evolved from lateralized behaviours of more ancient vertebrates for social cohesion and communication between group members, in order to gain benefits from social cooperation and to avoid sever injuries that might rise from wrong signals. Therefore, the findings of Experiment 4 and 5 seem to support the hypothesis that population-level lateralization might have been favoured by natural selection because social individuals gain benefit from the gregarious life (Vallortigara & Rogers, 2005). This assumption implies that “social constrains” confer fitness advantages by forcing individual to align their asymmetries to those of the others, thus, population-level asymmetry should be particularly apparent in social species, where individuals gain benefits from each other’s proximity. Solitary species, on the other hand, do not need to manifest directional asymmetries, as they would not gain any increment of their fitness by aligning their preference with the rest of the population, since they do not gain advantages from the social life. This hypothesis seems to be supported by a study in which fish individuals of gregarious species were compared with those of solitary species in a detour task, in order to verify whether shoaling in fish is associated with a population bias in turning to one direction, either left or right (Bisazza et al., 2000). In other words, group level alignment of social behaviours might not only favoured the dilution effect, but might help conspecifics in their communication, by facilitating the recognition of signals for the prediction of behavioural responses. A similar study about social laterality in non-human primate solitary species, such as orang-utans (*Pongo* sp.) or lesser bushbaby (*Galago* sp.), could be helpful in revealing whether social constrains favour lateralization of social behaviours at the population-level.

Chapter 7

Experiments on lateralized behaviours in typical children

Handedness based on object animacy

7.1 Experiment 5

7.1.1 INTRODUCTION

The aim of this experiment was to extend the investigation about handedness based on the type of the target also to humans. In particular, we considered a group of typical children aged 3-4 years old. Typical pre-school children might represent good candidates to investigate the development of the influenced of target animacy on the preferential use of hands, as at this age the degree of handedness should be stable. According to Fagard and Marks (2000) handedness becomes steadily observable in the first bimanual skills at around one year of age. Although some aspects of handedness might become stabilized after the age of three years (Annett, 1970; Ingram, 1975), the degree of hand preference, either toward the right or the left, keeps increasing during early childhood (McManus et al., 1988). Furthermore, comparative developmental studies have been recently widespread, by comparing non-human primates abilities with those of human infants rather than human adults. Indeed, some researchers suggested that human infants might be cognitively and experimentally comparable with adult great apes (Weiss & Santos, 2006). For example, infants and children do not have a fully functioning linguistic system which might be comparable with those of great apes. In particular, preschool children would be interesting subjects for the investigation of language development, as according to the literature, asymmetrical neurological functions undergo developmental change throughout infancy and childhood (Albanèse, 1985; Wuillemin, Richardson, & Lynch, 1994) and cerebral lateralization seems to be related with the ability of infants and children to perceive and process linguistic patterns of speech. Based on the literature, we would expect for human participants to be (especially since they were already vetted as right-handed by parents and teachers) biased to an overall right hand preference.

The choice of this age-group was also based on the fact that the experimental conditions of this age group are comparable to those of zoo non-human primates. Indeed, compared to adults, children are easier to test for the assessment of both manipulative and social interactions, as plying activities are more likely to elicit manual interactions with animate and inanimate targets. Moreover, the school environment facilitates this kind of study, because different type of activities can be performed with children, without interfering with their spontaneous behaviours.

This study aimed to detect if a hemispheric specialization tied to the animacy of target objects extends to humans, and if so, it might be suggested that this brain/behaviour characteristic trait is not species-specific, but evolved prior to our split from a common human/ape ancestor.

7.1.2 MATERIALS AND METHODS

Subjects and housing

Participants were 10 typical children 3-4 years of age, with a mean age of 47,7 months (*range*: 40,5 – 53,2 months). Four individuals (all males) were participants from the United Kingdom and the data about this group was collected at the "Livingstone Primary School", Barnet, London (UK). The remaining 6 individuals (5 males and 1 female) were from Italy and the data collection was carried out at the "Berto Barbarani" infant school in Verona (Italy). Based on the observations of tool-use and drawing activities, children were pre-classified as right-handed by the teachers. Written consent for child participation was obtained from both parents in order to run the experiment.

The study involving UK subjects was carried out in 2 rooms: The "soft play" room, where children were induced to play freely but without toys, and a classroom where children performed table-time activities and snack time. These two different environments were selected in order to elicit both social and object-related behaviours with equal amount of time.

The study involving Italian subjects was carried out in 3 different rooms: The "lunch room", where the children had lunch or played freely with different types of toys, the "room of hands", where children attended more manipulative activities, such as painting, clay modelling, and so on, and an open space area for recess time. This latter room was formed by two separated sides: One where children could play with toys and with seeds placed in a wooden basin and one for disguising games. Like for the English children, the different experimental locations were selected in order to collect the same amount of time about social and manipulative activities.

Procedure and data coding

For this experiment it was employed the same procedure adopted for chimpanzees (Experiment 1) and gorillas (Experiment 2).

For the English group all video footage was taken between February and May 2009 using two synchronized digital video cameras (Panasonic NVGS11B), in order to capture both the focal individual in full frame and a wide-angle to encompass the subject, conspecifics, and surroundings, such as with gorillas sample (Experiment 2).

For the Italian cohort video registrations were made between May and June 2011 using a single camera, which view was wide enough to include the entire experimental group, in order to collect information about the manual activities during both object manipulation and social interactions. The group was observed during different experimental sessions that varied according to the type of manual activity: *Free play*, in which children could freely use different structural games (e.g. LEGO® constructions, building a toy race track); *painting*, in which subjects were asked to use a paint brush and to draw whatever they preferred; *clay modelling*, in which subjects were asked to model a plasticine-like material into whatever they liked; *disguising*, which consisted in wearing and playing with second-hand dresses; *eating*, in which children used forks, knifes, and spoon to eat their lunch, while interacting with each other; *seeds-playing*, which consisted in manipulating different type of cereal seeds, using also tools such as plastic bottles, funnels, and spades. All these experimental sessions took place within a specific area or room, so that the view of the camera could include almost equally all subjects and to avoid that children with no parents consensus came mistakenly within the view of the camera. Videos were then coded considering from time to time a different focal subject.

The same MDM method used for chimpanzees and gorillas was employed for the data coding of children, considering the same variable. In particular, it was employed

OBSERVERTRON®. Therefore, I collected information about unimanual activities directed toward inanimate and animate targets.

Statistical analyses

To analyse the data set a 2 (left hand, right hand) x 2 (animate target, inanimate target) repeated measures analysis of variance (ANOVA) was used, with paired-sample t-tests for post-hoc analyses. Binomial test was used to assess handedness at the individual level, for both animate and inanimate target. All subject data were based on 90 minutes of observation time. To normalize the weighting that each subject contributed to the data set, proportions for each subject of each response type in relation to the total number of actions for that subject were calculated, as in previous experiments.

7.1.3 RESULTS

Table 9 indicates the frequencies of both left and right unimanual actions towards animate and inanimate target objects.

Table 9

Typical Children Scoring on Unimanual Handedness Based on Target Animacy

Subject	**Left Inanimate**	**Right Inanimate**	**z-score**	**Left Animate**	**Right Animate**	**z-score**	**Total**	**Observation (min)**
TypIT 1	54	151	6,70*	11	6	-0,97	222	90
TypIT 2	80	119	2,69*	10	9	0,00	218	90
TypIT 3	101	100	0,00	8	12	0,67	221	90
TypIT 4	45	177	8,79*	7	9	0,25	238	90
TypIT 5	52	292	12,89*	14	24	1,46	382	90
TypIT 6	43	221	10,89*	18	17	0,00	299	90
TypUK 1	56	180	8,00*	36	25	-1,28	297	90
TypUK 2	53	89	2,94*	24	62	3,99*	228	90
TypUK 3	27	49	2,40*	11	19	1,27	106	90
TypUK 4	11	39	3,81*	5	4	0,00	59	90

The table reports only unimanual events during interactions with inanimate and animate targets

* Significant lateral asymmetry ($p < .05$)

The 2 (left hand, right hand) x 2 (inanimate target, animate target) ANOVA (frequency and proportion) revealed significant interactions of lateralized unimanual actions and target animacy (frequency: $F(1,9) = 10.07$, $p = .0013$; proportion: $F(1,9) = 42.97$, $p < .0001$) (see figure 26).

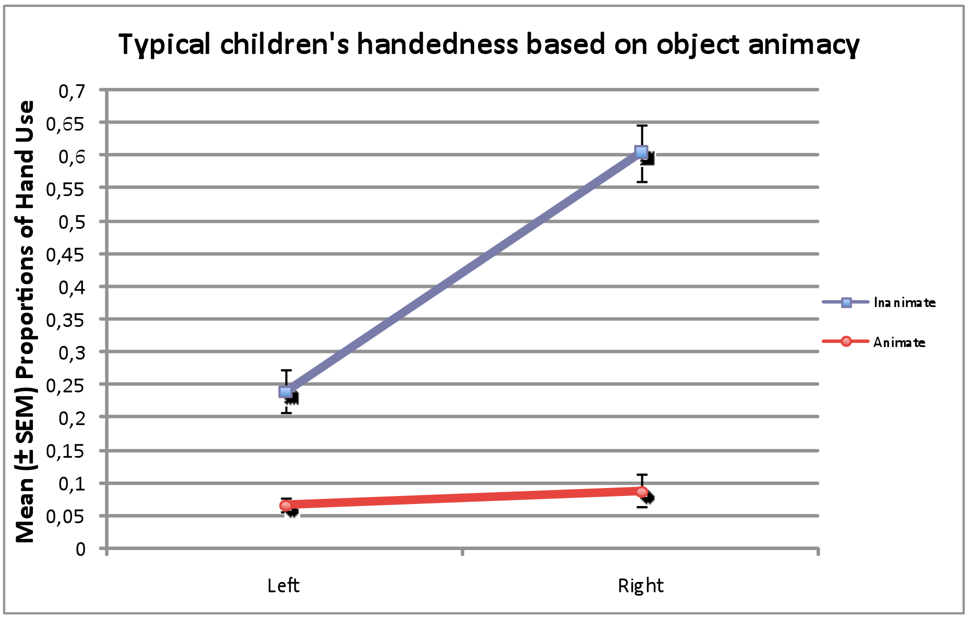


Figure 26. The chart depicts mean values of proportions relative to unimanual activities of left and right hand during contact with inanimate (blue line) and animate (red line) targets.

Main effects of target type (inanimate, animate) demonstrated higher overall amount of actions towards inanimate targets versus actions directed towards animate targets (frequency: F(1,9) = 35.89, p < .0001; proportion: F(1,9) = 137.03, p < .0001). Main effects of hand (left, right) were also identified (frequency: F(1,9) = 12.21, p = .0013; proportion: F(1,9) = 42.97, p < .0001) indicating a higher frequency of right handed actions compared to left handed actions. Post-hoc analyses were conducted using paired-sample t-tests to test the dominance of right-handed actions (frequency: M = 141.70, SE = 24.91; proportion: M = .60, SE = .04) compared with left hand actions (frequency: M = 52.20, SE = 7.92; proportion: M = .24, SE = .03) for inanimate targets only, (frequency: t(9) = -3.605, p = .0057; proportion: t(9) = -5.353, p = .0005), revealing a significant preference in using more frequently the right than the left hand. Right-handed actions (frequency: M = 18.70, SE = 5.33; proportion: M = .09, SE = .02) were also compared with left-handed actions (frequency: M = 14.40, SE = 2.98; proportion: M = .07, SE = .01) for animate targets only (frequency: t(9) = -1.022, p = .333; proportion: t(9) = -1.1067, p = .297) which did not demonstrate a significant difference.

7.1.4 DISCUSSION

The children revealed a significant right-hand preference in interacting with inanimate targets. Moreover, a significant preference in using more the right hand compared to the left upon animate targets was apparent.

These findings are consistent with those of chimpanzees and gorillas regarding the manual actions directed toward inanimate targets, corroborating the hypothesis that the left hemisphere might be dominant for the processing of hierarchical-sequences of motor activities. As Greenfield, (1991) postulated, this type of order-structure process is shared also by a very basic syntax of language, suggesting that language and right-hand preference might have developed through homologous evolutionary processes. Although the findings of this study are not able to make inferences on the causal relationship between the origin of language and hand preference, I offer the hypothesis that the left hemisphere might have been pre-adapted for the processing of ordered-structured activities, and that this ability might have been extended for both motor and language skills.

Furthermore, although pre-school children are still undergoing an increment of the strength of handedness, the degree of the preference should be already stable, as suggested by several authors (Bishop, 1990; Cornish & McManus, 1996; De Agostini et al., 1992; Michel et al., 2002). Thus, the pattern found in 3-4 years old children could be considered a reliable marker for the investigation of handedness based on animacy in humans.

The finding for self-directed behaviours and conspecific-directed manual actions are also consistent with the previous experiments on great ape handedness based on target animacy. Indeed, children showed a equal use of hands during interactions with animate targets, suggesting a greater involvement of the right hemisphere for actions that are supposed to have a relevant emotive purpose, compared to more ordered-structural and manipulative targets with less emotive valence.

These findings are the first to highlight in both human and non-human primates an early categorical neural distinction between objects that require functional manipulation and objects that require social manipulation, or both, which might have emerged prior to the evolutionary split of extant apes and modern humans. Moreover, they suggest that this categorical distinction at the cognitive level is already set at early development of humans, which potentially imply a genetic predisposition of cerebral lateralization for object animacy. Furthermore, the flexible nature of the MDM offers an opportunity to work toward a consistent experimental framework for future studies of naturalistic human and ape behaviour, leading to a better understanding of both the evolution and development of hemispheric specialization.

Lateralization for emotion processing

7.2 Experiment 6

7.2.1 INTRODUCTION

The investigation of developmental cerebral lateralization for the processing of emotions reports inconsistency in the literature about which age it becomes stable in humans and most of the studies are based on the perception of facial expressions. Therefore, the main aim of this experiment was to extend the investigation of lateralized behaviours during social interactions that was previously reported for great apes also to a cohort of 3-4 year-old typical children, in order to verify whether there is continuity between apes and humans in the manifestation of social lateralized behaviours and at which age they through across human development. However, this experiment was a pilot study as observations involved only the Italian group, previously considered for the study of handedness based on object animacy. This is the first study about whether the social context might induce individuals to manifest lateralized behaviours in humans and particularly in children, by adopting a pure observation of spontaneous activities.

7.2.2 MATERIALS AND METHODS

Subjects and housing

Participants were 6 typical children of 3-4 years old of age (average age: ~ 48,7), composed by 5 males and 1 female, which were observed in their native country in a school of Verona (Italy).

Procedure and data coding

For this experiment it was employed the same procedure adopted for chimpanzees (Experiment 3). Video registrations were the same employed for the Italian cohort in the Experiment 5.

Coding categorization was based on the same MDM method of the other experiments, employing OBSERVERTRON®, and the analysis of data considered the same variables of the Experiments 3 and 4..

Statistical analyses

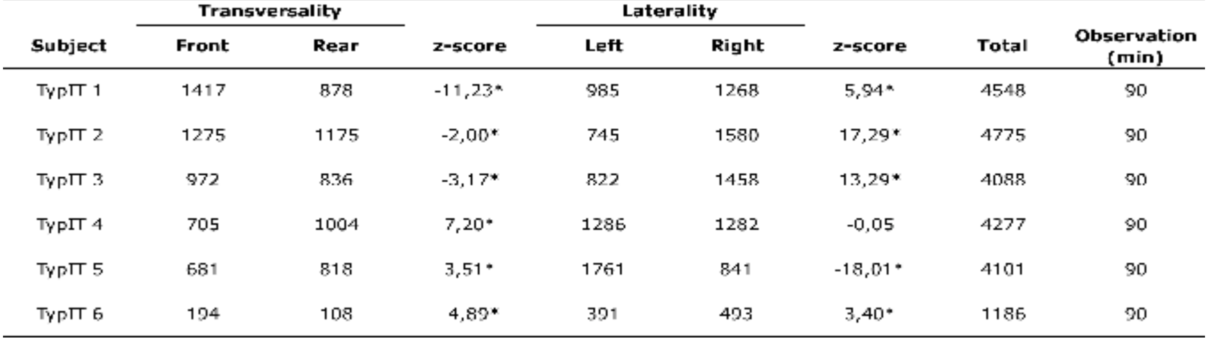
To analyse the data set a paired-sample t-tests was used to assess differences between frontal and rear sides and between left and right sides. The same type of analysis was run using a Wilcoxon test, a more conservative method (McGrew & Marchant, 1997) Moreover, a Friedman test was employed to estimate differences between front, rear, right, and left behavioural categories. Binomial test was used to assess side preference at the individual level, for both transversal and lateral condition. All subject data were based on 90 minutes of observation time and analyses were all based on frequencies. To normalize the weighting that each subject contributed to the data set, proportions for each subject of each response type in relation to the total number of actions for that subject were calculated.

7.2.3 RESULTS

Table 10 indicates the frequencies of transversal (front and rear) and lateral (left and right) side preference during social laterality.

Table 10

Typical Children Scoring on Transversal and Lateral Side Preference during social laterality



	Transversality			Laterality				
Subject	**Front**	**Rear**	**z-score**	**Left**	**Right**	**z-score**	**Total**	**Observation (min)**
TypIT 1	1417	878	-11,23*	985	1268	5,94*	4548	90
TypIT 2	1275	1175	-2,00*	745	1580	17,29*	4775	90
TypIT 3	972	836	-3,17*	822	1458	13,29*	4088	90
TypIT 4	705	1004	7,20*	1286	1282	-0,05	4277	90
TypIT 5	681	818	3,51*	1761	841	-18,01*	4101	90
TypIT 6	194	108	4,89*	391	493	3,40*	1186	90

Side of the focal subject showed to conspecific positioned within 3 meters away are reported in the table.

* Significant transversal or lateral asymmetry (p < .05)

Analyses with paired t-test were conducted to test the transversal condition, in order to verify the dominance of front side preference (frequency: M = 874, SE = 181.97, proportion: M = .218, SE = .025) compared with rear side preference (frequency: M = 803.17, SE = 149.304; proportion: M = .195, SE = .022) (frequency: t(5) = .61, p = .568; proportion: t(5) = .8497, p = . 434), which did not show any significant difference (see figure 27).

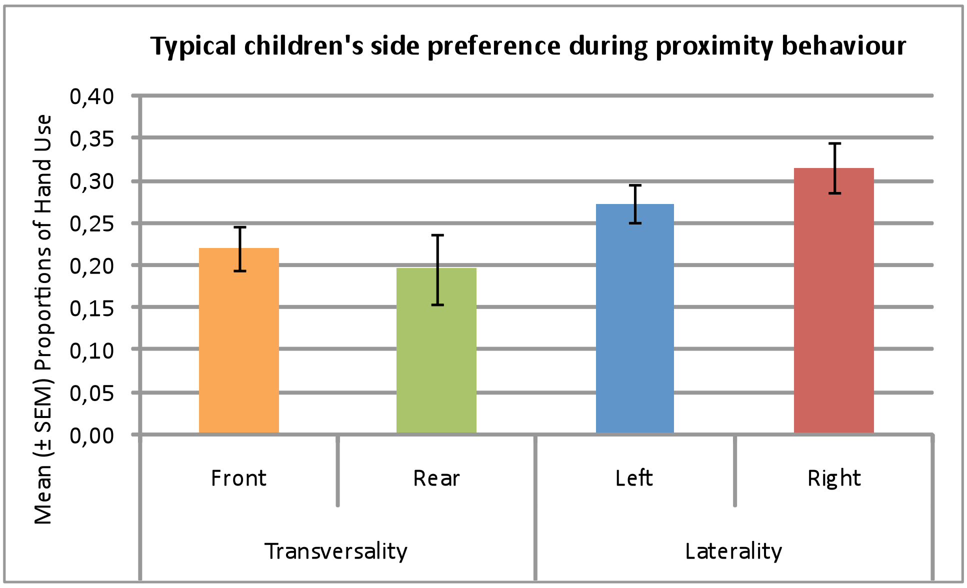


Figure 27. The chart depicts mean values of proportions relative to transversal (front and rear) and lateral (left and right) side preference during social laterality.

I also analysed the lateral condition, by comparing the dominance of right side preference (frequency: M = 1153.67, SE = 167.149; proportion: M = .314, SE = .029) with left side preference (frequency: M = 998.33, SE = 193.969; proportion: M = .272, SE = .041) (frequency: t(5) = .618, p = .563; proportion: t(5) = .713, p = .507), which also did not show a significant difference (see figure 27). Given the small sample size, a more conservative analysis was applied, thus Wilcoxon test was used to verify if there were significant differences in the transversal (frequency: Z = -.314, p = .753; proportion: Z = -.734, p = .463) and lateral conditions (frequency: Z = -.734, p = .463; proportion: Z = -.734, p = .463), both of which did not reveal any significant bias. Friedman test did not reveal significant differences between behavioural categories (frequency: χ^2 = 6.2, p = .102; proportion: χ^2 = 6.2, p = .102).

7.2.4 DISCUSSION

This study revealed that 3-4 years old typical children did not manifest any significant preference in keeping conspecifics either in the transversal (front or rear) and lateral (left or right) conditions.

The result of this experiment appears to be inconsistent with findings about chimpanzees and gorillas' side preference during social laterality. This discrepancy might be tied to the fact that pre-school children are still developing cerebral lateralization for emotion processing (Best & Queen, 1989). Indeed, studies reported in literature seem to be agree that although morphological and behavioural asymmetries may be present *ab initio* in newborn children (Grabowska et al., 1994), a strengthen of cerebral lateralization occurs across ontogenesis (Corballis and Morgan, 1978), which becomes fully established at adolescence (Miller & Turner, 1973). Furthermore, there is evidence that social environment strongly influences the elaboration and perception of emotion during infant and child's development especially at the cognitive level (Bard et al., 2004). For example, Trevarthen (1996), claimed that emotional dysfunctions can arise in children as a consequence of negative emotional experience with parents. Therefore, the manifestation and the degree of cerebral lateralization might strongly depend on environmental forces (Watling & Bourne, 2007).

This is the first study that assesses cerebral lateralization for emotion processing by observing whether children manifest lateralized behaviours during social interactions. To date, the investigation of developmental hemispheric specialization has been mainly focussed on hand preference and perceptual functions, such as the lateralized discernment of facial expressions. The small sample size of the current experiment might not have helped to reveal a real pattern, thus it is difficult to speculate about neural mechanisms underpinning lateralized behaviours related to emotional processing and a larger sample size might provide more interesting results about lateralized behaviours. Moreover, comparative studies across different ages might reveal how the degree of cerebral lateralization increases with the maturation of the individual and might also allow to make clearer inferences concerning at which age cerebral lateralization for the processing of emotions becomes stable.

Chapter 8

General discussion

Six experiments considered whether human and non-human primates manifest lateralized behaviours, which can be considered as a marker of cerebral lateralization for both language and emotional functions, employing a quantitative MDM, in order to compare results across species based on the same experimental conditions and to make inferences about the evolutionary aspects of the hemispheric specialization.

The main findings were related to a preferential use of hand during the interactions with either inanimate or animate objects and to the preferential body positioning with respect to the surrounding social environment during manual activities. The two groups of semi-captive non-human primates, nine chimpanzees and twelve lowland gorillas, exhibited a significant preference in using the right hand to interact with inanimate targets (i.e. objects and environmental items) and an equal use of hands upon animate targets (i.e. social partners and the self). Additionally, both groups of great apes overall showed to preferentially keep conspecific that were less than 3 metres far away to the front side of the body, during manual activities. Furthermore, when conspecifics were positioned either on the right or on the left side of the focal subject, both groups manifested a preference in keeping social partners on the left side, except for the gorilla alpha male, which showed a significant opposite pattern.

The same analyses were carried out in a group of ten typical children, aged around 3-4 years of age, who showed a significant preference in using the right hand upon inanimate targets and an equal use of hands upon animate targets. A pilot study on six subjects revealed significant preference in keeping social partners neither in the transversal condition (front or rear) nor in the lateral condition (left or right).

Results about lateralized behaviours in both human and non-human primates will be discussed in light of current evolutionary theories regarding the origins and the selective adaptation of cerebral lateralization.

8.1 Handedness based on object animacy

The results found in chimpanzees and gorillas suggest a hemispheric specialization for categorical meaning underpinning motor behaviours. Specifically, the significant unimanual right hand preference in interacting with inanimate targets found in both species might be related to a left hemisphere specialization for language processing, as both manipulative and linguistic activities are supposed to relay on hierarchical order-structured processes, in which specific events or unit constructions should follow a well-defined arrangement in order to achieve a goal (Biederman, 1987). In other words, as well as object manipulation is based on specific sequences of motor actions, a proto-syntax or a simple language grammar relays on simple units that have to be organized together in a specific order to construct a communicative sentence (Greenfield, 1991).

The two groups of great apes manifested also an equal use of hands upon animate targets, which, compared to the situation in which manual actions are directed toward inanimate targets, predicts a more contribution of the right hemisphere. Among scientists there is large agreement that the right hemisphere is specialized for the processing of emotive stimuli (Borod et al., 1998; Campbell, 1982). Thus, the greater employment of the left hand/right hemisphere upon animate than inanimate targets might be related to the emotive valence of manual actions. Indeed, interactions with conspecifics are likely to be linked to an emotional status, as well as self directed behaviours, which in most of the cases reflect a stressful condition (Leavens et al., 2004; Maestripieri et al., 1992). However, social contacts could also cover a structural and manipulative purpose. For example, grooming is considered one of the major social activities among primates (Dunbar, 2010), which apart of an hygienic function , it is supposed to play a bonding role (Dunbar, 2010). Nevertheless, this activity is highly manipulative and may require particularly fine and accurate finger activity, which needs to be performed through sequential and order-structured actions, in order to properly manage the interaction with the recipient or to fulfil a own physical necessity. Therefore, it is not excluded an involvement of the right hand/left hemisphere during a social physical interaction.

Historically, handedness was considered a prerogative of humans (Calvin, 1982; Frost, 1980; Steklis & Harnad, 1976). Although more recent studies have reported handedness also in non-human primates (for a review see Hopkins, 2006), there is still inconsistency on whether great apes manifest a population-level handedness and the methodological diversity between experiments does not help to compare the different results and to trace a definitive conclusion. It has been recently claimed that the degree of manifestation of handedness in non-human primates is task-dependent and it is particularly elicited during complex manual tasks, such as bimanual feeding, coordinated bimanual actions, bipedal reaching, and throwing (Hopkins 2006). Moreover, recent findings have demonstrated that similar conditions are applicable also to human handedness, as the high percentage of right-handers within the population is generated from tasks related to object manipulation and tool use (Annett, 2002), while non-object related tasks seem to decrease the degree of right hand use (e.g. Dimond & Harris, 1984). The current study is in line with most of the findings reporting variability of the strength of hand preference related to the type of the task in non-human primates. However, it seems to highlight that complex manual activities might not represent a necessary condition for the manifestation of handedness, especially at the population-level, but a simple distinction of object animacy could be sufficient to elicit a manual preference.

This is not the first study reporting an influence of target animacy on great apes' handedness. Indeed, Aruguete and collaborators (1992) found similar results in a group of captive zoo chimpanzees. However, results were not discussed in light of evolutionary implication of the cerebral lateralization for language abilities and the processing of emotions.

The investigation of handedness based on object animacy involved also a group of 3-4-year-old typical children. The study about children allows understanding the nurture and nature of particular human behaviours (Bard, 2008) and consents to make more reliable comparisons between human and non-human primates. Indeed, it has been argued that non-human primates, such as great apes, share more cognitive abilities with infants than with adult humans (Bard et al., 2004). Moreover, children and apes can be observable in similar environments. For example, pre-school children have many possibilities to manifest social interactions with both relatives and non-relatives and, due to their predisposition to exploration, they are more likely to manipulate different kind of objects, compared to adults. The studies on handedness development, however, have been mainly carried out with questionnaires addressed to the parents or through the observation of simple manipulative activities. Therefore, the current study tried to assess handedness in pre-school children by observing spontaneous activities in a social environment with the employment of a quantitative method, previously used for great apes' observations, in order to detect lateralized behaviours and make comparisons between human and non-human primates. Specifically, not all the lateralized manual activities were considered, but only unimanual actions directed toward either inanimate or animate objects, in order to verify whether different neural mechanism may underlie lateralized behaviours. The significant right bias for manual actions directed toward inanimate targets in the children of this study seems to confirm the assumption that there is a causal relationship between the specialization of the left hemisphere for language functions and right handedness for object interaction and manipulation processes (Greenfield, 1991).

The results of this study support the evidence that a stable handedness for object manipulation seems to be already observable in pre-school children of 3-4 years of age, as previously reported in literature (Fagard & Marks, 2000). Moreover, it might be argued that the animacy of the objects influences the preferential use of hands in children, which is supposed to be underpinned by an hemispheric specialization for categorical meaning and for hierarchically order-structured activities, such as language and tool use.

The comparative nature of this study highlights the consistency of pattern in both great apes and humans. Therefore, the findings strongly suggest a continuity in the evolution of hemispheric specialization for object animacy, which might have been emerged before hominids split from great apes. Most important, the results of this study seem to support the evolutionary validity of the tool theory (Byrne & Byrne, 1993; Corballis, 2002; Greenfield, 1991; Mercader et al., 2007), thus the hypothesis of a causal relationship between left-hemispheric specialization for language functions and right-handedness. Indeed, this association might have derived from early human experiences with tool-use, underpinned by the left-hemisphere neural circuitry that was specifically selected for orchestring hierarchical sequences of events. The relationship between tool use and language functions has been demonstrated also through fMRI studies, in which an overlap of activity between the two different skills was detected within the Brodmann area 44 (Broca' area), in both human (Higuchi et al., 2009) and non-human primates (Nelissen et al., 2005; Obayashi et al., 2001). Therefore, tool use might have played a causal role in the evolution of gestural communication (Bradshaw & Nettleton, 1982; Gibson, 1993), which also relies on ordered-structured processes by involving skilled serial motor activities, such as the movements of arms, hands and fingers (Frost, 1980). The emergence of modern speech might have been a consequence of the co-evolution for the selective advantages to communicate with vocalization, the changes in the vocal tract and the predisposition of the left hemisphere for motor skilled actions. Indeed, speech is produced by the movements of the tongue, lips, and vocal chords, which require precisely timed and sequenced actions to convey communication (Frost, 1980). The findings of this study also suggest that the emergence of a neural categorical differentiation might have played a causal role in the evolution of language abilities and consequently have shaped the manifestation of right-handedness for tool use and gestural communication.

This study provides further evidence that handedness and cerebral lateralization should not be considered unique hallmarks of human beings, but they could have evolved from our closest ancestors and even earlier in lower vertebrates (Bisazza, Rogers, & Vallortigara, 1998; Vallortigara & Rogers, 2005; Vallortigara et al., 1999). Moreover, although language skills develop throughout childhood until adult age, there seems to be evidence of a left hemispheric specialization for language at childhood (Albanèse, 1985; Wuillemin et al., 1994) and the results of this study about handedness appear to corroborate these assumptions.

8.2 Social laterality and hemispheric specialization for the processing of emotions

Compared to language lateralization, hemispheric specialization for emotions in both human and non-human primates has been less investigated. Nevertheless, different species of vertebrates, including non-human primates, manifest lateralized perceptive and motor behaviours that are particularly relevant during arousing situations, suggesting an evolutionary origin for hemispheric specialization underpinning the processing of emotions (for a review see Wallez & Vauclair, 2011). The majority of experiments carried out in non-human primates have mainly focussed on the perception of facial expressions (Fernández-Carriba et al., 2002; Hauser, 1993; Hook-Costigan & Rogers, 1998; Wellez & Vauclair, 2011), reporting a greater expressivity in the left than the right side of the face or a better perception of expressions with the left than the right visual field. These findings are in line with similar human studies (humans: Aljuhanay et al., 2010; Gilbert & Bakan, 2002; Lane et al., 1995), suggesting a major involvement of the right hemisphere. Only few studies have investigated the role played by handedness during activities with an emotional valence and within this context the left hand seems to be more employed than the right hand for face or body touching in human (Dimond & Harries, 1984) and non-human primates (Dimond & Harries, 1984; Leavens et al., 2001; Rogers & Kaplan, 1995). To date, only two studies assessed hemispheric specialization for emotion by observing lateralized behaviours in a social environment, but only in monkey species (mangabeys: Baraud et al., 2009; gelada baboons: Casperd & Dunbar, 1996). Although a significant preference have been reported in approaching the left side of conspecifics, the study of Baraud and colleagues (2009) seems not to go any further from the investigation of asymmetrical facial expressions. Indeed the results have been discussed in light of the existing assumptions that the left-side of the face is more expressive than the right side (Campbell, 1978; Gilbert & Bakan, 2002; Lane et al., 1995). Thus individuals prefer to approach their conspecific to the side that at the best manifests an emotional status, in order to predict the recipient's behaviour as fast as possible (Baraud et al., 2009).

Although the current study reflects the investigation of Baraud and collaborators' (2009) experiment, the interest was addressed to the focal subject, by observing which side of the body he/she preferred to show to the closest conspecifics (less than 3 metres away) during manual activities. Besides an overall preference in keeping conspecifics frontally, the analysis of the lateral condition revealed a significant left side preference in both chimpanzees and gorillas, which suggests a more involvement of the right hemisphere compared to the left one during interactions with social partners. Although a physical contact may not occur between two or more conspecifics, the social environment can influence the behaviour of the single individuals any time. As Barresi & Moore (1996) pointed out, social individuals spend most of their time trying to understand and interpret the other's behaviour, in order to facilitate social communication and social coherence (de Vignemont & Singer, 2006) and to avoid deleterious physical confrontations. Keeping conspecifics in the left side allows to expose the more expressive side of the face, the left one (Fernández-Carriba et al., 2002; Hook-Costigan & Rogers, 1998; Wallez & Vauclair, 2011), so that approaching individuals can have a better perception of the approached individual's intentions (Casperd & Dunbar, 1996), which is line with what Baraud et al. (2009) have proposed. Additionally, human studies have revealed a lower threshold of the left side of the body in perceiving pain in right-handed subjects (Göbel & Westphal, 1987) and a recent fMRI study demonstrated that the right hemisphere seems to be dominant in pain perception (Symonds, Gordon, Bixby & Mande, 2006). In particular, authors found a major involvement of specific areas within the right hemisphere, whose activation resulted to be more intense during pain stimulation, compared to the same areas housed within the left hemisphere, such as the anterior cingulate, the middle frontal gyrus, the medial and superior frontal gyri, and regions in the inferior frontal gyrus and inferior parietal lobule (Symonds et al., 2006). Furthermore, since the right hemisphere is specialized activating during emergency situations (MacNeilage et al., 2009), the left side of the body is supposed to be more reactive compared to the right side. According to these assumptions, thus, the left hand and probably the left side of the body are more sensitive to physical interactions, either positive or negative, and are more likely to be exposed to the social environment, in order to have a better perception of what happens around and to react as fast as possible towards stimuli.

A similar left lateralization during social interactions have been reported in other vertebrate species, such as toads (Robins et al., 1998), lizards (Deckel, 1995), domestic chicks (Rogers, Zappia, & Bullock, 1985), and also in other non-human primates species (Casperd & Dunbar, 1996), suggesting that such lateralized behaviours may have an homologous origin (Robins et al., 1998). Therefore, the findings reported in chimpanzees and gorillas for social laterality in this study seem to further give support for a right hemisphere dominance for the processing of emotions, which have been selected prior to human evolution. Moreover, this hypothesis seems to be further supported by the consistency of the equal use of hands during self-directed behaviours and contacts with social partners in chimpanzees, gorillas, and typical children, as the left hand/ right hemisphere is more involved than the right hand/left hemisphere during manual actions that are supposed to have an emotive purpose (e.g. self-touching, social grooming, etc.), compared to manual actions that have a more functional and structural purpose (e.g. too-use, object manipulation, etc.).

One interesting finding that emerged from the analysis of social laterality in the group of gorillas was the significant preference of the alpha male in keeping conspecifics in his right side. This outcome might be interpreted in relation to both social and survival aspects.

Indeed, considering that gorilla groups are formed by one alpha male, several adult females, and juveniles (Doran & McNeilage, 1997), male subjects might have evolved different strategies that have influenced their lateralized social behaviours, which could be related not only to their dominant role, but also to the fact that have to interact with females for copulation. Indeed, compared to females, males are supposed to be more prone to perform approaching behaviours, manifesting a more risky attitude both toward group members or other competing males that may attempt to conquer the harem. The *motivational withdrawal hypothesis* (Demaree et al., 2005) seems to represent a plausible explanation for the evidence of an asymmetrical opposite pattern between sexes. The theory states that the right hemisphere is dominant for the processing of negative emotions and drives individuals away from stimuli of the environment (i.e. withdrawal motor responses), while the left hemisphere directs behavioural responses toward stimuli (i.e. approaching motor responses) (Demaree et al., 2005). As a result, the right part of the body should be more involved during responses of avoidance and the left side during approaching behaviours. I offer the hypothesis that females prefer to keep conspecifics to their left in order to expose the more reactive side to perform avoiding behaviours as they are supposed to protect themselves from the attacks of other group members, whereas male prefer to expose the right side, in order to be more reactive during approaching behaviours, especially to succeed in copulation and in defending the harem from external attacks. Therefore, the result found in the gorilla male suggests that hemispheric specialization for the elaboration of emotions might depend on the predisposition of the individuals to approach or withdraw an external stimuli, that could have been pre-determined as a evolutionary selective value. Indeed, this kind of differentiation in the processing of emotions at the hemispheric-level might be particularly evident between sexes or across the social ranks, in which high-social rank individuals (e.g. males in patriarchal societies and females in matriarchal societies) are supposed to be more prone to approach stimuli and thus to manifest motor right side biases, compared to low-social rank individuals that tend to manifest preservative behaviours and thus left-side biases. The same sex differences in the manifestation of lateralized behaviours influenced by the social environment have not been found in chimpanzees, probably due to the fact that at the time of data capture there was not a stable alpha male. Additionally, the social system of chimpanzees is different from that of gorillas, the former based on a multi-male and multi-female society (Goldberg & Wrangham, 1997). The differences in the raring-history between the two groups might also represent another possible explanation.

Overall, the findings related to social laterality in great apes seem to discard neither the right hemisphere nor the valence hypothesis for the processing of emotions. Although the right hemisphere might be more dominant than the left one in the processing both positive and negative emotions, there is a tendency of manifesting different lateralized behaviours in accordance with the social circumstances, which might be actually evident at the individual level and according to some particular conditions, such as the different social rank. Therefore, as Davidson, Ekman, Saron, Senulis, and Friesen (1990) suggested, originally hemispheric specialization might not have been based on a emotional valence (positive, negative), but rather on whether the emotion requires the individual to approach or avoid an external stimulus. This type of asymmetry has a more adaptive value and might not necessary involve only affective lateralized functions, but also non-affective ones, such as simple reflexive and automatic responses (Rutherford & Lindell, 2011). Then with the appearance of more complex social dynamics in humans, these behaviours might have been interpreted as a different perception of expression of emotional valence. I would suggest that sex differentiation of social lateralization behaviours deserves more attention and further studies on other groups of semi-free ranging gorillas might be useful to confirm or reject this hypothesis. Therefore, more data collection needs to be carried out.

The investigation of social laterality in the group of 3-4-year-old typical children revealed significant preference in keeping conspecifics either during frontal (front/rear) and lateral (left/right) conditions only at the individual level, while no group-level bias was detected. This finding might lead to the conclusion that there seems not be evidence of a population-level cerebral lateralization for behaviours related to the social environment in humans. However, two alternative hypotheses might explain this outcome. First, emotions are strongly dependent on social environment (Watling & Bourne, 2007), and since 3-4 year-old children are still learning how to emotionally relate with other social individuals, cerebral lateralization might not have been yet completed for the processing of emotions (Watling & Bourne, 2007). Therefore, children might show a bilateral processing of emotional-like contents as a strengthening of cerebral lateralization is expected to occur during ontogeny (Corballis and Morgan, 1978) until it becomes fully established at adolescence (Miller & Turner, 1973). Second, given the complexity of emotion processing in humans, a simple right hemisphere model could not fit the cerebral lateralization of humans to explain the manifestation of social lateralized behaviours, especially in children. Some researchers tried to apply the motivational withdrawing model also to humans, especially in the field of psychopathology, such as during the manifestation of anxiety, and it was first labelled as *reinforcement sensitivity theory* (RST) (see Rutherford & Lindell, 2011). According to this paradigm, two behavioural manifestations can be distinguished: responses to conditional reward, that guide the individual toward stimuli, and responses to conditioned punishment, that guide the individual away from stimuli. Although Sutton & Davidson (1997) demonstrated high EEG activity in the right and the left hemisphere during the manifestation of withdrawing and approaching behaviours, respectively, subsequent researchers were not able to replicate the results concerning the higher EEG activity in the right hemisphere during the manifestation of approaching behaviours (Coan & Allen, 2003), suggesting that the cerebral lateralization for withdrawing behaviour might be more complicated to define compared to approaching behaviours (Coan & Allen, 2004). Therefore, it has been suggested that the motivational approach-withdrawal model is not fully applicable to human cerebral lateralization for the processing of emotions, as a more complicated system might underlie its neural processes. According to Lang, Bradley, and Cuthbert (1990), the emotionality of behavioural responses is determined by the valence factor, which determines approaching or withdrawing responses and also by the arousal factor, which determines the intensity of responses. Therefore, humans' behaviours during affective circumstance might depend not only on a reflexive response towards a stimulus, but also on the emotional valence of the contex and the valence model might be suitable to explain the complexity of lateralized behavioural manifestations in humans.

The study on children's social laterality showed an individual-level lateralization in keeping conspecifics either in the left or in the right side of hemispace and this might be due to the fact that each child can manifest a personal preference in positioning towards conspecifics, which depends on their own attitude or on personal experience with the social environment. Indeed, Trevarthen (1996) suggested that emotional dysfunctions affecting parents can seriously influence the emotional expression of their children. For example, some individuals can manifest a more risky attitude and thus be more prone to approach social stimuli, whereas others might tend to be more cautious and avoid stimuli, as a consequence of a bad experience, such as a shock.

It seems fair to highlight that the small sample size might have not allowed to obtain a clear statistical analysis at the group-level (Hopkins & Cantalupo, 2005), although five out of six children (4 were significant) manifested a preference in keeping conspecifics in their right side, which might suggest a tendency to manifest an approaching attitude, probably because at this age children are particularly prone to explore different social relations, not only to increase the cognitive information about emotional processing, but also because social confrontations are more likely to establish the rank position within the group.

Although this kind of study might be considered an alternative way to investigate social laterality in both human and non-human primates in a natural environment, more data is needed in order to increase the sample size and the statistical power of the analysis and to shed light on the evolution, development and origins of cerebral lateralization for the processing of emotions.

8.3 Advanced behavioural studies and the validity of a MDM

With the advancement of our understanding of brain function and organization, we can nowadays make predictions about brain lateralization based on observations of naturalistic behaviour. Although Altman (1974) had very good ideas about focal sampling back in the 1970s, she did not have the technology to take, code and store video footage like we do today. Therefore, the history of naturalistic behavioural observation has primarily been of a qualitative nature. While qualitative studies have had their benefits, we can now conduct empirical studies of naturalistic behaviour from a quantitative perspective. New methods are now emerging and the studies of the current dissertation have adopted and adapted the MDM to investigate the naturalistic behaviours of great apes and human children. Indeed, this method can help to code behaviours of individuals in their naturalistic setting. Moreover, the methodology is not exclusive to primate populations and could be flexibly adapted to any species of animals, both human and non-humans one, and therefore strengthens the method as a tool for comparative studies of naturalistic behaviour. The MDM also allows investigating different type of behaviours, in order to infer underling cognitive processes without invasive methods. Furthermore, the possibility of off-line coding makes this method powerful, as more activities related to both the different part of the body of the individual and to the social environment can be collected in a single frame, allowing to produce a large data sets so that many different types of analyses and comparisons can be conducted.

8.4 Conclusion

The results of the studies concerning handedness based on object animacy show strong consistency in human and non-human primates in using the right hand upon inanimate targets, suggesting a causal relationship between left hemisphere language centres and right-handedness, as well as an early cerebral specialization for categorical meaning that emerged prior to human evolution. In particular, the finding appears to support the tool-use hypothesis (Byrne & Byrne, 1993; Corballis, 2002; Greenfield, 1991; Mercader et al., 2007), according to which a co-evolution of handedness for tool-use and language activities might have occurred, as both rely on hierarchical order-structured activities. Having replicated these findings in two species of great apes and in human children, it is conceivable to speculate that sequences of actions to reach a goal could be described as a very basic syntax or a proto-syntax and that these types of activity might have paved the way for the evolution and the development of language skills. Therefore, the neural circuitry that drives grammatical structure might not be unique to humans, but was rather inherited from an evolutionary ancestor common to both great apes and humans.

Both great ape species manifested a preference in keeping conspecific in their left side and this finding suggests a more involvement of the right hemisphere compared with the left one in processing lateralized behaviours that are influenced by the social context. This result is further supported by the mix-handed finding during contact with animate targets, suggesting a right-hemisphere specialization for the processing of emotions (Borod, 1993; Borod et al., 1998; Campbell, 1982). Since other vertebrate species have been shown to manifest a similar lateralization during social interactions (Casperd & Dunbar, 1996; Deckel, 1995; Robins et al., 1998; Rogers et al., 1985) there seems to be agreement in the literature about an evolutionary adaptive value of the right-hemisphere specialization for the controlling of lateralized behaviours during affecting situations (Robins et al., 1998). However, more data would be useful to investigate whether hemispheric specialization for emotion processing might also involve the left hemisphere during particularly contexts or according to the individual predisposition to approach or withdraw external stimuli (Demaree et al., 2005). Moreover, more data is necessary to shed light on the emergence of hemispheric specialization for emotional contents in human development, as preschool-children seem to still be affected by the experience, which apparently plays a key role in shaping cerebral lateralization for processes related to emotions.

Although this is not the first study that raises methodological issues, it is conceivable to highlight the need for a consistent investigative framework under which to assess a comprehensive range of behaviours, in order to better understand the neural regions that dive specific types of lateralized actions. In this context, the MDM represents one plausible methodological tool to approach a behavioural observation from a bottom-up perspective comparison both within and between species and within their natural environment.

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