Hand preferences in bonobos (*Pan paniscus*) for a variety of actions: spontaneous daily actions (non-social and social), bimanual coordination ("tube task"), tool-use ("termite fishing") and induced gestures (begging)

By

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Abstract

The present database on hand preferences in non-human primates provides inconsistent and inconclusive findings and is plagued by important methodological issues (e.g. small samples, inappropriate measures, comparability issues). In this thesis, I studied hand preferences in bonobos (*Pan paniscus*). This species exhibits outstanding features that make it an invaluable model for investigating the evolution of human brain lateralization and handedness. The previous data on laterality in bonobos are scarce and they are from small samples and for relatively simple tasks. I conducted a comprehensive study that was based on a large sample and a variety of actions. I studied a sample of 94 bonobos (40% of the worldwide captive population) from four different populations (three European zoos and one sanctuary in DR Congo). I examined a wide range of actions, ranging simple tasks to very complex tasks, and including both spontaneous actions and experimentally induced actions. Based on previous research and gaps in the database, the following four studies were conducted:

1 - Study of hand use for spontaneous actions (non-social): The bonobos were observed during their spontaneous daily activities. I recorded hand use for 140 behaviours. I investigated the effects of several variables, including posture, activity of the other hand and grip type.

2 - Study of hand use for manipulation and bimanual coordination: The bonobos were tested with the “tube task”, which is a complex task that requires a manipulative bimanual coordinated precise action: one hand extracts food from a tube that is held by the other hand.

3 - Study of hand use for tool-use: I recorded hand use for spontaneous tool-use actions and for an enrichment task that requires using a stick as a probe to extract food from holes (artificial “termite fishing” task).

4 - Study of hand use for social actions and gestures in different contexts: a). I studied the behaviours that occurred spontaneously during the social interactions (intra-specific) and during the interactions with humans (inter-specific). b). I also assessed hand preference for induced inter-specific gestures in an experiment that involved begging towards a human observer.

The results show significant laterality in almost all of the actions studied, indicating that the bonobos exhibit manual laterality. The preferences were present on an individual basis, with similar numbers of right-handed and left-handed subjects. There was no group-level bias, for any of the actions studied. I tested the effect of factors that have been proposed or shown to influence laterality, including: external factors (e.g. living conditions, rearing history, experimental design) and internal factors (e.g. sex, age). I found no significant effect of the settings, rearing history, sex and age. However, there was an effect of age in one case: in study 2, adults were more right-handed than younger subjects. I investigated the effects of task-related factors that may influence laterality; and that have been proposed as selective pressures for the emergence of human handedness. The results indicate that laterality was influenced by: postural demands (posture, activity of the other hand); precision of the action; grip type; manipulation; bimanual coordination; tool-use; throwing and gestural communication. Notably, the laterality was very marked for the “tube task”, the “termite fishing” task and the begging experiment, which suggests that the factors involved in these tasks could be important factors regarding laterality.

Key words: Bonobos. *Pan paniscus*. Laterality. Brain lateralization. Handedness. Evolution. Hand preference. Primates.

Glossary

The words defined in this glossary are “**in bold**” in text on their first occurrence

- ABSHI: ABSHI is the absolute value of HI. It gives information about the strength of preference, from 0.0 to 1.0. see methods section p. 111.

- Behaviour: A behaviour is an action, for instance : “feeding”.

- Behavioural pattern: Behavioural patterns are the behaviours split according to the posture and action of the other hand, for instance : “feeding while seated with the other hand holding a food item”.

- Bout: A bout is the unit of measurement that is used in this thesis to ensure data independence. One bout is either one event (response/trial), or one sequence of identical events. For instance, we count only one bout if the subject dips the right hand into the tube ten times without any intervening action that breaks the sequence (e.g. dropping the tube). see methods section p.95 and p.118.

- Bout length: A bout can be an event or a sequence of identical events, and the length of a bout is the number of events in the bout. For instance the bout length is ten if the bout includes ten identical events that occurr in a sequence. see methods section p.95 and p.118.

- Complexity: This term refers to the degree of complexity of the task. Task complexity is a general term that can include and combine different factors. For instance, a task can be complex because it is novel, or because it requires a precise fine action, complex balance control, manipulation, several stages, several elements to be combined or involvement of the two hands (in different or coordinated complementary roles). There is no definition for task complexity, but it is generally admitted that a complex task is a task that is demanding and involves high cognitive skills. see p. 19.

- Frequency: Frequency is the unit of measurement that is used in study 2 and study 3 for comparison with bouts. One frequency data point is one event (response/trial). The event could be isolated or included in a sequence. Namely, we count ten right hand responses if the subject dips the right hand into the tube ten times in a sequence. see methods section p.95 and p.118.

- Group-level laterality (group-level bias): Laterality is said to be present at the group-level when the majority of individuals display the same preference, i.e. when the numbers of right-handers and left-handers are significantly different.

- Hand performance: The term “hand performance” is used to refer to the efficiency of the hand. Studying hand performance means comparing the efficiency of the two hands of the individual for performing a task.

- Hand preference: Hand preference occurs when the individual uses one hand significantly more than the other hand.

- Handedness: I chose to use this term only to refer to the pattern of laterality that is observed in humans (defined p. 11). Be aware that several other researchers apply this term to the laterality that is observed in non-human primates as well.

- HI: HI gives the direction of preference from -1.0 to +1.0. Negative values indicate a left hand bias and positive values indicate a right hand bias. This index is informative of hand use and does not tell whether the subject is lateralized or not. see methods section p. 111.

- Individual-level preference / individual-level laterality: Preferences are said to be present at the individual-level when the individuals exhibit significant preferences; but the numbers of right-handers and left-handers in the group are similar (i.e. no group-level bias).

- Laterality: “Laterality” refers to asymmetries in the behaviour, i.e. the preferential use of one side of the body over the other. When I use the term “manual laterality”, I refer to hand preferences. When I say “there is evidence of manual laterality” it means that there is evidence of significant hand preferences (whether they are present in a minority or majority of individuals, and whether they are present at the individual-level or group-level is not considered).

- Lateralization: “Lateralization” refers to functional asymmetries of the cerebral hemispheres.

- Precision: I use the term precision to refer to actions that require precise fine movements.

- Total: “total” in tables means “total number of responses per subject: right hand responses + left hand responses”. This is analyzed as the “number of data points per subject”.

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Section I :

Introduction

Chapter 1: Handedness in humans

The research work presented in this thesis investigates **hand preference** in bonobos, which is a species of great interest as such, and with regard to the issue of the evolution of **handedness**. The term “right-handedness” refers to the pattern of **laterality** observed in humans and described as follows.

In humans, about 90% of individuals preferentially use the right hand for complex actions (Annett 1985; Fagard 2004; Faurie 2004; Faurie and Raymond 2004). The proportion of left-handers is around 10%. The number of ambidextrous is extremely small and laterality is present in almost all individuals (Annett 1985; Fagard 2004; Faurie 2004; Faurie and Raymond 2004; Vuoksimaa et al. 2009). This right-handedness is present in all human cultures, all over the world (Faurie 2004; Raymond and Pontier 2004). Indeed, the 90% proportion of right-handers is relatively constant between populations and cultures. There is some cultural variation, with extreme reported values of 73 and 100% (Faurie and Raymond 2005), but everywhere right-handers represent the great majority of the population (Coren and Porac 1977; Fagard 2004; Faurie 2004; Faurie and Raymond 2004; Marchant et al. 1995; Marchant and McGrew 1998; Raymond and Pontier 2004). Right-handedness would be an ancient trait that already existed in the first hominids. The archaeological data (reviewed in Cashmore et al. 2008; Uomini 2009) provide evidence for population-level handedness from the Neanderthals, and some data from older hominids suggest that it could have been present earlier (Uomini 2009). Therefore, the commonly held opinion is that right-handedness would have always existed in humans, and remained unchanged until today (Coren and Porac 1977; Fagard 2004; Faurie 2004; Faurie and Raymond 2004).

Neurologically, this preference for using the right hand may be related to a specialization of the left hemisphere for manual functions (Cameron and Rogers 1999; Corballis 1989; Fagard 2004; Fagot and Vauclair 1991; McNeilage et al. 1987). Brain

lateralization refers to the two cerebral hemispheres having different functions (i.e. each hemisphere having its own functional specializations). It is generally admitted that when one hemisphere is specialized for a particular function, this makes the related side of the body better, and leads the individual to use this side preferentially. Thus, asymmetries in the behaviour are thought to be related to hemispheric specialization.

Brain lateralization was first reported in the mid-1800s for language related functions (Broca 1865), which are mainly located in the left hemisphere, like manual functions. Since then, many other functions have been studied and shown to be lateralized (e.g. face recognition, emotional processes) (Fagard 2004). Within this area of research, handedness has been and remains the most studied asymmetry (the keyword “handedness” gives 42000 articles in “Pubmed” this day of February 2010). Indeed, handedness is the most obvious behavioural manifestation of brain lateralization in humans. Moreover, it is seen as one of the features that “sets man apart from other animals” (McNeilage et al. 1987).

Why humans show lateralization in virtually all subjects and right-hand preferences in 90% of individuals? What are the proximate and ultimate causes of this outstanding feature? This question is still unresolved, in spite of intensive research over 1.5 centuries (see Fagard 2004; Faurie 2004; Faurie and Raymond in preparation for reviews). The topic remains matter of considerable scientific debate and inquiry.

- The proximate causes of right-handedness are largely unclear. This topic stands beyond the scope of this research. To summarize, the data suggest a genetic determination of hand preference, but other (non-genetic) factors would also influence laterality (review in Doyen 2004). There is evidence of behavioural asymmetries early in life. For instance, foetuses display right-biased arms movements and right thumb suckling (Hepper et al. 1991; Hepper et al. 1998). Neonates show a right bias for turning their head that is correlated to hand preference later in life (Güntürkün 2003; Hopkins and Bard 1995; Rönnqvist and Hopkins 1998). Moreover, the literature suggests that handedness is a heritable trait (Doyen 2004; Fagard 2004; Vuoksimaa et al. 2009). These points support the hypothesis for a genetic determination of handedness. However, the genetic determinants remain unknown so far (Doyen 2004).

Other factors may also influence hand preference, including cultural pressures, learning, pregnancy or birth stressors (Hopkins 2006; Vuoksimaa et al. 2009).

- The ultimate causes of right-handedness are investigated in this research. It is universally admitted that handedness is a trait that stems from Natural Selection. However, despite important research effort, the evolutionary origins of human handedness remain an unresolved issue (e.g. see previous review articles Cashmore et al. 2008; Corballis 1989; Fagot and Vauclair 1991; Falk 1987; Harris 2000; Hopkins 2006; Lehman 1993; McNeilage et al. 1987).

According to "the theory of Evolution" (Darwin 1859), for a trait to be selected by way of Natural Selection, it should provide significant advantages in terms of fitness. The current data indicate that brain lateralization would indeed have an important role in improving brain efficiency (Vallortigara 2000; Vallortigara and Rogers 2005). The dominance of one hemisphere over the other would provide computational advantages, such as saving neural space by avoiding replication of functions, allowing simultaneous processing of different processes and avoiding hemispheric competition (Corballis 1989; Rogers 2000; Rogers 2002). There is empirical evidence that brain lateralization would improve cerebral abilities, and that, consequently, behavioural efficiency would be enhanced. The data suggest that lateralized individuals would indeed perform better than unlateralized individuals, (humans, non-human primates and other animals (Crow et al. 1998; Faurie 2004; Fragaszy and Mitchell 1990; McGrew and Marchant 1992; McGrew and Marchant 1999; Pascual et al. 2004; Rogers 2000; Rogers et al. 2004; Sovrano et al. 2005)). Therefore, brain lateralization would provide advantages, by improving brain and behavioural efficiency (Rogers 2002; Rogers and Andrew 2002; Rogers et al. 2004; Vallortigara and Rogers 2005).

In this thesis, I investigated hand preferences in bonobos as a possible indicator of brain lateralization. Within the last three decades, there has been an important research effort to examine brain lateralization and related laterality in non-human animals. Researchers have tested many different species to determine whether these animals also display laterality and brain lateralization. Moreover, studying non-human animals can help in understanding the evolution of human features, such as handedness. It is very unlikely that brain lateralization emerged *de novo* in humans (McNeilage et al. 1987; McNeilage 1993). This sophisticated complex feature has likely been shaped by long evolutionary processes, and precursor forms could be expected earlier in evolution. Studying non-human animals can thus provide invaluable clues for discussing evolutionary hypotheses on human brain lateralization and handedness. Among them, non-human primates are the most likely to exhibit incipient forms of human features because of their phylogenic proximity to humans. Thus, many researchers have studied our closest living relatives and have used them as models for investigating the evolution of human handedness.

In this research work, I studied hand preferences in bonobos (*Pan paniscus*), which is a particularly interesting species that has rarely been studied before (see section I.4)..I investigated whether the bonobos exhibited significant laterality and what was the pattern of laterality. I also tested which of the factors that are proposed to influence laterality can actually affect laterality in bonobos (including both factors that are related to the individual and factors that are related to the task).

In section I.2 of this introduction, I first present the hypotheses on handedness that were examined in this research. In section I.3, I summarize the previous data on hand preference in non-human primates (with a focus on great apes), and I explain the methodological issues and gaps that plague the literature on laterality in non-human primates. In section I.4, I present my research work, starting with the model of study: bonobos, and the previous data on manual laterality in this species. Then, follows the description of the studies of this PhD research. Study 1 examined hand preferences in spontaneous daily actions (non-social). Study 2 assessed hand preferences for an experimental bimanual coordinated manipulative task (the “tube task”). Study 3 focused on hand use for tool-use actions. Study 4a investigated hand preferences for spontaneous social actions and gestures. Study 4b examined hand use for an experimentally induced begging gesture. The following sections present the methods used (section II) and the results of each individual study (section III) (summarized in Table 37). Finally, a general discussion is presented (section IV), which interprets the data in relation to the hypotheses investigated and to the previous data in non-human primates.

Chapter 2: Hypotheses on handedness

As discussed in the previous chapter, lateralization would be a means to improve brain and behavioural efficiency (Rogers 2002; Rogers and Andrew 2002; Rogers et al. 2004; Vallortigara and Rogers 2005). In evolution, brain lateralization is thought to have emerged to improve brain skills, to solve increasing cognitive problems (Rogers and Andrew 2002). What are these problems? What adaptive function does lateralization serve? What is lateralization an adaptation to? Namely, what caused brain lateralization to appear? What were the factors involved in the selection of this feature? These questions remain unresolved. Many different explanatory models have been proposed. Most ideas view handedness as a unique-to-human feature and relate it to other human typical traits, like tool-use, bipedalism or language. In this chapter, I present the main hypotheses on handedness, which are examined in this thesis. These are theoretical models or models that are based on observations done in non-human primates. I describe each hypothesis as it was formulated by the authors and I explain what the hypothesis predicts concerning hand preference in non-human primates. These numbered predictions are investigated in this thesis using bonobos. The other hypotheses and predictions tested in this thesis are presented in the following chapters, referred to as "prediction X". They are all summarized in Table 2.

- The "tool-use hypothesis" and the "throwing hypothesis"

The "tool-use hypothesis" proposes that right-handedness may have emerged in humans as an adaptation to complex bimanual coordination for tool manufacture and use (Frost 1980; Kimura 1979). Specifically, Kimura (1979) proposed "that cerebral asymmetry of function developed in conjunction with the asymmetric activity of the two limbs during tool-use, the left hemisphere, for reasons uncertain, becoming the hemisphere specialized for precise sequential limb positioning". Tool-use is an extremely complex behaviour as it involves spatio-temporal coordination of both hands together and of the hands with the object(s). The “throwing hypothesis” proposes that throwing would be “the best candidate for handedness” (Calvin 1983a; Calvin 1983b). Throwing indeed requires a finely tuned action (particularly aimed throwing toward a target) (McGrew et al. 1999) that necessitates great accuracy in the spatial and time dimensions, i.e. extremely complex spatiotemporal skills. Therefore, the high perceptual and motor cognitive requirements of tool-use, including throwing, are proposed as selective pressures involved in the emergence of brain lateralization and handedness.

Predictions 1: These hypotheses predict a marked laterality, i.e most individuals being lateralized, strong individual preferences and a **group-level right bias**, for tool-use and throwing in non-human primates. Moreover, tool-use actions should be more strongly lateralized than non-tool-use actions.

- The “bipedalism hypothesis”

The “bipedalism hypothesis” proposes that the appearance of right-handedness in humans is related to the emergence of bipedalism. This link could be a direct link related to the high postural demands of this posture. Indeed, bipedal posture is a relatively unstable posture, with a high center of gravity and few points for support, leading to complex problems in balance control. Lateralization could have evolved as a solution to improve cerebral skills for postural control problems, i.e. maintaining balance in the bipedal posture (Falk 1987; Larson et al. 1989; Sanford et al. 1984; Westergaard et al. 1998a). The link between bipedalism and handedness could also be an indirect link, related to the release of the hands from their role in locomotion and postural support (see below). By relieving the hands of their postural duties, bipedalism makes them available for other activities that are proposed to be involved in the emergence of right-handedness (e.g. tool-use) (Bradshaw 1991).

Predictions 2: This hypothesis predicts that, when assuming a bipedal posture, non-human primates should exhibit a laterality that is more similar to that of humans. The bipedal posture should elicit a strong laterality, i.e. most individuals being lateralized, strong individual preferences and a group-level right bias.

- Language related hypotheses

Several hypotheses propose an evolutionary link between handedness and language. One reason for this is that language and manual functions are lateralized in the same (left) hemisphere in humans (Annett 1985; Broca 1865; Knecht et al. 2000). There are two possible directions for a causal relationship between language and handedness. On the one hand, the specialization of the left hemisphere for linguistic functions could have appeared first, and be secondarily used by manual functions (Falk 1987). On the other hand, the specialization of the left hemisphere for sequential manual actions could have appeared first and established a favourable ground for language (Hewes 1973).

In this research, I tested hypotheses related to gestural communication. Indeed, current research on the evolution of language and handedness (e.g. Pollick and De Waal 2007; Vauclair 2004; Vocoid conference 2007) gives a great deal of attention to gestures. The “gestural origins of language” hypothesis (Hewes 1973) proposes that gestures are the communication that preceded speech in the evolution. It suggests that gestural communication was already lateralized in the left hemisphere.

Predictions 3: This hypothesis predicts that gestures should elicit a strong laterality and group-level right bias in non-human primates (Corballis 2002; Vauclair 2004). We should observe a greater right hand use for gesturing compared to other actions. Moreover, the laterality for gesturing should be unrelated to the laterality observed for non-communicative manual actions.

- The “postural origins hypothesis”

The “postural origins hypothesis” (McNeilage et al. 1987) is an evolutionary model that places the origins of human handedness early in primate evolution. In 1987, McNeilage and collaborators examined the available data on laterality in non-human primates. They found evidence of group-level hand preference, with left-hand preferences for reaching, while right-hand preferences occurred for manipulation, among other things. They suggested that the negative findings in non-human primates (no evidence of human-like handedness) could be related to using inadequate measures, testing young individuals (with undeveloped laterality) or asking for a uniform hand preference across all tasks. They proposed that “primate handedness patterns evolved with structural and functional adaptations to feeding, that they are precursors to aspects of human left- and right-hemisphere specialization patterns, and that they evolved in the following order” (McNeilage et al. 1987). First, the left hand may have been specialized for visually guided reaches, the right hand being specialized for postural support (McNeilage 1993). This evolved as an adaptation to unimanual predation in prosimians, along with the prehensile hand. Later, the right hand may have become specialized for manipulations and bimanual coordination. This emerged along with the opposable thumb and the decrease of postural demands in monkeys. Finally, the right hand may have become dominant for all activities in humans. With regard to great apes, they are expected to be intermediate between monkeys and humans. This model is presented in Table 1.

Predictions 4: The “postural origins hypothesis” (McNeilage et al. 1987) predicts a left hand preference for visually guided reaches and a right hand preference for postural support (particularly in lower primates); and a right hand preference for manipulation and bimanual coordination in higher primates (monkeys and apes). Moreover, this hypothesis suggests an effect of task **complexity**, with right-hand preference arising only beyond a certain minimum demands.

Table 1: Model of McNeilage et al. (1987)
(table replicated from the original publication).

Group	Left side	Right side
Prosimians (circa 65 million years ago)	Visually guided reaching, initially in upright feeding posture (right-hemisphere control)	Part of a complementary postural control system (left-hemisphere control)
Monkeys (circa 40 million years ago)	1. Generalization of the prosimian asymmetry (right-hemisphere control) 2. Subordinate role in bimanual coordination (primarily left-hemisphere control)	1. Fine hand-arm movement control (left-hemisphere control) 2. Dominant role in bimanual coordination (left-hemisphere control)
Great apes (circa 18 million years ago)	Intermediate between monkey and man?	
Hominids (circa 7 million years ago)	Left-side reaching preference disappears	Right hand-arm becomes dominant for all unimanual tasks

- Release of the hands from postural duties

Several hypotheses propose that release of the hands from postural duties would be the key condition necessary for the emergence of handedness (McGrew and Marchant 1997a; McNeilage 1993). Indeed, in all primates (except humans), the hands have a major role in locomotion and postural support, which may be unfavorable to the development of laterality. In fact, laterality would be disadvantageous whenever both hands must be equally able to perform a task; and a typical task that requires equivalent skills of the two hands is postural support. In the trees, when moving or still, both hands must be equally competent to grasp branches efficiently, because the environment is symmetrical (Marchant and McGrew 2007). On the ground, the hands are also used for support and locomotion (except in bipedal locomotion). In humans, the hands are free, permanently available to be used in a variety of tasks other than postural support. This release of the hands from postural duties occurred along with two features: permanent bipedalism and terrestriality, a combination that is unique to humans (Marchant and McGrew 2007). Therefore, handedness may have emerged only in humans because of this unique favorable ground to the development of laterality.

Predictions 5: This hypothesis predicts that, in non-human primates, the behaviours performed in the trees should display no laterality, leaving both hands equally able to perform the crucial task of preventing the animal from falling (Marchant and McGrew 2007). However, a strong laterality may occur in the actions performed when seated on the ground with both hands free. It also suggests that laterality should be more likely to appear when both hands are equally available for use compared to when one hand is used to support body weight (Byrne and Byrne 1991; McGrew and Marchant 1997a).

- The “hypothesis of task complexity”

In 1991, Fagot and Vauclair (Fagot and Vauclair 1991) examined the extant data on laterality in non-human primates, taking into account the **complexity of the task**. They proposed that hand preference would depend on the task’s demands. Specifically, they distinguished two categories of tasks according to their complexity: “low-level” tasks and “high-level tasks”.

- Low-level tasks are those that are simple (grossly regulated) or familiar, highly practiced. An example of such tasks is reaching for food on the ground.
- High-level tasks are those that are novel or complex and demanding, i.e. tasks that require high spatiotemporal or cognitive skills. Task complexity can be related to different factors, including: **precision** of the action, novelty of the task, complex balance control, manipulation, need for several stages to solve the task, need for several elements to be combined, need to involve both hands (in different or coordinated complementary roles), need to use the subordinate hand as postural support.

When analyzing the data available, the authors found that low-level tasks appeared to induce only individual preferences. They suggested that both hands (hemispheres) would be able to perform these simple tasks. Here, hand preference would not be related to hemispheric specialization, but would rather stem from various factors (e.g. the position of the object relative to the hands). By contrast, high-level tasks appeared to elicit group-level biases. The authors proposed that only one hand (hemisphere) would be able to perform these complex demanding tasks. Here, hand preference would reflect the specialization of the contralateral hemisphere. So, for complex tasks, only one hemisphere would be competent to solve the task, which leads to a preferential use of the associated hand. Under the assumption that the competent hemisphere is the same for all the individuals of the group, group-level biases should appear. This idea implies that only complex tasks, that require the specific skills of one hemisphere, could elicit laterality. The authors suggested that the negative findings reported in non-human primates (no group-level bias) could be due to the use of inadequate tasks, i.e. tasks that are not sufficiently complex.

Predictions 6: The “hypothesis of task complexity” (Fagot and Vauclair 1991) predicts that: a) both motor and cognitive aspects of the tasks should influence hand preference, b) “the more skilled action the task requires, the stronger the group-level bias should be”. Thus, laterality should depend on the task. Complex tasks should elicit group-level laterality. Within the same line, the presence or absence of laterality and the strength of laterality should also be affected by task complexity, with a stronger laterality expected in complex than simple tasks.

- Artefactual preferences in non-human primates

Several researchers have proposed that the hand preferences observed in non-human primates are just artefacts, coming from experimental or/and environmental factors (Deuel and Dunlop 1980; McGrew and Marchant 1997a; McGrew and Marchant 2001; Warren 1980). According to Warren (Warren 1980), the preferences could be learnt throughout the experiment. That is, the animal would learn to prefer using one hand through its repetitive trials on a given task. The preferences would not be related to brain lateralization. Moreover, being learnt on one task, the preferences cannot be generalized to other tasks. The hand preferences of non-human primates have also been suspected to be due to the captive conditions or human-rearing (McGrew and Marchant 1997a; McGrew and Marchant 2001; Warren 1980) (discussed in section I.4.3.6.). Therefore, some have suspected the laterality of non-human primates to be an artificial phenomenon, with little biological validity, and thus irrelevant for discussing evolutionary hypotheses.

Predictions 7: The predictions of these hypotheses are as follows. The strength of preference should increase with practice on a given task. The preference should randomly vary between tasks. The preference should not be stable across time. Laterality should appear in experimental tasks, not in spontaneous actions. Laterality should appear in captive animals only, not in wild animals. Captivity-related factors, such as the degree of daily interactions with humans (keepers and public), the amount of space available, the asymmetry of the environment and the closeness to natural settings, should influence laterality. Human-rearing should affect laterality. The hand preferences should be random, not hereditary. Hand preferences should not be present at the group-level.

- The social related hypothesis

I now present a recent hypothesis on brain lateralization, which is not particularly related to handedness but proposes an interesting explanation for group-level biases. The social related hypothesis (Vallortigara and Rogers 2005) is based on the influence of social factors. It suggests that laterality may evolve in two steps. Firstly, laterality would appear on an individual basis, to provide computational advantages (Rogers 2000; Rogers 2002; Vallortigara 2000) (see section I.1). The advantages of lateralization in terms of brain efficiency are indeed valid on an individual basis. The second step would be an alignment of the direction of the asymmetries in most individuals of the population, as a result of social pressures (Ghirlanda and Vallortigara 2004; Vallortigara and Rogers 2005). Indeed, when asymmetrical organisms have to interact together, it may be essential for an individual to adapt its laterality according to the asymmetries of the others (i.e. for school cohesion in fishes) (Ghirlanda and Vallortigara 2004). The crucial point proposed here is that **individual-level laterality** would stem from natural selection, and would be maintained unless there are requirements for a social alignment.

Predictions 8: Thus, this hypothesis proposes that social pressures are the crucial factor for alignment of laterality at the group-level. It predicts that group-level laterality should appear in social related behaviours. Moreover, laterality should be more marked in social compared to non-social actions. Importantly, it suggests that individual-level laterality is advantageous and sufficient, when there are no selective pressures for aligning laterality between the individuals of the group.

Table 2: Hypotheses investigated in this thesis and their related predictions on hand preference in non-human primates.
This table gives a summary of the hypotheses that are explained above.
The number is the reference that is cited in text when referring to the hypothesis.

	hypotheses	predictions	number
theoretical hypotheses	the "tool-use hypothesis" and the "throwing hypothesis"	a marked laterality, i.e most individuals being lateralized, strong individual preferences and a group-level right bias, for tool-use and throwing in non-human primates. tool-use actions should be more strongly lateralized than the other actions.	1
	"bipedalism hypothesis"	when assuming a bipedal posture, non-human primates should exhibit a laterality that is more similar to that of humans. the bipedal posture should elicit a strong laterality, i.e. most individuals being lateralized, strong individual preferences and a group-level right bias.	2
	language related hypotheses	gestures should elicit a strong laterality and group-level right bias in non-human primates. we should observe a greater right hand use for gesturing compared to other actions. the laterality for gesturing should be unrelated to the laterality observed for non-communicative actions.	3
	the "postural origins hypothesis"	a left hand preference for visually guided reaches and a right hand preference for postural support (particularly in lower primates). a right hand preference for manipulation and bimanual coordination in higher primates (monkeys and apes). an effect of task complexity, with right-hand preference arising only beyond a certain minimum demands.	4
	release of the hands from postural duties	in non-human primates, the behaviours performed in the trees should display no laterality. however, a strong laterality may occur in the actions performed when seated on the ground with both hands free. The laterality should be more likely to appear when both hands are equally available for use compared to when one hand is used to support body weight.	5
	the "hypothesis of task complexity"	a) both motor and cognitive aspects of the tasks should influence hand preference, b) "the more skilled action the task requires, the stronger the group-level bias should be". thus, laterality should depend on the task. complex tasks should elicit group-level laterality. the presence or absence of laterality and the strength of laterality should also be affected by task complexity, with a stronger laterality expected in complex tasks.	6
	manipulation bimanual actions	manipulation and bimanual actions should elicit a particularly marked laterality and a group-level bias. the right hand should be preferred for manipulation and for the most active component in bimanual coordination.	6'
	precise actions	precise actions should elicit a marked laterality and a group-level right bias in non-human primates.	6''
	grip type	the grip type used may influence hand preference (morphology of the hand, precise versus unprecise grip)	6'''

(table 2 continued)	hypotheses	predictions	number
	hypotheses for artefactual preferences in non-human primates	the strength of preference should increase with practice on a given task. the preference should randomly vary between tasks. the preference should not be stable across time. laterality should appear in experimental tasks only, not in spontaneous actions. laterality should appear in captive animals only, not in wild animals. captivity-related factors, such as the degree of daily interactions with humans (keepers and public), the amount of space available, the asymmetry of the environment and the closeness to natural settings, should influence laterality. human-rearing should affect laterality. the hand preferences should be random, not hereditary. hand preferences should not be present at the group-level.	7
	the "social related hypothesis"	individual-level laterality is advantageous and sufficient, unless there are selective pressures acting for a social alignement. group-level laterality may appear in social related behaviours. laterality should be more marked in social compared to non-social actions.	8
	maternal behaviours	maternal behaviours may exhibit a specific laterality.	8'
hypotheses based on the specific features of bonobos	phylogeny	Because they are so close to humans in the phylogeny, bonobos could be expected to exhibit a laterality that is close to that of humans	9
	language	If language and handedness were related, and if bonobos displayed the highest language skills of all non-human primates, then they should exhibit a manual laterality that is the closest to that of humans (especially for communicative actions)	10
	bipedalism	If bipedalism was an important factor in the evolution of handedness, if there was a link between bipedalism and handedness; bonobos, which are thought to be the most biped of all non-human primates, should exhibit a more human-like laterality, compared to other non-human primates species	11
	tool-use	If tool-use was involved in the emergence of handedness, and if tool-use was actually limited in bonobos compared to chimpanzees, then laterality should be weaker in bonobos. chimpanzees should exhibit a laterality that is closer to human-handedness compared to bonobos	12
other hypotheses about possible influential factors	posture	The posture of the subject may influence laterality	13
	activity of the other hand	The activity of the other hand may influence laterality	14
	sex	The sex of the individual may influence laterality	15
	age	The age of the individual may influence laterality. immature subjects may exhibit a different laterality compared to other individuals	16
	kinship	kinship may influence laterality	17

Above, I have presented the main hypotheses on handedness. These hypotheses can be tested by studying hand preferences in non-human animals. Indeed, data on laterality in non-human species can provide clues for understanding which of the factors proposed as selective pressures for handedness have a real influence on laterality. There has been important research on non-human primates. The next chapter presents the current literature on laterality in non-human primates.

Chapter 3: Manual laterality in non-human primates

Lateral preferences in the behaviour of non-human animals have been examined in many recent studies (review in Rogers and Andrew 2002). Among these species, non-human primates have received the greatest attention. In this research, I focus on great apes because, as our closest living relatives, they are particularly valuable models for studying the evolution of human features. Great apes also display very interesting characteristics in terms of brain lateralization and handedness. Their hands are close to that of humans regarding morphology and manipulative skills (Byrne et al. 2001). They can manufacture and use tools (McGrew and Marchant 1997b). They can use bipedal locomotion (De Waal and Lanting 1998; Susman et al. 1980; Videan and McGrew 2001; Videan and McGrew 2002). They exhibit some abilities for language (Savage-Rumbaugh et al. 1977; Savage-Rumbaugh et al. 1978; Savage-Rumbaugh et al. 1985; Savage-Rumbaugh et al. 1986; Savage-Rumbaugh 1987) (see the famous chimpanzee Washoe, the gorilla Koko, the orang-utan Chantek and the bonobo Kanzi). All these features have been proposed as possible factors involved in the emergence of brain lateralization and handedness. In addition, great apes exhibit neuro-anatomical brain asymmetries (Cantalupo and Hopkins 2001; Gannon et al. 1998; Holloway and De La Coste-Lareymondie 1982; Hopkins et al. 1998; Hopkins et al. 2000b; Hopkins and Pilcher 2001; Hopkins and Cantalupo 2004; Hopkins et al. 2007). Therefore, great apes are good models for investigating the origins of brain lateralization and handedness. Finally, great apes are the closest to humans in the phylogeny. Assuming that the feature did not appear *de novo* in humans, manual laterality could have been present earlier in evolution; and precursor forms of handedness may exist in other primates (McNeilage et al. 1987). Great apes are the best candidates for exhibiting precursors of human traits, as they have shared a common ancestor with humans relatively recently. Therefore, data on hand preference in great apes can provide essential clues for discussing evolutionary hypotheses on human handedness.

I now present the current data on manual laterality in non-human primates (with a focus on great apes), and then I explain the issues and gaps that plague the extant database.

3.1. Main results on manual laterality in non-human primates, with a focus on great apes:

Hand preference has been extensively studied in non-human primates, from prosimians to great apes. The data for all species are reviewed in (Cashmore et al. 2008; Corballis 1989; Fagard 2004; Fagot and Vauclair 1991; Falk 1987; Harris 2000; Hopkins 2006, Hopkins and Cantalupo 2005; Lehman 1993; McGrew and Marchant 1997a; McNeilage et al. 1987; Papademetriou et al. 2005; Warren 1980). To summarize, these data show that non-human primates do exhibit manual laterality. Indeed, previous works have consistently found evidence of hand preferences, for a variety of different actions (both spontaneous and induced actions), including : reaching (reaching from a tripedal posture: data reviewed in (Fagot and Vauclair 1991; Papademetriou et al. 2005), reaching from a bipedal posture: data reviewed in (Westergaard et al. 1998a), feeding (holding food to the mouth: e.g. (Harrison and Nystrom 2008; Hopkins et al. 1993c; Hopkins and DeWaal 1995; Marchant and McGrew 1996; Parnell 2001; O'Malley and McGrew 2006; Rogers and Kaplan 1996; Shafer 1997), holding food to the mouth while the other hand holds other food items: (Hopkins 1994; Hopkins et al. 1993c; Hopkins and DeWaal 1995; O'Malley and McGrew 2006; Peters and Rogers 2008), bimanual manipulation of an object or food item (e.g. (Byrne and Byrne 1991; Byrne and Corp 2003; Corp and Byrne 2004; Hopkins 1995; Hopkins 1999; Hopkins et al. 2001c; Hopkins et al. 2003; Hopkins et al. 2004; Hopkins et al. 2005a; Rogers and Kaplan 1996)), throwing (Colell et al. 1995b; Hopkins et al. 1993a; Hopkins et al. 2005c; Marchant 1983, Westergaard et al. 2000), carrying (Fletcher and Weghorst 2005; Harrison and Nystrom 2008; Hopkins et al. 1993c; Hopkins and DeWaal 1995; Marchant 1983) and other actions, such as tool-use and gestures that are discussed in the next chapter as particular cases (sections I.4.3.4 and I.4.3.5 respectively).

The individual preferences observed displayed various degrees, from a weak preference towards one hand to an exclusive use of one hand, depending on the task. The proportion of unlateralized subjects in the group also varied according to the task. Globally, laterality appeared to be weak for simple tasks, like tripedal reaching for which most subjects are unlateralized (chimpanzees: (Colell et al. 1995b; Finch 1941; Hopkins 1993; Marchant and Steklis 1986); bonobos: (De Vleeschouwer et al. 1995; Hopkins et al. 1993c; Hopkins and DeWaal 1995); gorillas: (Fagot and Vauclair 1988; Olson et al. 1990); orang-utans: (Heestand 1986; Hopkins 1993; Olson et al. 1990)), and strong for complex and more demanding tasks, like bimanual coordination for which most individuals are lateralized (gorillas: (Byrne and Byrne 1991); chimpanzees: (Byrne and Corp 2003; Corp and Byrne 2004)) (also see Table 3 for the “tube task”). Among all the tasks studied, bimanual coordination and manipulations, including tool-use, stood out with the strongest laterality (very marked laterality with extremely strong preferences and most individuals being lateralized).

When considering the distribution of lateralized individuals, the preferences were generally present on an individual basis. That is, the numbers of right-handers and left-handers in the group were similar, indicating no **group-level bias**. In fact, there is evidence of group-level biases for certain behaviours including : bimanual coordination on the “tube task” (chimpanzees: (Hopkins 1995; Hopkins 1999; Hopkins et al. 2001c; Hopkins et al. 2004; Hopkins et al. 2005a), orang-utans: (Hopkins et al. 2003)), bipedal reaching (chimpanzees: (Hopkins 1993); gorillas: (Olson et al. 1990)), bimanual feeding (chimpanzees: (Hopkins 1994)), throwing (chimpanzees: (Hopkins et al. 2005c)), carrying (bonobos: combining data from (Hopkins et al. 1993c; Hopkins and DeWaal 1995)) and begging (chimpanzees: (Hopkins et al. 2005b)). However, such findings are relatively scarce, and they are disputed on issues like the methodology, the statistics and the subjects (McGrew and Marchant 1997a; Papademetriou et al. 2005). Importantly, these group-level biases are always smaller than the extreme bias that is observed in humans (90% of individuals of one kind) as the significant biases found in non-human primates are generally in the order of 65%.

Therefore, the current data provide evidence of significant manual laterality in non-human primates. However, the database is highly inconclusive, and the question of manual laterality in non-human primates remains a matter of considerable scientific debate and inquiry (Hopkins and Cantalupo 2005; McGrew and Marchant 1997a; Palmer 2002). In fact, the extant database is plagued by substantial problems that prevent us from getting an understandable overview of the pattern of laterality. The results are often inconsistent and contradictory between studies, which makes the data available very difficult to interpret. Moreover, there are important methodological issues that hamper data interpretation and there are notable and disturbing gaps in the literature. These methodological issues and gaps are presented below.

3.2. Methodological issues and gaps of previous research on laterality in non-human primates:

3.2.1. Methodological issues:

- Small sample sizes

One of the most important issues with studies in non-human primates is the small size of the samples studied (Hopkins et al. 1993c; Hopkins 2006; Marchant and McGrew 1991). Because of the limited availability of primate subjects, most studies have considered small samples (fewer than 10 individuals) and very few studies had large samples. In studies on apes, “the paucity of subjects in the typical study of laterality is indicated by the fact that in 78 reports that specify numbers, only 20 (26%) had 10 or more subjects” (Marchant and McGrew 1991). This was still pointed out recently by Hopkins (Hopkins 2006) reporting that “for all apes, only 5 studies had sample sizes exceeding 59 individuals of the same species”.

Testing small samples raises important problems in several ways. First, small samples are problematic in terms of representativeness and generalization of the results. Testing a large sample is indeed necessary for obtaining a representative sample of the species and avoiding chance findings. For instance, it would not be reliable to conclude that orang-utans are right-handed based on the study of only a few subjects. Small samples also do not allow investigation and control for the possible effects of individual characteristics (e.g. stratification by age and sex). Finally, small sample sizes are problematic with regard to statistical power (Hopkins 2006). Indeed, a large sample size is required to reliably detect a group-level bias; particularly for a bias in the order of 65%, like those observed in non-human primates (Hopkins 2006; Hopkins and Cantalupo 2005; McGrew and Marchant 1997a). Power calculations (see section II.1.2) indicate that a minimum sample of 53 subjects is necessary for detecting a 65% bias, which is a size that very few studies display. Therefore, the absence of group-level bias that is generally reported in the literature, has been suspected to be related to small sample size issues (Hopkins and Cantalupo 2005; McGrew and Marchant 1997a).

- Statistics

Interpretation of the available data is strongly hindered by statistical issues. These problems include: lack of standardization of the methods (notably to classify the subjects as lateralized or unlateralized), lack of data independency, small samples of data per subject. These issues are discussed in the methods section (section II.3).

- Inadequate measures

Since the first studies in non-human primates, research has demonstrated and stressed the influence of task complexity on laterality (e.g. Kounin 1938). Indeed, studies have consistently reported that the more complex the task is, the stronger the laterality (e.g. Anderson et al. 1996; Byrne and Byrne 1991; Colell et al. 1995a; Fagot and Vauclair 1988; Fagot and Vauclair 1993; Fragaszy and Mitchell 1990; Phillips and Sherwood 2005; Schweitzer et al. 2007; Spinozzi et al. 1998; Trouillard and Blois-Heulin 2005; Vauclair and Fagot 1993; Warren 1980). Complex and demanding tasks would induce marked preferences (e.g. Boesch 1991; Byrne and Byrne 1991; Byrne and Corp 2003; Corp and Byrne 2004; Fragaszy and Adams-Curtis 1993; McGrew and Marchant 1992; McGrew et al. 1999). Moreover, group-level biases would be more likely to appear in complex tasks (e.g. bipedal reaching (Hopkins 1993; Olson et al. 1990; Sanford et al. 1984) or bimanual coordination (Hopkins and Cantalupo 2005; Spinozzi et al. 1998)). Therefore, it is generally admitted that laterality, i.e. significant preferences and group-level biases, is more likely to appear in complex than simple tasks (Fagot and Vauclair 1991).

Consequently, complex tasks would be the most appropriate measures to use for revealing manual laterality (Fagot and Vauclair 1991; Kounin 1938; Marchant and McGrew 1991). However, simple tasks have been the most commonly used measures. In their review of the methods used in apes studies, Marchant and McGrew (1991) pointed out that "the typical task for assessing laterality of function was one-handed, non-sequential and gross in movement". As laterality is more likely to appear in complex than simple tasks, the use of simple tasks is problematic. It makes negative results difficult to interpret, because they could be related to the simplicity of the task rather than reflecting a real absence of laterality (Byrne and Byrne 1991; Hopkins 2006).

- Comparability issues within non-human primates

From the earliest studies in non-human primates (e.g. Kounin 1938), researchers have shown that hand preference varies between tasks (Fagot and Vauclair 1991; Hopkins 2006; Hopkins and Cantalupo 2005; McGrew and Marchant 1997a; Papademetriou et al. 2005; Warren 1980). This has been consistently reported and is generally admitted: both the strength and direction of preference vary according to the task (e.g. Chapelain et al. 2006; Harrison and Byrne 2000; Heestand 1986; Hook-Costigan and Rogers 1995; Hopkins et al. 1993c; Hopkins and Pearson 2000; Marchant and McGrew 1996; Sanford et al. 1984; Spinozzi and Cacchiarelli 2000; Spinozzi and Truppa 1999; Teichroeb 1999; Ward and Cantalupo 1997; Westergaard et al. 1998b). Therefore the results depend on the task that is used to assess laterality. This is an important point that implies that standardization of the methods between studies is necessary for allowing data comparisons between studies and species. Disappointingly, a variety of tasks has been used in the literature. There are also important between-studies differences in the definition of the behavioural categories, the data collection procedures, the statistics and also in the definition of terms such as "lateralized individual" and "handedness" (these issues are discussed in section II). Therefore, it is very difficult to compare the findings between studies and species.

The fact that hand preference varies between tasks also has implications regarding the level of analysis required. As laterality may depend on the action considered, it is preferable to analyse each action separately. Examining overall limb use (merging different actions together), as was done in many studies, could hide significant effects for individual actions, mask the asymmetries and lead to false negative findings (Fagot and Vauclair 1991).

- Comparability issues between non-human primates and humans

There is also an important issue when trying to compare data from human and non-human primates. Indeed, it is very difficult to compare the data because the methods used with humans are different from those used with non-human primates (Harris 2000; Hopkins et al. 1993c; Hopkins and Cantalupo 2005; Seltzer et al. 1990). Generally, the tasks used with humans measure hand preference for complex tasks, such as precise actions and tool-use (Fagard 2004; Faurie 2004; Seltzer et al. 1990), whereas the tasks used with non-human primates are usually much simpler (Marchant and McGrew 1991). This difference of complexity may strongly affect the results and obviously hinders between species comparisons.

3.2.2. Gaps in the database:

- Species studied

There is a great imbalance between the species that have been studied. Research has focused on macaques and chimpanzees, which are over-represented in comparison to other species (Fletcher and Weghorst 2005). There has been very little consideration for orang-utans and bonobos.

- Actions studied

The actions studied far from include the whole repertoire of asymmetrical behaviours. They are generally restricted to a small number of behaviours, i.e. the behaviours that occur the most frequently. Among the different actions considered, bimanual manipulations and tool-use are very important tasks (see section I.3.1), but the data are only from chimpanzees, there are almost no data from other species. The same issue applies regarding gestures.

- Spontaneous versus induced actions

Whilst manual laterality has been studied for a variety of tasks, from natural spontaneous actions to artificial experimental tasks, very few studies have considered and compared both kinds of actions in the same subjects (Marchant and McGrew 1991). This is a problem because laterality may differ between the two kinds of actions (Warren 1980) (see section I.2).

- Variables considered

Many studies have not considered several variables that may influence laterality (described in I.4.3.6). For instance, the posture of the subject, the grip type used, the activity of the other hand, the sex and age of the subject have not always been considered or taken into account.

- Settings: captive versus wild

Most studies have been conducted on captive subjects. In their review of apes studies, Marchant and McGrew (1991) reported that "of the 80 studies, only 10 were done on free-ranging" apes (Marchant and McGrew 1991). The imbalance is still valid today, with very little investigation on wild compared to captive animals (Hopkins 2006; Marchant and McGrew 1996). This is problematic because the validity of findings from captive animals has been questioned (McGrew and Marchant 1997a; McGrew and Marchant 2001; Warren 1980). This issue is discussed in section I.4.3.6.

- Settings: location

Most studies have tested only one group of individuals. Very few works have considered several populations of subjects, housed at different locations. This is a problem because, within a species, there may be some variability between populations from different locations (McGrew and Marchant 1997a). Moreover, it is difficult to make inferences about a species-level pattern of laterality based on the study of only one population at one location.

3.2.3. Conclusion:

Therefore, the current database is plagued by important methodological issues that may be responsible for the findings reported. These problems obviously make the available data very difficult to interpret and the database inconclusive. These important issues must be addressed in future research. Specifically, particular care should be taken to study a large sample of subjects that includes different populations. With regard to the methods, it appears essential to examine a wide range of actions, including both spontaneous and induced actions, and actions with various degrees of complexity (ranging from simple tasks to very complex tasks). Moreover, the data collection and data analysis should be designed in order to allow for reliable comparisons with other studies.

In the above chapters, I have presented the hypotheses on handedness that were examined in this thesis. I have summarized the current data and explained the issues and gaps of previous works on laterality in non-human primates. In the next chapter, I present the study carried out for this PhD thesis. Based on the issues and gaps described above, I designed four studies to investigate manual laterality in bonobos. Bonobos are a particularly interesting model of study for which there are limited reliable data available. The following chapter explains why bonobos are an invaluable model for investigating the evolution of human brain lateralization and handedness, and gives a comprehensive review of the previous data in this species. This is followed by the description of the four studies.

Chapter 4: Presentation of my research work on bonobos

4.1. Model of study: bonobos (*Pan paniscus*)

Bonobos have rarely been studied before and there is a lack of data on laterality in this species. This is a very disturbing gap because data on hand preference in bonobos can provide essential clues for discussing hypotheses about hand preferences in non-human primates and evolutionary hypotheses on human handedness. Indeed, bonobos are a very important species in which to investigate laterality. Several hypotheses propose that they should exhibit a laterality that is the closest to that of humans. Bonobos are indeed particularly close to humans for several traits that are relevant regarding the emergence of handedness. These specific traits are described below.

- Phylogeny

The genus *Pan,* including bonobos and chimpanzees, is the closest to humans in the phylogeny of living species. Bonobos and chimpanzees belong to the homininae sub-family, hominini kind, like humans. The divergence between the *Homo* and *Pan* lineages is estimated to have occurred between 5 and 6 million years ago (Wildman et al. 2003), which means that there was a common ancestor living only a few million years ago. *Pan* species are the closest living relatives of humans. Molecular data indicate that *Homo* and *Pan* are closer to each other than to any other living hominid taxon (Takahata and Satta 1997). Bonobos and humans share 98.4% of their coding DNA sequences (Wildman et al. 2003).

This great closeness between bonobos and humans makes them the best candidates for exhibiting precursors of human features, and for sharing common traits, and thus invaluable models for studying the evolution of human features.

Prediction 9: Because they are so close to humans in the phylogeny, bonobos can be expected to exhibit a laterality that is close to that of humans.

- Language

Bonobos are thought to display outstanding linguistic abilities. The works of Savage-Rumbaugh and collaborators with the bonobo Kanzi (e.g. Savage-Rumbaugh et al. 1977; Savage-Rumbaugh et al. 1985; Savage-Rumbaugh et al. 1986; Savage-Rumbaugh 1987) are particularly fascinating. Regarding comprehension of spoken English, Kanzi is thought to demonstrate the rudimentary language comprehension skills of 2.5 year-old-children. This bonobo also displays impressive symbolic communicative skills. He communicates with people using lexigrams (geometric symbols) that he presses on a keyboard. What Kanzi acquired was spontaneously learnt through observational learning, without any training or conditioning. In fact, these researchers think that the linguistic skills of bonobos would surpass those of the other apes.

If this is true, this feature would make bonobos extremely interesting regarding hypotheses that propose a relationship between language and handedness (Corballis 2003; Hewes 1973; Vauclair 2004).

Prediction 10: If language and handedness were related, and if bonobos displayed the highest linguistic skills of all non-human primates, then they should exhibit a manual laterality that is the closest to that of humans (especially for communicative actions).

- Bipedalism

Bonobos are well known for their terrestrial bipedalism. Their bipedalism occurs in many contexts, including: during displays (e.g. dragging branches), for vigilance (standing upright for looking around), when foraging (e.g. for elevated food items; for aquatic food), when playing, when crossing streams and when walking through open short-grass plains (Myers Thompson 2002; Susman 1984). Bipedalism is also particularly related to carrying items (Susman et al. 1980; Susman 1984; Videan and McGrew 2001; Videan and McGrew 2002). In fact, bonobos would be the non-human primate that most frequently use bipedal locomotion (De Waal and Lanting 1998; Susman et al. 1980; Susman 1984). However, the available data so far are scarce and do not enable us to tell whether wild bonobos display more habitual use of bipedalism than chimpanzees (Myers Thompson 2002). Recent work in captivity suggests no difference in the overall rate of terrestrial bipedalism, but rather a difference in the use of it : carrying and vigilance for bonobos, displaying for chimpanzees (Videan and McGrew 2001).

With regard to anatomy, bonobos have been characterized as excellent bipeds, with an anatomical predisposition for bipedalism (De Waal and Lanting 1998; Videan and McGrew 2001; Videan and McGrew 2002). Compared to chimpanzees, they would have a more centrally positioned foramen magnum, longer thigh bones, lower intermembral index, heavier lower limb muscle, longer feet and a different distribution of body weight (De Waal and Lanting 1998; Myers Thompson 2002; Susman 1984). These specific features of bonobos regarding bipedalism are of great interest with regard to the hypothesis proposing bipedalism to be involved in the emergence of right-handedness.

Prediction 11: If bipedalism was an important factor in the evolution of handedness, if there was a link between bipedalism and handedness; bonobos, which are thought to be the most biped of all non-human primates, should exhibit a more human-like laterality (compared to other non-human primates species).

- Tool-use

Tool-use in bonobos is an interesting topic, especially because the current data available suggest that they may differ greatly from chimpanzees. Chimpanzees are outstanding tool users. They “can be characterized as customary users of a wide variety of tools in nature” (review in (McGrew 1994; McGrew and Marchant 1997b). For instance, chimpanzees are well known for using probes for termite-fishing (Lonsdorf and Hopkins 2005; McGrew and Marchant 1999; McGrew and Marchant 1992) or ant-dipping (Boesch and Boesch 1990; Marchant and McGrew 2007; Nishida and Hiraiwa 1982), using hammers and anvils for nut-cracking (Boesch 1991) and using leaves as sponges (Boesch 1991). In contrast, bonobos are thought to rarely use tools in the wild (McGrew 1994 ; McGrew and Marchant 1997b). Indeed, there are scarce reports of tool-use in wild bonobos so far. These reports include: using leaves as protection against the rain, using leaves as napkins to clean themselves, using a twig as a toothpick, using a branch to deter insects, using a stick to scratch themselves and using branches in displays (Ingmanson 1996). Therefore, in the wild, tool-use in bonobos seems to be very limited compared to the extensive tool-use of chimpanzees. Moreover, bonobos would use tools in different contexts, i.e. for self-directed actions and for communicative behaviours, but not for acquisition of food. Thus, the current data available suggest that bonobos would rarely use tools and would not rely on tool-use for subsistence. However, field research on bonobos is relatively recent and the knowledge is limited compared to that on chimpanzees, so no final conclusion can be drawn.

If this is true, this particular feature of bonobos and the differences with chimpanzees would be of particular interest regarding the hypothesis proposing tool-use as a selective pressure for handedness (Frost 1980; Kimura 1979).

Prediction 12: If tool-use was involved in the emergence of handedness, and if tool-use was really limited in bonobos compared to chimpanzees, then laterality should be weaker in bonobos. Chimpanzees should exhibit a laterality that is closer to human handedness compared to that of bonobos.

Conclusion:

To summarize, bonobos are an excellent model species for studying the evolution of human handedness for several reasons. First, *Pan* is the closest taxon to humans in the phylogeny. Second, bonobos display linguistic abilities and bipedalism that may be greater than that of other ape species. Bipedalism and language are traits that are proposed to have driven the evolution of handedness, so these hypotheses predict that bonobos should exhibit a pattern of laterality that is the closest to that of humans of all non-human primates. Regarding tool-use, another factor proposed as selective pressure for handedness, bonobos may exhibit limited tool-use. Therefore, bonobos are an invaluable model of study, especially for testing evolutionary hypotheses proposing that these factors are involved in the emergence of handedness. Data on hand preference in bonobos are thus extremely important to research on the origins of human handedness.

4.2. Previous data on hand preference in bonobos:

I now present a detailed review of the previous data on hand preference in bonobos. Table 1app in appendix gives the details of each study. I present the different studies and their findings one by one. A general discussion follows, which discusses and points out the gaps and issues of these previous studies on bonobos.

The definitions of the behaviours are those of the authors (i.e. in their own words). There is some variability in the methods used (e.g. definition of the behaviour, recording, statistics, etc…), which hinders between studies comparisons and interpretation.

Regarding statistics, I solved the comparability issue by retesting the raw data of the studies (when available) with the statistical methods used in my study (for individual-level laterality and group-level laterality).

- Ingmanson 1998 and Ingmanson 2005 (N=?)

Ingmanson's work is the only research done on wild bonobos (Ingmanson 1998; Ingmanson 2005). Ingmanson observed group E1 and group E2 at Wamba (DR Congo) in 1987-1988. She recorded hand use for several spontaneous actions. The actions analyzed included: picking up an object, branch dragging and grooming. She also examined data on a bimanual coordinated manipulative action: "the peeling of sugar cane, where one hand is used in power grip and the other for small manipulations". For peeling sugar cane, she reported that "individuals tended to be very consistent in the use of either the right or left hand". No effect of sex was found. Regarding the distribution of lateralized individuals, there was equal numbers of right-handed and left-handed subjects in the whole population. However, "within a unit group, individuals tended to be consistent with each other". Namely, most individuals (65%) used their right hand for the power grip in E1, while 78% of the individuals in E2 preferred the left hand. This between-group difference also appeared for picking up an object, with 95% of right-handers in E1 and 88% in E2. For branch dragging, 60% of the individuals preferentially used the left hand. When considering the different tasks, "individuals tended to be statistically consistent within a task, but not necessarily between tasks". Unfortunately, these very interesting data have only been published as abstracts and the number of subjects tested, the methods and the results are not available.

- Hopkins *et al*. 1993 (N=11)

Hopkins and collaborators (Hopkins et al. 1993c) considered manual preference in 11 bonobos from the Yerkes regional primate center field station (Lawrenceville, GA) and the Yerkes main center (Atlanta, GA) (USA). They studied spontaneous hand use during daily feeding and extra feeding sessions. The behaviours considered were: feeding, carrying, self-touching, face-touching, leading limb, gesturing and reaching. The results showed that the bonobos exhibited individual preferences and that there was a high proportion of unlateralized individuals. When testing the percentage of right-hand use with T-test (see section II.3.2), the authors found a right bias for leading limb and a left bias for carrying.

The authors investigated the effect of several possible influential variables, including: posture, activity of the other hand and age. They reported that "the bipedal condition had the effect of increasing the use of the left hand in the carrying measure and increasing the use of the right side for the leading limb measure". Regarding the activity of the other hand, they found that "of all the bimanual feeding patterns, subjects most favoured using their right hand for feeding while holding food items with their left hand". With regard to age, they reported that "the older subjects were more consistent in the use of the right hand in feeding than were the younger subjects, averaged across all feeding contexts. This was also the case for reaching, but not for any of the remaining observational measures".

These authors also assessed hand use in an experiment that tested the effect of posture (N=8). In one condition, the bonobos had to adopt a bipedal posture with both feet on the floor, to reach for a raisin placed at height in the cage mesh. In the other condition, the bonobos had to reach for a food item on the floor from a tripedal posture. The results indicate that the percentage of right-hand use was higher in the bipedal compared to the tripedal posture (71% vs 53.8%).

- Christel 1994 (N=5) and Christel *et al*. 1998 (N=3)

Christel and collaborators performed detailed analyses on the grasping behaviour when reaching for small food items, including investigation of grip types and manual preference. In the first study (Christel 1994), the sample of 41 subjects included humans, monkeys and apes, with 5 bonobos. In the second study (Christel et al. 1998), the sample comprised 5 humans and 3 bonobos. In both studies, the ape subjects had to reach for small food items spread on the ground of the enclosure. The first study (Christel 1994) found that "averaging over all actions, all five bonobos showed a significant right hand preference" and the hand preferences were more pronounced in the preferred grip type" (over all species subjects). The second study (Christel et al. 1998) reported that "all three bonobos have a strong right-hand preference".

- Hopkins and De Waal 1995 (N=10)

Hopkins published another bonobo study in collaboration with De Waal (Hopkins and DeWaal 1995). The same spontaneous behaviours as in (Hopkins et al. 1993c) were studied in 10 bonobos from the San Diego zoo (USA). These data were from videos recorded in 1983-84. The results show that the bonobos exhibited individual-level preferences. There were many individuals with no preference, except for the leading limb in locomotion. I could not retest the data because no raw data were available, so I considered the z-score given in the paper. Regarding the distribution of the individuals, a group-level right bias appeared for the leading limb. When testing the percentage of right-hand use with T-test, the authors found significant biases for carrying and reaching (left bias) and for leading limb and gesturing (right bias).

These authors also investigated the effect of several variables. With regard to the activity of the other hand, they reported that "the bonobos tended to hold food items in the left hand and process or feed with the right hand".

They combined these new data with the data from their previous study (Hopkins et al. 1993c). In the combined sample, they found a group-level left bias for carrying. However, this was not exactly the same behaviour that was considered in the two studies because it included carrying infants in (Hopkins et al. 1993c) and concerned only objects and food in (Hopkins and DeWaal 1995). This difference can be disturbing because infant carrying may induce a specific laterality (see review on cradling preferences in Damerose and Vauclair 2002). In the combined sample, the group-level right bias for leading limb was confirmed. The authors also reported that "the bonobos tended to hold food items with the left hand and feed with the right hand. They also tended to eat food items with the right hand when the left hand was inactive". Analysing an enlarged sample allowed for a better investigation of the effects of age and sex. With regard to sex, there was “a greater prevalence of right-handed gesturing on the part of male versus female bonobos”. With regard to age, “older bonobos had a stronger right-hand bias in reaching” and “subadults tended to posturally support with the left hand and to feed with the right hand, whereas adults did not show this pattern. Moreover, in the behavioural context of feeding while the opposite hand was inactive, adults exhibited higher percentages of right-hand use compared to the subadults”. All these analyses were based on the percentage of right-hand use.

- De Vleeschouwer *et al.* 1995 (N=5)

De Vleeschouwer and collaborators (De Vleeschouwer et al. 1995) studied hand preferences in an experiment that assessed the effect of posture on laterality. The sample consisted of 5 bonobos from Planckendael zoo (Belgium). The experiment required the subject to adopt different postures to reach for a food item. The postures were chosen for their increasing demands in terms of maintaining balance. The 7 evoked postures were: 1. sitting. 2. tripedal standing. 3. bipedal standing with support of one hand (food placed 1.5m above the ground). 4. bipedal standing without support (food placed at the end of a rope, 1.5m above the ground). 5. jumping (food placed at the end of a rope, 2m above the ground). 6. jumping via support on a ridge along the wall (food placed at the end of a rope, 2.5m above the ground). 7. hanging on bars (food placed at the end of a rope, 2.5m above the ground). The authors reported that the bonobos showed individual preferences. However, I could not retest the data because no raw data were available. The authors were interested in the percentage of left-hand use and its variation across postures. They reported that “all subjects showed an increasing left-hand preference over the first four postures; this is the transition from a sitting posture, by way of a tripedal posture, to a bipedal posture, with or without support” and that “all individuals reacted in the same way over these first four postures”.

- Colell *et al.* 1995 (N=2)

Colell and collaborators (Colell et al. 1995b) assessed hand preferences in several apes (31 chimpanzees, 3 orang-utans), including 2 bonobos from N’Sele zoo (Kinshasa, DR Congo). In the bonobos, hand use was recorded for reaching for small food items thrown by the observer (on the ground or in the air). The two bonobos were right-handed for this task.

- Shafer 1997 (N=14)

The study of Shafer (1997) assessed hand use in spontaneous behaviours in 14 bonobos from 2 captive groups (San Diego zoo (some bonobos were the same subjects as in Hopkins and DeWaal 1995) and the San Diego wild animal park) (USA). The behaviours studied were: self-touching, touching others, hitting/knocking other, throwing, feeding, manipulating large objects, manipulating small objects, digging/sifting, tool-use, gesturing, hanging and “others”. This is the only study that included social actions. The author analyzed overall limb use (all behaviours merged together) and found a group-level right bias in the number of individuals (11 right-handers and 2 left-handers). When analyzing each behaviour separately, the bonobos exhibited individual preferences. The number of unlateralized individuals was high; except for feeding and manipulating. There was a slight right bias (non-significant trend) for manipulation of small objects (9 right-handers versus 2 left-handers). There was no difference between the data from the two zoos. With regard to age, the author reported that “infants and juveniles were not as strongly lateralized as adolescents and adults”, based on analysis of overall limb use. Sex differences could not be tested.

- Harrison and Nystrom 2008 (N=22)

The most recent study was done by Harrison and Nystrom in 2000 (published in 2008) (Harrison and Nystrom 2008). These authors studied 3 captive groups of bonobos (Berlin zoo and Stuttgart zoo in Germany, Twycross zoo in England). The sample included 22 individuals, which was the largest sample tested at that time. They examined hand use for spontaneous daily activities. The behaviours analyzed were: leading limb, scratching, gesturing, “carry and object manipulation”, feeding and tool-use. They recorded the posture adopted by the subject and the grip type used. The results show that the bonobos exhibited individual preferences. The number of unlateralized individuals was very high, except for feeding and tool-use. No significant effect of sex, age or settings appeared, based on analysis of overall limb use. However, “more females appeared to favor the right hand”.

Conclusion:

In conclusion, the available data in bonobos are limited. There has been relatively little investigation on manual laterality in this species (fewer than 10 published studies). This is particularly obvious when comparing with their close kin, the chimpanzees, which are the second most studied species (Fletcher and Weghorst 2005). Thus, despite their outstanding characteristics, little attention has been given to bonobos so far.

Together the previous findings indicate that bonobos exhibit significant manual preferences in a variety of actions (Table 1app in appendix). However, a high proportion of individuals were unlateralized for most of the actions studied. Only for certain behaviours (e.g. feeding and manipulating in Shafer 1997), feeding and tool-use in Harrison and Nystrom 2008) were many individuals lateralized. The preferences were present at the individual-level. No group-level bias was found for any of the actions studied, with the exceptions of carrying (left bias) and initiating locomotion (right bias) (combined data from Hopkins et al. 1993c; Hopkins and DeWaal 1995).

However, these results have to be considered with caution because there are important issues with previous studies in bonobos. The first problem is that all the studies have tested very small groups of subjects : almost always fewer than 15 animals. Probably because captive bonobo groups are rare. As seen above (section I.3.3), studying small samples strongly hinders detection of group-level biases and is suspected to lead to false negative findings (Hopkins 2006; Hopkins and Cantalupo 2005; McGrew and Marchant 1997a). Small samples are also problematic for investigating the effects of individual factors (e.g. sex, age). Finally, these small bonobo samples do not allow making inferences at the species level.

Regarding the methods, the actions studied were sometimes imprecisely defined (e.g. manipulating small objects (Shafer 1997)) or analyzed in categories (e.g. “carry and object manipulation” (Harrison and Nystrom 2008)). This makes the data difficult to interpret and hampers comparison with other studies. In this respect, there is a disturbing issue regarding “gestures” (in all studies) and “tool-use” (in Harrison and Nystrom 2008) because these actions were analyzed as a global category (“gestures”, “tool-use”) that gathered different kinds of gestures or tool-use actions together. This approach is criticisable because hand preference depends on the action considered (see section I.3.3), so grouping different actions together could hide significant effects for individual actions (Fagot and Vauclair 1991). Therefore, the negative findings might be related to this problem, instead of indicating a real absence of laterality. Along the same line, several authors have performed analyses on overall limb use (merging all actions together) (e.g. Harrison and Nystrom 2008; Shafer 1997). Thus, in several previous studies, the findings are difficult to interpret because based on analyses of categories instead of individual actions.

Furthermore, when considering the current bonobo data, we are faced with an incomplete database that is plagued by several notable gaps. The first important gaps concern manipulation, bimanual coordination and tool-use. As seen above (sections I.2 and I.3.1), these actions are especially relevant regarding evolutionary hypotheses and they appear to stand out with the strongest observed laterality. There are almost no data for these actions in bonobos and those available are difficult to interpret (see above for tool-use). Regarding manipulations, Harrison and Nystrom (2008) have studied "carry and object manipulation" defined as "transport an object for at least 3 consecutive steps; manoeuvre an object for some purpose other than feeding or tool use". Manipulations were not examined alone, which impairs interpretation (see section I.3.3). Shafer (1997) has studied object manipulation, distinguishing large and small objects manipulations, but these categories were still vague. Large object manipulation was defined as "the manipulation of any object (usually large or heavy) with the whole arm or arms, distinguished by elbow flexion, as opposed to finger/wrist flexion". Small object manipulation was defined as, "the manipulation of any object with just the hands or fingers, distinguished by wrist and/or finger flexion, including small tool use". Thus, there has been no detailed examination of a manipulative action, apart from the observations of Ingmanson on the peeling of sugar cane (Ingmanson 1998; Ingmanson 2005).

In fact and importantly, there are very few data for complex tasks in bonobos. Most of the data available concern simple tasks. This lack of data is an important issue given the importance of studying complex tasks to reveal laterality (see section I.3.3). Moreover, there are few experimental studies, and they were limited to one kind of action: reaching (i.e. reaching for food from different postures) (Christel et al. 1998; Colell et al. 1995b; De Vleeschouwer et al. 1995; Hopkins et al. 1993c). No other behaviour has been studied in experimental conditions, which is a pity because experimental work is a powerful tool that allows for controlled tests conditions in which we can assess the effect of one isolated factor. Also, only one study has assessed hand preference in the same subjects in both spontaneous and induced actions (Hopkins et al. 1993c). Finally, there has been no specific work on communicative actions (e.g. gestures) despite the outstanding feature of bonobos in terms of communicative skills.

When considering the spontaneous actions that have been examined in previous research, they included: feeding, carrying, initiating locomotion (leading limb), gesturing, reaching, touching face, self-touching, touching others, hitting/knocking, throwing, manipulating large objects, manipulating small objects, digging/sifting, hanging, scratching and tool-use (Harrison and Nystrom 2008; Hopkins et al. 1993c; Hopkins and DeWaal 1995; Shafer 1997). This range of actions is far from including all the behaviours of the bonobo repertoire and complementary data are necessary to make the sample more comprehensive and representative. Moreover, there has been no study of social actions (only Shafer (1997) included two social actions: “touch other” and “hit/knock other” and Ingmanson (2005) included grooming).

Finally, I would like to highlight that several factors have never been investigated in bonobos. The first one is the effect of rearing history, which has been suspected to create artefactual laterality (McGrew and Marchant 1997a; McGrew and Marchant 2001; Warren 1980). Consistency of hand preference over time has also never been examined, while finding a consistency of laterality over time would demonstrate the stability of the feature. The effect of kinship has also never been considered, while the question of heritability is a very important issue. Finally, the effects of individual factors like sex and age, which have been shown to influence laterality in other species (see section I.4.3.6), could not be reliably investigated due to the small samples studied.

To conclude, there are scarce data on laterality in bonobos, and they are based on small samples of subjects, behaviours and variables, and they mainly concern simple tasks. The studies are few and they are plagued by important methodological problems and gaps. Important data are missing, notably for bimanual coordination, for tool-use and for individual gestures. Therefore, the data available are limited and the findings are difficult to interpret and generalize. Further investigation is required.

4.3. Presentation of the four studies:

Based on the points raised above, I chose to study hand preferences in bonobos, in a large sample of subjects and for a wide variety of actions. I aimed to provide new data on manual laterality in this important species for which relatively little is known. My objective was to complement the scarce previous data, to address the issues that have not been reliably investigated and to fill the disturbing gaps.

I asked the following questions :
Do bonobos exhibit laterality ?
How marked is the laterality: do they show weak or exclusive preferences, low or high proportion of unlateralized subjects, individual-level or group-level laterality ?
Which factors influence laterality : do sex, age, rearing history or settings affect laterality ?
Moreover, I was particularly interested in investigating the effects of the factors that have been proposed as selective pressure for the emergence of human handedness (see evolutionary hypotheses described in section I.2). Assuming that brain lateralization was selected to increase cognitive skills for the performance of highly complex tasks (Fagot and Vauclair 1991; McNeilage et al. 1987; Rogers 2002; Rogers and Andrew 2002; Rogers et al. 2004; Vallortigara and Rogers 2005), the complex tasks that elicit laterality in non-human primates could be viewed as selective pressures for the emergence of human handedness. Thus, I asked which factors elicit laterality in bonobos, testing which attributes of the task could elicit or influence laterality. Do high postural demands (e.g. bipedal posture), precision of the action, manipulation, bimanual coordination, tool-use or throwing elicit or influence laterality ?

To answer these questions, I assessed hand preferences in a large sample of bonobos on a variety of different tasks. I considered many task-related factors that may make a task complex and require laterality. Namely, I studied a wide range of tasks of varied complexity (ranging from simple tasks to very complex tasks). I studied different tasks within the same subjects, which is a good approach for understanding which factors can

induce laterality. Moreover, the actions studied included actions that occurred spontaneously during daily activities and actions that were experimentally induced for the study. I examined laterality for each action separately. I also compared the laterality between actions (at the group-level and at the individual-level).
Four studies have been designed and conducted during this PhD research. These studies assessed hand preferences for: spontaneous daily actions (non-social) (study 1), manipulation, bimanual coordination (study 2), tool-use (study 3), spontaneous social actions and gestures (study 4a) and induced begging gestures (study 4b).

This study was the first comprehensive study on hand preferences in bonobos. This was also the first time that laterality was studied in bonobos for manipulative bimanual coordination, tool-use and gestural communication (studies 2, 3 and 4b). The objective of this work was to investigate whether bonobos exhibit manual laterality and to determine which factors - related to the task or to the individual – elicit or influence laterality in bonobos. The following paragraphs present each of the studies and the factors that have been examined.

4.3.1. Total sample studied: 94 bonobos

Previous research is plagued by small sample size issues, with most studies using samples that were too small to allow reliable analyses and interpretation (Hopkins et al. 1993c; Hopkins 2006; Marchant and McGrew 1991). Therefore, for this work, I wanted to study a large number of subjects. Captive bonobos are very rare, with about 230 individuals worldwide: 169 bonobos in zoos (ISIS record 2008) and 58 bonobos at Lola Ya Bonobo sanctuary. I went to four different countries to study four different bonobo groups and enlarge the sample. The total sample studied included 94 subjects. This is the largest bonobo sample ever considered (the previous largest sample was N=22 in Harrison and Nystrom 2008). This sample represents 40% of the worldwide captive bonobo population, which makes it a highly representative sample. This exceptional sample size would allow for reliable assessment of group-level laterality (Hopkins 2006). Indeed, such a sample would be appropriate to detect a human-like extreme group-level bias (90% of individuals of one kind), as well as a smaller bias like those previously observed in chimpanzees (65%) (see section I.3.3 and II.1.2). Moreover, this sample size would allow investigation of the effects of individual related factors, such as sex, age, rearing history and kinship. Finally, studying several populations of subjects that are housed at different locations enhances the reliability to make inferences at the species-level (McGrew and Marchant 1997a).

4.3.2. Study 1: spontaneous daily actions

I first present the study on laterality for spontaneous actions (non-social). This work examined hand use in behaviours that are part of the daily routine of the animals. My investigation considered all behaviours that can be asymmetrical. Among others (see methods section II.2), the studied behaviours included: feeding, carrying, reaching, self-touching, throwing, manipulating and hanging, which have been examined in previous studies (reviewed in section I.3.1 and I.4.2). Non-manual behaviours (e.g. postural asymmetries) have also been recorded. This study aimed to provide essential new data for naturally occurring actions and complement the data from previous bonobos studies on spontaneous actions, which have only considered small samples of subjects, behaviours and variables.

- Biological validity of spontaneous actions

I first studied spontaneously occurring actions, because they have the best ecological validity. Most of the behaviours considered in this study occur in the wild and belong to the natural repertoire of the species (DeWaal 1988). Studying spontaneous actions provide data on the natural behaviour of the subject, that is, on behaviours that have been shaped by Natural Selection (Fletcher and Weghorst 2005; Marchant and McGrew 1996; McGrew and Marchant 1997a; McGrew and Marchant 2001). Therefore, such data would best reflect the selective pressures involved in the evolution of laterality.

Studying spontaneous actions in captive animals also provide crucial clues to the discussion on the validity of findings from captive animals. As will be discussed below, there are disturbing discrepancies between the findings from field studies and captive studies that may be due to the use of different methods. We need to collect data that allow comparisons between captive and wild animals, i.e. we need to study daily spontaneous activities in captive animals. The pattern of laterality observed in captive animals for spontaneous actions can be expected to be similar to the one observed in wild animals.

- Variables considered

In this study, I considered several variables that have been proposed or shown to influence laterality.

Posture: Predictions 13: The posture of the subject may influence laterality.

It is relevant to think that the posture assumed by the subject can influence hand preference as the hands have to be used simultaneously for postural support and for other activities (except when seated or bipedal on the ground) (Fletcher and Weghorst 2005; Fragaszy and Adams-Curtis 1993; Marchant and McGrew 1996; Marchant and McGrew 2007; McGrew and Marchant 2001). The posture is likely to influence hand preference because when one hand is used for postural support, it is then unavailable for other actions (McGrew and Marchant 1997a).

Regarding evolutionary hypotheses, posture has been proposed to be an important factor in the emergence of handedness, as described in section I.2 (“postural origins hypothesis”, “bipedalism hypothesis”, release of the hands from postural duties).

Moreover, postural demands may influence laterality with respect to complexity. Indeed, if laterality increases with task complexity (Fagot and Vauclair 1991), the complexity of balance control may influence hand preference. Namely, tasks with high postural demands should elicit a marked laterality. High postural demands can be related to the number of points of support, the position of the center of gravity and generally, to instability (level of stability).

To investigate hypotheses for an influence of posture, researchers can test the effect of posture on laterality in non-human primates. Previous data suggest that posture can indeed influence hand preference. However, most previous works have examined the effect of the bipedal posture (e.g. Chapelain et al. 2006; De Vleeschouwer et al. 1995; Hopkins 1993; Hopkins et al. 1993c; Olson et al. 1990; Sanford et al. 1984; Westergaard et al. 1997b; Westergaard et al. 1998a; Westergaard et al. 1998b), while few studies have tested other postures (Chapelain et al. 2006; De Vleeschouwer et al.

1995; Forsythe et al. 1988; Larson et al. 1989). I considered several postures, including: seated, tripedal, quadrupedal and bipedal postures. Moreover, I assessed the effect of having one hand used for postural support, which has also rarely been done before (Diamond and McGrew 1994; Miller and Paciulli 2002).

Activity of the other hand: Predictions 14: The activity of the other hand may influence hand preference (Byrne and Byrne 1991). Hypotheses propose that laterality should be more likely to appear when both hands are equally available for use compared to when one hand is engaged into an action, supporting body weight or other activities (Byrne and Byrne 1991; McGrew and Marchant 1997a). Also, the other hand activity is interesting to examine in relation to the hypotheses that propose bimanual actions as selective pressure for laterality. Previous studies have shown that the other hand activity could influence hand use in some cases (i.e. for feeding) (Hopkins 1994). Therefore, when studying hand use, it is important to record the activity of the two hands simultaneously, to test whether the fact that the subordinate hand is inactive, engaged in postural support, engaged in a supportive action (different or same role as the dominant hand) can influence laterality.

In this study, I have systematically recorded the posture and activity of the other hand, to investigate and control for the possible effects of these factors on laterality.

Complexity: Predictions 6: The complexity of the task may influence laterality. I examined a wide range of actions that presented a variation of complexity, from simple tasks (e.g. tripedal reaching for big items) to complex tasks (e.g. peeling a fruit that is held by the other hand). The following factors of complexity have been examined: precision of the action by comparing precise versus imprecise actions; complex balance control by comparing actions with different degrees of postural demands; manipulation by examining tasks requiring manipulative actions; bimanuality (i.e. need to involve the two hands in different or coordinated complementary roles) by examining bimanual actions; throwing by considering aimed throwing and postural demands by comparing different postural patterns. All these factors have been proposed as elicitors of laterality.

- Summary of study 1

To summarize study 1, I observed the bonobos during their spontaneous daily activities. I recorded hand use for behaviours that belong to the natural repertoire of the species (including all behaviours that can be asymmetrical). The **behaviours** analyzed were split into **behavioural patterns**, according to the posture and action of the other hand. I examined each behaviour and behavioural pattern separately, I also compared them to each other and I combined them into relevant categories, to investigate hypotheses regarding the effect of possible influential variables.

4.3.3. Study 2: manipulation and bimanual coordination: the "tube task"

I now present the study on laterality for manipulation / bimanual coordination. There are almost no reliable data on manipulation and bimanual coordination in bonobos, and almost no data for complex tasks of any kind (see section I.4.2). Thus, I wanted to assess hand preferences in bonobos on a task that was complex and that required a bimanual coordinated manipulative action. This study aimed to investigate hypotheses proposing that brain lateralization emerged to improve brain and behavioural efficiency for complex survival processes (Rogers and Andrew 2002), here for bimanual manipulations in food processing (Byrne and Byrne 1991; Fagot and Vauclair 1991).

- Task complexity: manipulation / bimanual coordination

I examined hand preference in bonobos for a manipulative task that requires the use of both hands in a coordinated way, along with a precise action. Bimanual coordinated actions, with different but complementary roles (one hand manipulates an item that is held by the other hand), have been shown to elicit a particularly marked laterality in non-human primates (see section I.3.1). In fact, my review shows that bimanual coordination (including tool-use) elicited the strongest laterality of all the actions studied. It is thus extremely important to examine hand preferences in bonobos on this highly complex task.

- Comparability with other studies

I used an experimental task called the “tube task” (Hopkins 1995) that requires the individual to hold a tube with one hand while reaching for food inside with a finger of the other hand. I specifically chose this task because it has been used in other studies (reviewed in Table 3). As emphasized above, it is essential to standardize the methods between studies to allow reliable data comparisons (Fagot and Vauclair 1991; Hopkins and Cantalupo 2005; McGrew and Marchant 1997a) because the strength and direction of laterality varies according to the task. In fact, the “tube task” has been used in many previous studies and may become the long-awaited standard measure of hand preference in non-human primates.

In great apes, all species have been tested with this task - orang-utans (N=19), gorillas (N=31) and a very large sample of chimpanzees (N=467) (see Table 3). Only bonobos have not been tested with this task, so it was essential to do this testing.

- Previous data on the “tube task”

Previous studies using the “tube task” have reported a strong laterality. This indicates that the task would be a sensitive measure of hand preference (Hopkins and Cantalupo 2005; Meunier and Vauclair 2007; Vauclair et al. 2005; Westergaard and Suomi 1996). Moreover, the preferences appeared to be stable across time (up to several years), which shows the reliability of the task (Hopkins et al. 2001c; Hopkins et al. 2005a; Meunier and Vauclair 2007; Vauclair et al. 2005; Westergaard and Suomi 1996). Table 3 presents a review of the previous data for the “tube task”. All studies reported a marked laterality: most individuals lateralized and strong individual preferences. Several group-level biases were found: a left bias in orang-utans (Hopkins et al. 2003), a left bias in infant rhesus macaques (Westergaard et al. 1997a) and a right bias in baboons (Vauclair et al. 2005). Of particular interest is the group-level right bias that was found in chimpanzees, because it is relatively close to human-handedness and is not anecdotal as it has been replicated in several studies (Hopkins 1995; Hopkins 1999; Hopkins et al. 2001c; Hopkins et al. 2004; Hopkins et al. 2005a).

Therefore, given the previous findings in other species, one could expect bimanual coordination to be the task that should reveal a very strong laterality and a group-level handedness in bonobos.

Table 3: Review of the studies that used the "tube task" to measure hand preferences.
right-handed: number of right-handed subjects, left-handed: number of left-handed subjects, not-lateralized: number of unlateralized subjects. B test: p value for the Binomial test that I performed on the number of right-handed versus left-handed subjects, significant values indicating group-level bias are in bold. Empty cells are cases when the data were not available or extractable from the article.

study	species	location	number of subjects	measure	number of data points per subject	number of test sessions	right-handed	left-handed	not-lateralized	B test
Hopkins (1995)	chimpanzees, *Pan troglodytes*		110	Frequency*	from 17 to 515	2 test sessions separated by several days	59	32	19	**0.006**
Hopkins (1999)	chimpanzees, *Pan troglodytes*		188	frequency	min 20		95	53	40	**7E-04**
Hopkins et al. (2001c)	chimpanzees, *Pan troglodytes*	Yerkes Research Center, Georgia	109 (some are the same as in Hopkins 1995)	frequency	mean 118.52	4 (2 sessions per day on 2 successive days)	54	33	22	**0.031**
Hopkins et al. (2001c)	chimpanzees, *Pan troglodytes*	Yerkes Research Center, Georgia	109 (some are the same as in Hopkins 1995)	Bouts*	mean 23.78	4 (2 sessions per day on 2 successive days)	24	15	70	0.2
Hopkins et al. (2004)	chimpanzees, *Pan troglodytes*	Alamogordo primate facility, New Mexico	148	frequency	min 20	at least 2 test sessions				
Hopkins et al. (2004)		University of Texas, bastrop	117	frequency						
Hopkins et al. (2004)		Yerkes Research Center, Georgia	202	frequency						
total for these 3 populations			467	frequency			272	162	33	**1E-07**
total for these 3 populations			452	bouts			269	183	0	**6E-05**

table 3 continued	**species**	**location**	**number of subjects**	**measure**	**number of data points per subject**	**number of test sessions**	**right-handed**	**left-handed**	**not-lateralized**	**B test**
Hopkins et al. (2005a)	chimpanzees, *Pan troglodytes*	Yerkes Research Center, Georgia	180 (some are the same as in Hopkins et al. 2001)	bouts		8 (4 tests sessions per day on two days)	67	30	83	**2E-04**
Hopkins et al. (2003)	gorillas, *Gorilla gorilla*		31	frequency		4 (2 sessions per day on 2 successive days)	15	12	4	0.701
Hopkins et al. (2003)	orangutans, *Pongo pygmaeus*		19	frequency		4 (2 sessions per day on 2 successive days)	4	15	0	**0.019**
Vauclair et al. (2005)	baboons, *Papio anubis*	Station de Rousset sur Arc, France	104	frequency	from 15 to 311, mean 80		52	33	19	**0.05**
Meunier and Vauclair (2007)	white-faced capuchins, *Cebus capucinus*	Centre de primatologie, Strasbourg, France	13	frequency	min 50		6	6	1	1.226
Phillips and Sherwood (2005)	tufted capuchins, *Cebus apella*		7	frequency	mean 34 (s.d. 18)	4 test sessions separated by several days	3	3	1	1.313
Westergaard and Suomi (1996)	tufted capuchins, *Cebus apella*		45	frequency	from 20 to 175, mean 81	2 test sessions separated by 1 to several days	19	20	6	1
Westergaard and Suomi (1996)	tufted capuchins, *Cebus apella*		45	bouts	25	2 test sessions separated by 1 to several days	19	20	6	1
Westergaard and Suomi (1996)	rhesus macaques, *Macaca mulatta*		55	frequency	from 20 to 128, mean 66	2 test sessions separated by1 to to several days	28	15	12	0.066
Westergaard et al. (1997a)	infant rhesus macaques, *Macaca mulatta*		19	frequency	from 20 to 50, mean 42	2 test sessions	3	12	4	**0.035**

table 3 continued	**species**	**location**	**number of subjects**	**measure**	**number of data points per subject**	**number of test sessions**	**right-handed**	**left-handed**	**not-lateralized**	**B test**
Schmitt et al. (2008)	barabary macaques, *Macaca sylvanus*	“la forêt des singes”, Rocamadour, France	28	frequency						
Schweitzer et al. (2007)	De Brazza's monkeys *Cercopithecus neglectus*	Station de Paimpont, France	12	frequency	from 82 to 279, mean 202.4	20 test sessions (1 session per day)	3	9	0	0.146
Lilak and Phillips (2008)	tufted capuchins, *Cebus apella*	Laboratory of Hiram College; Northeastern Ohio Universities College of Medicine (Ohio)	11	frequency		4 test sessions	5	5	1	1.246
Begg-Reid and Schillaci (2008)	gorillas, *Gorilla gorilla*	Metro Toronto Zoo in Ontario, Canada	6	frequency	from 27 to 71, mean 45.33	2 test sessions	3	1	2	NA
Bennett et al. (2008)	rhesus macaques, *Macaca mulatta*	NIH animal center	124	frequency	min 15	at least 2 test sessions	49	50	25	1

- Summary of study 2

This experimental study was the major piece of this PhD research. To summarize study 2, I assessed hand preferences using the “tube task” to provide so far missing precise data in bonobos for complex tasks, specifically bimanual coordinated manipulation. The “tube task” was chosen because it would be an efficient measure of hand use, it has been used in previous studies and with all apes except bonobos. Moreover, group-level right biases have been found in chimpanzees with this task. The hypotheses predict that bonobos should exhibit strong laterality, with most subjects being lateralized, strong individual preferences and a group-level right bias for the “tube task”.

4.3.4. Study 3: tool-use

I now present the study on laterality for tool-use actions. There are no reliable data for tool-use in bonobos. Data in this species can provide crucial clues for discussing the hypothesis proposing tool-use as a selective pressure for handedness (Frost 1980; Kimura 1979). The objective of this study was to provide so far missing precise data on hand use for different tool-use actions in bonobos.

- Previous data on tool-use

The data on laterality for tool-use are almost only from chimpanzees. All the studies have reported a very strong laterality (with the exception of Marchant and McGrew 2007). Namely, most individuals were lateralized and the individual preferences were extremely strong, with often an exclusive use of one hand (McGrew and Marchant 1996; McGrew and Marchant 1997b; McGrew et al. 1999). This applies for all the tool-use actions studied, including: using a probe to extract termites from their nests (termite fishing) (Lonsdorf and Hopkins 2005; Marchant and McGrew 1996; McGrew and Marchant 1992; McGrew and Marchant 1999; Nishida and Hiraiwa 1982), using a sponge to drink water from tree holes (wadge dipping) (Boesch 1991), using hammers and anvils to crack open nuts (nut cracking) (Boesch 1991; Matsuzawa et al. 2001; Sugiyama et al. 1993) and pounding *strychnos* fruits on anvils (McGrew et al. 1999). The only reported case of weak laterality for tool-use was for ant-fishing (Marchant and

McGrew 2007) and this action was performed in the trees where postural constraints may discourage laterality (Marchant and McGrew 2007). Regarding the distribution of the individuals, no group-level bias was found in chimpanzees for tool-use (although (Lonsdorf and Hopkins 2005) reported a group-level left trend for termite fishing). In orang-utans, individual preferences were found for making, modifying and using tools; with tool-use evoking the strongest laterality relative to other tasks (O'Malley and McGrew 2006). The studies on tool-use are further reviewed in (Marchant and McGrew 2007; McGrew and Marchant 1997b).

In conclusion, laterality was found to be extremely strong: most individuals were lateralized and extremely strong preferences occurred (McGrew and Marchant 1996; McGrew and Marchant 1997b; McGrew et al. 1999). In fact, tool-use showed the strongest laterality compared to other tasks. Thus, the data suggest a special laterality associated with tool-use actions.

In bonobos, there are very few previous data. Shafer (1997) studied hand use for "using sticks and grass blades to poke into holes in a log occasionally stocked with honey". The bonobo studied exhibited almost exclusive left hand use. Harrison and Nystrom (2008) studied "tool-use" defined as "use an object to alter more efficiently the form, position or condition of another object, another individual or the users themselves", merging different actions together. Five bonobos displayed no preference, 3 were left-handed and 4 were right-handed. The lateralized subjects exhibited almost exclusive preference (the mean percentage of use of the preferred hand was 90%) (Harrison and Nystrom 2008). Therefore, the previous bonobo data suggest some strong laterality for tool-use, at least in some individuals.

- Summary of study 3

Therefore, in study 3, I assessed hand preferences for tool-use in bonobos. I first recorded data on spontaneous tool-use occuring during daily activities. The behaviours studied included: using a stone to crack open nuts on an anvil, using a container to take water in the pond, using a container to drink, using a stick to scratch itself, using a rag to clean the wall or ground, using a stick as a rake to get out-of-reach items.

I also studied a tool-use action that was elicited during an enrichment procedure. This induced action was "dipping a stick into a hole" to extract food, a task similar to the "termite fishing" task. This task was a very complex action that involved manipulation, coordination with the objects, a sequential action and precise movements. Thus, it was considered as the most complex task studied in this research work. The “tool-use hypothesis” (Frost 1980; Kimura 1979) predicts a very marked laterality, with most subjects being lateralized, strong individual preferences and a group-level right bias for tool-use in bonobos.

4.3.5. Study 4: spontaneous social actions and gestures (a) and induced begging gesture (b)

Study 4 investigated hand preference for social manual actions and gestures. There are almost no data in bonobos for these actions. I considered the “social related hypothesis” (Vallortigara and Rogers 2005) by studying laterality in social manual behaviours. This hypothesis proposes social pressures as the key factor for alignment of laterality at the group-level. It predicts group-level laterality in social related behaviours. Moreover, among social actions, gestures received particular attention in relation to the hypotheses related to language (see section I.2), which suggest that a particular laterality may be associated with gestural communication. Given the outstanding linguistic abilities of bonobos, data on hand preference for gesturing in this species are of great interest. I aimed to provide so far missing detailed data on laterality for social actions and gestures in bonobos.

- Previous data on social actions

Few previous laterality studies have included some social actions (e.g. Boesch 1991; Fletcher and Weghorst 2005; Marchant and McGrew 1996; McGrew and Marchant 2001) and no notable pattern appeared regarding these actions. In bonobos, there are almost no data on laterality for social actions. Only Shafer (1997) considered two social actions, defined as follows: “touch other: any touch of another bonobo (except hit or knock, includes hugging) and “hit/knock: any hit or slap to another bonobo, glass, grass, rock, etc”. The results show that many bonobos were unlateralized. However, the actions were studied as categories that gathered different types of actions, which is problematic as laterality may vary depending on the action (see section I.3.3).

Among social actions, maternal behaviours have been shown to exhibit a specific laterality in humans (e.g. Damerose and Vauclair 2002; Donnot and Vauclair 2005; Harris 2002; Manning 1991; Manning and Chamberlain 1991; Salk 1973; Vauclair and Donnot 2005) and the data suggest that this may also be the case in non-human primates (e.g. Hopkins 2004; Manning and Chamberlain 1990) (hypothesis 8'). Therefore, I paid special attention to mother-infant behaviours, such as picking up and carrying the infant during displacement and cradling the infant when seated.

- Previous data on communicative gestures

Data on laterality in gestures are mainly restricted to chimpanzees. Significant laterality was found in gestural communication, for both spontaneous and induced gestures. Regarding spontaneous actions, chimpanzees showed very strong, quasi-exclusive, individual preferences, and almost all the individuals were lateralized, for clapping the hands together to attract the attention of humans (Fletcher 2006). Regarding induced actions, chimpanzees showed a group-level right bias for begging for food from the experimenter (Hopkins and Leavens 1998; Hopkins and Wesley 2002; Hopkins et al. 2005b). Moreover, these authors suggest that there may be a specific laterality associated to gestural communication. Indeed, they found no correlation between the laterality observed in gestures and that observed in other actions (simple reaching, "tube task", bimanual feeding (Hopkins and Leavens 1998; Hopkins and Wesley 2002; Hopkins and Cantero 2003)). Also, the chimpanzees were more right-handed (Hopkins et al. 2005b) and more individuals showed exclusive hand use for gesturing in comparison to other actions (Hopkins and Wesley 2002). However, in two of these studies (Hopkins and Leavens 1998; Hopkins and Wesley 2002), the samples of data were very small, i.e. only 1 to 3 trials per subject, which does not allow statistical analysis and prevents reliable data interpretation.

I here review the previous data on laterality for gesturing in bonobos.

- Hopkins and collaborators (Hopkins et al. 1993c; Hopkins and DeWaal 1995) studied spontaneous gestures defined as: "animal uses its hand for communicative purposes, such as clapping to another animal or by itself and begging toward the caretakers or observers", merging different actions together. In the first study, 5 bonobos were unlateralized, 2 were left-handed and 2 were right-handed (Hopkins et al. 1993c). In the second study (Hopkins and DeWaal 1995), all 5 bonobos were unlateralized. The authors reported a group-level right-bias in hand use (right skewed **HI values** and 67% right hand use), which also appeared when they combined the samples of the two studies.

- Shafer (1997) assessed laterality in spontaneous gestures defined as: "any hand motion interpreted as signalling to another bonobo or as solitary gestures", merging different actions together. The gestures studied included: hand and finger waves, hand flaps, arms sweeps in various directions, "high fives" (clapping one hand with that of another bonobo), begging, and gestures that seemed to say "stop", "go away", or "leave me alone" or, more often, "come play" (both playful and sexual solicitation). The author found that 9 bonobos were unlateralized and 1 individual was right-handed.
- Harrison and Nystrom (2008) studied spontaneous gestures defined as: "use hand for communicative purposes towards another (e.g. reconciliatory), keeper or public (e.g. begging)", merging different actions together. The data showed that 18 bonobos were unlateralized, 1 was left-handed and 2 were right-handed.

Therefore, the available data suggest a very weak laterality for gesturing, with most subjects being unlateralized. However all previous studies have analyzed "gestures" as a global category. They gathered different kinds of gestures together, without examining each action separately. This is problematic as laterality depends on the type of action (see section I.3.3). Specifically for gestures, differences of laterality between gesture types have been reported (between begging and pointing) (Hopkins and Leavens 1998; Hopkins and Wesley 2002; Leavens et al. 1996). Therefore, gathering all "gestures" together may hide significant effects for individual gesture types and yield false negative results. Thus, the few current data available are difficult to interpret.

In addition, gestures have only been considered as part of the spontaneous daily behaviours recorded. They have never been the focus of any specific attention. Finally, no study has assessed hand use for gesturing in a controlled experimental design. Therefore, despite of its outstanding features in terms of language, bonobos have never been specifically studied for gestural communication. I aimed to examine hand use for gestural communication in bonobos, for both spontaneous and induced actions.

- Summary of study 4

I investigated hand preference for different kinds of social manual actions and gestures. From an evolutionary perspective, the most relevant behaviours to study are species-typical gestures that occur spontaneously (not experimentally induced) between the conspecifics (intra-specific), i.e. in the conditions where Natural Selection has acted. Therefore, I first considered actions that occurred in spontaneous daily activities and that belong to the natural repertoire of the species (DeWaal 1988; Pika et al. 2005). Within the same vein, I firstly examined actions that were directed towards conspecifics, because these actions present the best ecological value. Secondly, I considered gestures that were directed toward humans during spontaneous actions. Finally, I designed and carried out an experiment to assess hand preference for induced gestures that were directed towards humans.

In sum, hand use was studied in three different contexts:

1. in spontaneous intra-specific interactions: The bonobos were observed during their daily social interactions and hand use was recorded for spontaneous social actions and gestures.
2. in spontaneous inter-specific interactions: I recorded the hand used when the bonobos spontaneously gestured toward humans (e.g. keepers, public) in the daily behaviour.
3. in induced inter-specific interactions: The bonobos were tested in an experiment that involved begging towards a human observer. Out-of-reach food was presented to the bonobos to induce gesturing.

This study is the first to include a range of social actions. Regarding gestures, this is the first work that examined each gesture separately (not different gestures merged together). This approach was to allow investigation of the effects of several possible influential factors, including: the type of gesture, the meaning of the gesture, the emotional valence of the gesture, the identity of the perceiver, the context of emission. This is also the first study to assess laterality for gesturing in bonobos with an experimental design, hereby yielding data for comparison with chimpanzees. I also aimed to compare laterality for spontaneous versus induced actions, and for intra-specific versus inter-specific actions. This study was to provide crucial important new data in bonobos. In accordance with the language related hypotheses (Corballis 2002; Hewes 1973; Vauclair 2004), their outstanding linguistics abilities (e.g. (Savage-Rumbaugh et al. 1977; Savage-Rumbaugh et al. 1986) and the previous findings in close related species (Hopkins and Leavens 1998; Hopkins and Wesley 2002; Hopkins et al. 2005b), bonobos could be expected to exhibit very strong preferences and a group-level right bias for gesturing.

In the four studies, I investigated the effects of several possible influential factors that are presented in the following paragraphs.

4.3.6. Possible influential factors considered in studies 1 - 4:

As seen above (section I.2), the hand preferences of non-human primates have been suspected to be artefacts, stemming from experimental or/and environmental factors (McGrew and Marchant 1997a; McGrew and Marchant 2001; Warren 1980). If this was the case, they would have little biological validity. Thus investigating these hypotheses is crucial. I tested them by examining the effects of factors that have been proposed to affect hand preference. I assessed the effects of external factors, including: experimental biases, living conditions and rearing history. I also considered the effects of the internal factors, sex and age, that may influence laterality. Finally, I examined kinship to assess heritability of hand preference. These different issues are explained in the following paragraphs.

- Experimentally induced actions

The character of the action - spontaneous versus experimental - has been proposed to influence hand preference. In fact, according to Warren (Warren 1980), significant hand preferences should appear only in experimental tasks, not in spontaneous actions. Some previous data indicate that experimental tasks would be more likely to induce strong laterality (e.g. Chapelain et al. 2006; Fagot and Vauclair 1991; Fragaszy and Adams-Curtis 1993; Heestand 1986; McGrew and Marchant 1997a; Rothe 1973; Trouillard and Blois-Heulin 2005) compared to spontaneous actions that would elicit a weak laterality (this would be the case even in humans (Fagard 2004; Faurie 2004; Marchant et al. 1995)). I assessed laterality in a wide range of actions, including both naturally occurring behaviours and experimentally induced actions. I collected data in the same subjects for both spontaneous and induced actions, which has rarely been done before (Marchant and McGrew 1991), and only once in bonobos (Hopkins et al. 1993c). I compared the two kinds of actions to investigate the effect of the spontaneous versus experimental character of the action and test Warren's hypothesis (Warren 1980) (see predictions 7).

- Captive settings

Ideally, to investigate the evolution of a trait, researchers should study animals in their natural environment. According to McGrew and Marchant (McGrew and Marchant 1997a), “the more natural the settings, i.e. close to the environment of evolutionary adaptation, the more valid the results are likely to be”. However, detailed observations of hand use are rarely possible in wild individuals. For instance, the animals may not be habituated enough to the presence of humans for allowing close range observations, the conditions of observations may be difficult (bad visibility), the frequency of observations may be too low (infrequent contacts with the animals). With regard to bonobos, detailed behavioural studies were not possible in the wild at the time of the study (McGrew. pers. com., Hohmann pers. com.).

Studying captive animals can also provide valuable data for discussing evolutionary hypotheses. However, studying captive rather than wild animals is based on the assumption that the captive conditions do not influence the results. This assumption has been questioned. Indeed, some have suggested that laterality would appear in captive animals only, being produced by captive related factors (e.g. asymmetrical cages, experimental procedures or contact with right-handed humans) (McGrew and Marchant 1997a; McGrew and Marchant 2001; Warren 1980). Therefore, researchers should test these hypotheses (predictions 7), and provide evidence to support the validity of work on captive animals.

The best way to do that would be to prove that the results are the same in captive and wild animals. Unfortunately, there has been little investigation in wild compared to captive animals. Moreover, there are some disturbing differences between the findings from wild and captive animals. Namely, most field studies have reported a weak laterality, with most individuals being unlateralized and no group-level bias (Boesch 1991; Marchant and McGrew 1996; McGrew and Marchant 1997a; McGrew and Marchant 2001; Parnell 2001; Sugiyama et al. 1993), while captive studies have often reported a stronger laterality, with many individuals being lateralized and occasionally, group-level biases (Fagot and Vauclair 1991; Fagot et al. 1991; Hopkins 1993; Hopkins 1995; Hopkins and Cantalupo 2005; Hopkins et al. 2005a; Olson et al. 1990; Sanford et al. 1984; Spinozzi and Cacchiarelli 2000; Westergaard et al. 2001).

Alternatively to the hypothesis that laterality would be an artefact of the captive conditions (McGrew and Marchant 1997a; McGrew and Marchant 2001; Warren 1980), the difference observed may be related to the methods used. Indeed, there are differences in the methods used in captive and field studies: field studies mainly focused on spontaneous activities, while captive studies were mostly interested in experimental tasks (Marchant and McGrew 1991). This difference strongly hinders data comparison, because studying spontaneous or induced actions may yield different results (i.e. stronger laterality in experimental than spontaneous actions (see above)). There is also a difference of complexity, with captive studies considering generally more complex tasks than field studies (Fletcher and Weghorst 2005; Hopkins and Cantalupo 2005). Therefore there are differences of methodology that makes it difficult to compare data from wild and captive animals. These methodological differences may explain the inconsistencies between captive and wild findings (Fletcher and Weghorst 2005; Hopkins 2006; Hopkins and Cantalupo 2005; Marchant and McGrew 2007; McGrew and Marchant 1997a; McGrew and Marchant 2001). To investigate this hypothesis and conciliate the findings from both settings, we need to compare data from wild and captive animals on comparable tasks. Studying daily spontaneous activities in captive bonobos can provide useful clues to this discussion.

Another way to investigate hypotheses on artefactual preferences would be to show that captive related factors do not influence the results. The factors that have been proposed to influence hand preferences of captive animals include: limited amount of space, little variety of external stimuli, interactions with right-handed humans, asymmetry of the environment and disturbed sociality (McGrew and Marchant 1997a). The possible influence of these variables is difficult to measure directly, especially because they probably have combined effects that cannot be disentangled. However, it is possible to investigate the effects of these factors by comparing laterality in different conditions (e.g. varying the amount of space available, the contacts with humans, the naturalistic degree of the environment) (McGrew and Marchant 2001).

In this study, I compared hand use between individuals that lived in four different settings (three zoos and one sanctuary). The settings of Twycross zoo, Stuttgart zoo, Apenheul zoo and Lola Ya Bonobo sanctuary varied significantly regarding all the above mentioned factors. There was a great variation between the settings, with a general gradient from very unnatural conditions at Stuttgart (very small concrete cages) and Twycross zoos (small cages with an outside grassy enclosure), to more natural settings at Apenheul zoo (grassy and woody island) to natural-like settings at Lola ya bonobo sanctuary (semi-free ranging forest habitat). These and other varying factors (e.g. variety of external stimuli, interactions with humans) are detailed in the methods section II.1.3. At the four places, hand use was assessed by the same observer and using the same methodology to allow for reliable comparisons. Comparing laterality (direction and strength) between the four places enable me to investigate the effect of these possible influential factors. If any factor related to the living conditions affects laterality, we should observe differences in laterality between these subjects.

- Rearing by humans

Within the same vein, rearing history has been pointed out as a factor that may affect laterality of captive subjects (see predictions 7). Specifically, rearing by humans is suspected to cause captive-born animals to be more right-handed than wild-born individuals (McGrew and Marchant 1997a). Most humans are right-handed so intensive interactions with humans (especially during development in infancy) might have an influence. An effect of human-rearing, i.e. human-reared individuals being more right-handed than mother-reared animals, has been occasionally reported (Hopkins and Cantero 2003; Hopkins et al. 1993b).

I investigated this issue in my study. This has never been done before in bonobos. The sample studied included different kinds of subjects: some bonobos were wild born and the others were born and raised in captivity, with various degrees of interactions with humans during infancy. To assess the effect of rearing history, I compared three categories of individuals: “parent-reared” bonobos (those that have been reared by their mother from birth to independence), “human hand-reared” bonobos (those that have been removed from their mother within the first weeks of life, and reared by humans during infancy (zoo nursery)) and “lola-reared” bonobos (those that have been reared by their mother from birth, but separated from it in early infancy, and then reared by humans until independence). If we observe differences in laterality (direction or strength) between these subjects, this would suggest an influence of humans on laterality.

In addition, to further investigate possible human influence, I examined the effect of interactions with humans on a daily basis throughout the life, by comparing the four bonobo populations that varied in the degree of daily interactions with humans (keepers and public) (details in methods section II.1.3).

- Sex and age

Predictions 15 and 16: The sex and age of the individual may influence laterality.

In humans, hand preference is not established and stable in young individuals (Fagard 2004). Shifts in the direction of hand preference are observed during the first years, the preference being typically stable by 3 years old. Moreover, the strength of hand preference may increase through middle childhood. Regarding sex effect, a greater number of men than women are left-handed, i.e. about 13% of left-handers in men and 11% in women (Fagard 2004; Faurie 2004). In non-human primates, the data suggest that these factors may also influence laterality (review in Fagot and Vauclair 1991). In fact, some have suggested that the effects of sex or age may account for the variation observed between individuals; and be responsible for the absence of group-level bias that is usually reported in the literature (Vauclair and Fagot 1987). Indeed, if males were left-handed and females right-handed, no bias would appear in the group. The same applies if laterality depended on age and a mixed age group was examined without considering this factor.

In the database, several studies have reported an influence of sex on hand preference in non-human primates (e.g. Corp and Byrne 2004; Milliken et al. 1989; Spinozzi et al. 1998; Ward et al. 1990). For instance, preferences of opposite direction between males and females have been found: in bushbabies and lemurs for reaching (Milliken et al. 1989; Milliken et al. 1991) and in chimpanzees for food processing (Byrne and Corp 2003; Corp and Byrne 2004), with most males being left-handed and most females being right-handed. These specific data suggest that males could be more left-handed than females. However, the database is inconsistent, with contradictory findings and many negative results (Hopkins 2006; McGrew and Marchant 1997a). Therefore, although its effect remains unclear, sex may have an influence on laterality. It is thus an important factor to investigate and take into account when studying hand preference.

With regard to age, it is reasonable to think that the age of the individual could influence hand preference, along with maturational processes (McGrew and Marchant 1997a). In the database some studies found that laterality increased with age, with immature animals exhibiting weaker or less consistent and stable preferences than adults (e.g. (Boesch 1991; Fletcher and Weghorst 2005; Hook and Rogers 2000; Hopkins 1994; Hopkins 1995; Milliken et al. 1991; Vauclair and Fagot 1987; Ward et al. 1990; Westergaard and Suomi 1993; Westergaard and Suomi 1994; Westergaard and Suomi 1996; Westergaard et al. 1997b; Westergaard et al. 2001). Moreover, some works found that the direction of preference also varied with age (e.g. Harrison and Byrne 2000; Westergaard and Suomi 1993; Westergaard and Suomi 1994).
Several authors have suggested that the negative findings of the database may result from testing young subjects (McNeilage et al. 1987). According to them, the results of studies that tested young subjects that may exhibit an incomplete maturation (undeveloped laterality) could be erroneous (Fagot and Vauclair 1991; McNeilage et al. 1987). The database is inconsistent and inconclusive and includes many negative findings regarding age effect (Hopkins 2006; McGrew and Marchant 1997a), but it suggests that age may influence laterality. Thus, age is a very important factor to examine and control for when studying hand preference.

In my study, I systematically examined the effects of sex and age. These factors have rarely been considered in bonobos before, and previous analyses were strongly impaired by the small size of the samples (Harrison and Nystrom 2008; Hopkins et al. 1993c; Hopkins and DeWaal 1995; Shafer 1997) (see section I.4.2). Thus, this is the first time that these factors were investigated in a large sample of subjects, which allowed for reliable analysis.

- Kinship

Prediction 17: kinship may influence laterality.
As seen in section I.1, the mechanisms that determine hand preference are largely unclear (even in humans) and the transmission of hand preference remains a very controversial topic (Fagard 2004; Faurie 2004; Hopkins et al. 2001b; Hopkins 2006; McGrew and Marchant 1997a). I here briefly summarize the data on laterality in relation to kinship in non-human primates. Some studies found no effect of kinship on hand preferences (e.g. Hook and Rogers 2000; McGrew and Marchant 1992; Vauclair

and Fagot 1987), while other studies suggested that the direction of preference could be heritable (Teichroeb 1999). In chimpanzees, Hopkins' studies suggest that hand preference would be heritable (Hopkins 1999; Hopkins et al. 2000a; Hopkins et al. 2001b). For instance, one study (Hopkins 1999) reported a concordance between the preferences of siblings, which suggests a genetical transmission. However this concordance was not found for siblings that were raised separately (one by the mother and one by humans), which suggests an influence of environmental factors. Therefore, there are previous data suggesting heritability of hand preference in non-human primates. However, the data are scarce and inconclusive. Very little is known, and the mechanisms of transmission remain to be clarified. These mechanisms are likely to include genetic as well as non-genetic factors (Teichroeb 1999). The non-genetic factors that have been proposed to influence hand preference in non-human primates include: learning by imitating the mother, contact with humans, pregnancy or birth stressors, and mother's cradling behaviour (Hopkins et al. 1993a; Hopkins et al. 2000a; Hopkins et al. 2001b; Hopkins 1999) (see Damerose and Vauclair 2002; Hopkins 2004 for reviews on cradling biases).

The question of heritability of hand preference is also important with regard to Warren's hypothesis of artefactual preferences (Warren 1980). Indeed, finding evidence of a transmission of laterality from parents to offspring would demonstrate the biological nature of the feature and definitely rule out these hypotheses.

Heritability of hand preference has never been investigated in bonobos. My large sample included pairs of related individuals, which allowed me to consider this issue. I compared the preferences in mother-infant pairs, father-infant pairs and sibling pairs to investigate the transmission of laterality in bonobos.

4.4. Summary of my research work

To summarize my research, I investigated manual laterality in bonobos, which is an outstanding species for studying hand preferences, notably in relation to evolutionary hypotheses on the emergence of human handedness. I aimed to complement the scarce previous bonobo data and to provide new data on points that have not been addressed before (or not reliably so) in bonobos. As seen above, previous studies are scarce (fewer than 10) and have only tested small samples of bonobos (generally between 2 and 14 subjects). I considered a very large sample of subjects (N=94) that represented 40% of the worldwide captive bonobos and included four different populations. I assessed hand preferences for the widest possible range of spontaneous actions (both non-social and social). I also tested the bonobos on different experimental tasks that were chosen to fill notable gaps of the database. I examined the effect of many different task-related factors; including manipulation, bimanual coordination, tool-use, throwing, postural demands and gestures; that have been proposed as selective pressure for the emergence of handedness. Therefore, this comprehensive study aimed to provide a new set of crucial data to complement the scarce and inconclusive previous bonobo data. It was also designed to yield data that are comparable to that of other species, to allow reliable comparisons between studies and species. Finally, I investigated the effects of different factors that have been shown or proposed to influence hand preference in non-human primates, including settings, rearing history, sex and age (McGrew and Marchant 1997a; Warren 1980) to assess any possible influence on the results. Table 2 summarizes the predictions that have been tested in this research work.

In the following section, I present the methods used for each of the studies described above. This is followed by the presentation of the results of each study (section III) (summarized in Table 37) and a general discussion (section IV).

Section II :

Materials and Methods

This section describes the methods that have been used in this PhD research. The methodology has been designed based on previous studies and taking into account the issues that hindered previous research. The first part of this section gives general information about the species studied and the subjects considered. The second part describes the methods that have been used in each of the 4 studies. The third part presents the statistics used.

Chapter 1: Presentation of the subjects studied

1.1. The bonobo species:

In the introduction, I have highlighted the importance of studying bonobos, given their outstanding characteristics as a model species and because the previous data available are scarce (notably compared to chimpanzees). I now give general information about the species and its biology.

In contrast to chimpanzees that have long been known and studied, bonobos were only described in 1929 (Schwarz 1929) and recognized as a species distinct from the common chimpanzees in 1933 (Coolidge 1933). Behavioural research on bonobos started in the mid-1970s, and field research has been limited (two main field sites: Wamba and Lomako). Therefore, little is known about bonobos in comparison to chimpanzees, while both are equally close to humans.

- Habitat

The bonobo species is endemic to the Democratic Republic of Congo. Bonobos live in a mosaic of primary and secondary forests, as well as seasonally inundated swamp forests (De Waal and Lanting 1998; Hohmann et al. 2002). Their habitat was long thought to be restricted to a moist evergreen lowland dense forest (e.g. study sites of Lomako and Wamba) (Hohmann et al. 2002), but they have recently been studied in a dry forest/savanna mosaic habitat (study site of Lukuru) (Myers Thompson 2003). Bonobos divide their time between the trees and the ground. They are accomplished arborealists and spend a lot of time in the forest canopy (Susman 1984). They also spend a considerable amount of time on the ground (e.g. when foraging for herbaceous vegetation, when travelling between arboreal food spots) (Hohmann et al. 2002; Susman 1984). *Pan* species exhibit a great variety of locomotion modes that is thought to surpass that of other primates and allows access to the widest variety of arboreal and terrestrial food resources (Susman 1984). On the ground, bonobos use quadrupedal knuckle-walking, and sometimes adopt tripedal or bipedal locomotion (especially when carrying items); in the trees, they use quadrupedalism, quadrumanous climbing and scrambling, bimanual suspension (arm swinging), leaping and diving and bipedalism (Susman et al. 1980; Susman 1984).

- Diet

Bonobos are primarily frugivorous, with 50 to 90% of their diet being composed of fruits (De Waal and Lanting 1998; Hohmann et al. 2002; Kano 1995; Susman 1984). They complement their diet with other plant products, including a large part of terrestrial herbaceous vegetation, in the form of leaves, shoots, flowers and pith; and more than 110 species of plants are consumed. Bonobos also eat vertebrates (e.g. duikers, monkeys, squirrels, forest antelopes, snakes) and invertebrate preys (e.g. caterpillars, earthworms, millipedes) (Fruth and Hohmann 2002; Hohmann and Fruth 2008; Surbeck and Hohmann 2008; Surbeck et al. 2009) but this is a very small part of their diet. Thus, bonobos exhibit a very diverse diet in the wild.

- Life history

Bonobos can live up to 60 years in captivity, and their lifespan is estimated to be over 40 years in the wild (Rowes 1996). Males reach sexual maturity around the age of 9 years and females around the age of 8 years. Females first give birth at the age of 10.5 years old (Kano 1995). The gestation period is 7.5-8 months. Infants are sustained only by nursing during the first year of life. Infants are not weaned before 4-5 years old. The female nurses her young up to 4-5 years and is unable to conceive during that time; so the interbirth interval is 4-6 years (De Waal and Lanting 1998; Kano 1995; Rowes 1996).

1.2. Subjects studied:

Table 4 presents the subjects studied in this research, along with their characteristics (age, sex, rearing, location, kinship) and the studies in which they were analyzed.

- Total sample of subjects: N=94

- As seen in section I.3.3, most previous studies have considered small samples of subjects, which is very problematic for analysis and interpretation (Hopkins et al. 1993c; Hopkins 2006; Marchant and McGrew 1991). Testing a large sample is indeed necessary: a) to consider a representative sample of the species; b) to allow investigation of the effects of individual characteristics (e.g. sex, age, rearing history); c).to allow reliable assessment of group-level laterality for many different actions (especially for infrequent behaviours that are performed by a small proportion of subjects). In fact, I performed power analyses to determine the sample size that would be necessary to reliably detect a bias in the order of 65% like those found in chimpanzees (65% of right-handers when excluding unlateralized subjects) (Hopkins 1995). If I use a threshold of 5% for error type I (α) and 10% for error type II (β), the sample size necessary to detect a 65% bias is 53 subjects. If I accept a higher risk of missing an existing bias (error type II) and use β=20%, the minimum sample necessary is still large: 40 subjects.

Therefore, I have considered the largest possible bonobo sample. The total sample studied included 94 bonobos, which represents 40% of the worldwide captive bonobo population (ISIS 2009). This is the largest bonobo sample ever studied (four times larger than the previous largest sample N=22). Thus, the sample studied would be the first appropriate bonobo sample for allowing reliable analyses (global and detailed (for each action)) and interpretation (individual-level and species-level).

- The sample included four different populations of bonobos. Indeed, the subjects were from four different locations: three zoos and one sanctuary. 10 bonobos were housed at Twycross zoo, Twycross (England), 16 bonobos, separated in two groups, were housed at the Wilhelma zoo, Stuttgart (Germany), 9 bonobos were housed at Apenheul, Apeldoorn (Holland), and 58 bonobos, separated in four groups, were housed at Lola

Ya Bonobo sanctuary, Kinshasa (Democratic Republic of Congo). As seen in section I.3.3, studying a large sample and different populations allows reliable interpretation and generalization of the findings (McGrew and Marchant 1997a).

- Each of the bonobos tested was examined for hand/arm injuries, current or old (finger mutilations are frequent in the rescued bonobos of the sanctuary) because such injuries may influence hand use. In the analyses on hand preference, I kept only the individuals that had no hand/arm injuries (recent or old), to avoid any possible bias in hand use. In total, 8 subjects were excluded from the analyses on hand preference due to injuries (Mobikisi, Kisentu, Kikwit, Kindu, Bandundu, Keza, Etumbe and Lomami).
- Several (15) of the subjects have been studied previously for laterality in spontaneous daily actions (Table 4). They were tested several years before my study: May to November 2000 by (Harrison and Nystrom 2008) N=14 and June to August 1992 by (Hopkins et al. 1993c) N=1. The data of these subjects allow for testing consistency of hand preference over time (5 and 14 years interval), which has never been done before in bonobos.

- Group composition

Figure 1 shows the distribution of the subjects based on sex and age.

Sex: In the sample studied, 49 bonobos were males and 45 were females.

Age: The sample included: 36 adults, 13 adolescents, 33 juveniles and 12 infants, ranging in age from 3 months to 40 years, at the time of the study. Therefore, more than half of the analyzed subjects could be considered mature (i.e. belonging to the adolescent or adult category). Age classes were based on Badrian and Badrian (1984) as follows: infants: 0 to 3 years old (3 excluded); juveniles: 3 to 6 years old; adolescents: 7 to 9 years old; adults: 10 years and older. Because of the small number of infants, I combined infants and juveniles into one group for the analyses. For analyses on age categories, I analyzed age groups defined as follows:

ageregpt1, group 1: infants + juveniles; ageregpt1, group 2: adolescents + adults.
ageregpt2, group 1: infants + juveniles + adolescents; ageregpt2, group 2: adults.
Ageregpt3, group 1: infants + juveniles, group 2: adolescents, group 3: adults.

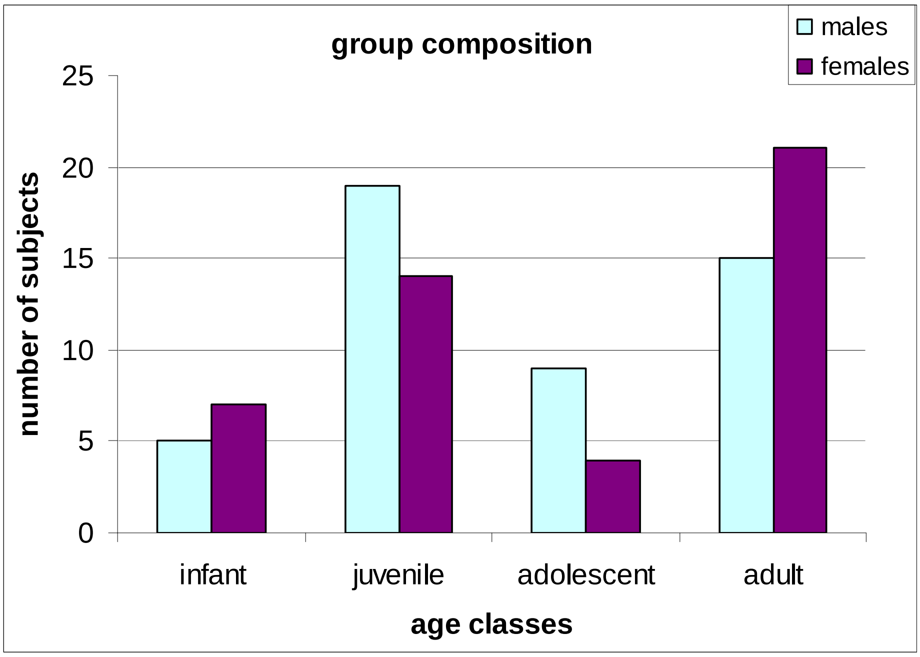

Figure 1: Distribution of the subjects studied based on sex and age.

- Rearing history

The bonobos studied had different rearing histories. Some subjects were wild born and others were born and raised in captivity, with varied degrees of interactions with humans during infancy. I distinguished three types of rearing history (defined below). In the sample, 33 bonobos were "parent-reared", 8 bonobos were "human hand-reared" and 53 bonobos were "Lola-reared".

- "Parent-reared" individuals are those that have been reared by their mother from birth to independence.

- "Human hand-reared" individuals are those that have been removed from their mother within the first weeks of life, and reared by humans during infancy (zoo nursery).

- "Lola-reared" individuals are all the bonobos living at Lola Ya Bonobo sanctuary (with the exception of Mbano and Bisengo that were parent-reared). All the bonobos of the sanctuary were orphans rescued from the bushmeat traffic and pet trade (except the infants born at the sanctuary). In the forest, the bonobos are killed for their meat. The cute infants are often captured and illegally sold as pets. Some of them are confiscated and entrusted to the sanctuary. These bonobos have thus been separated from their mother in early infancy. This separation generally occurred around 2-3 years (they cannot survive it when this happens before they are 1 year old). The history between the wild life in the forest and the arrival at the sanctuary is specific to each subject, living from a few months up to several years in a human environment. On arrival at the sanctuary, the infants are placed in a nursery with other bonobo infants, and with 4 human surrogate mothers who take care of them for several years. When they become independent (around the age of 5 years), they are placed in the enclosure within a mixed age bonobo group. Thus, “Lola-reared” bonobos have been reared by their mother from birth, but have been separated from her in early infancy, and then reared by humans until they are independent.

Table 4: Characteristics of the subjects studied.
Sex: 1 for male, 2 for female. Age classes based on (Badrian and Badrian 1984): infants < 3 yr; juveniles: 3 - 6 yr; adolescents: 7 - 9 yr; adults: 10+ yr. Asterixes indicate the subjects that have been previously studied on spontaneous actions by Harrison and Nystrom (2008) or Hopkins et al. (1993). The 8 subjects in italic were excluded from the analyses on hand preference due to hand/arm injuries.

location	name	sex	date of birth	age at the beginning of the study (in years)	age class	rearing	mother	father	origin (zoo of birth or wild born)	analyzed in studies:
Stuttgart zoo	Banbo	2	03-Sep-02	4	juvenile	hand	Banja	Keke	Twycross	1, 2, 3b
Stuttgart zoo	*Chipita	2	1993	13	adult	hand			Wild Born	1, 2, 3b
Stuttgart zoo	*Daniela	2	17-Jun-68	38	adult	parent			Frankfurt	1, 2, 3b, 4a
Stuttgart zoo	Dankie	1	13-Aug-05	1	infant	parent	Daniela	unknown	Stuttgart	4a
Stuttgart zoo	David	1	27-Jul-01	5	juvenile	parent	Daniela	Kirembo	Stuttgart	1, 2, 3b, 4a
Stuttgart zoo	*Diwani	1	11-Aug-96	10	adolescent	parent	Daniela	n° 54	Stuttgart	1, 2, 3b, 4a
Stuttgart zoo	Kasai	1	27-Dec-04	2	infant	parent	Chipita	Diwani	Stuttgart	4a
Stuttgart zoo	Khaya	2	19-Oct-01	5	juvenile	hand	Banja	Keke	Twycross	1, 2, 3b
Stuttgart zoo	Kianga	2	17-Jul-05	1	infant	parent	Kombote	unknown	Stuttgart	
Stuttgart zoo	*Kirembo	1	10-Dec-92	14	adult	parent			Stuttgart	1, 2, 3b, 4a
Stuttgart zoo	*Kombote	2	1966	40	adult	hand			Wild Born	1, 2, 3b
Stuttgart zoo	*Lina	2	28-Jul-85	21	adult	parent			San Diego	1, 2, 3b, 4a
Stuttgart zoo	*Louisoko	1	19-Apr-98	8	adolescent	parent	Lina	n° 54	Stuttgart	1, 2, 3b
Stuttgart zoo	Lucuma	1	29-Oct-02	4	juvenile	parent	Lina	Kirembo	Stuttgart	1, 2, 3b, 4a
Stuttgart zoo	Mixi	2	18-Dec-01	5	juvenile	parent	Chipita	Kirembo	Stuttgart	1, 2, 3b
Stuttgart zoo	*Zorba	1	1980	26	adult	hand			Wild Born	1, 2
Twycross zoo	*Banja	2	01-Feb-90	15	adult	parent			Koln	1, 2, 3b, 4a
Twycross zoo	Bokela	2	14-Oct-03	2	infant	parent	Banja	unknown	Twycross	1, 4a
Twycross zoo	Cheka	2	18-Mar-96	9	adolescent	parent			Frankfurt	1, 2, 4a, 3a, 3b
Twycross zoo	*Diatou	2	21-Oct-77	28	adult	hand			Stuttgart	1, 2, 3b, 4a
Twycross zoo	Gemena	2	07-Nov-05	0	infant	parent	Cheka	unknown	Twycross	4a
Twycross zoo	*Jasongo	1	02-Aug-90	15	adult	hand			Wuppertal	1, 2, 3a, 3b, 4a

table 4 continued	**name**	**sex**	**date of birth**	**age at the beginning of the study**	**age class**	**rearing**	**mother**	**father**	**origin (zoo of birth or wild born)**	**analyzed in studies:**
Twycross zoo	*Kakowet II	1	07-Jun-80	25	adult	hand			San Diego	1, 2, 3b, 4a
Twycross zoo	*Keke	1	02-Jan-94	11	adult	parent	Diatou	Kakowet II	Twycross	1, 2, 3b, 4a
Twycross zoo	*Kichele	2	19-Apr-89	16	adult	parent	Diatou	n° 54	Stuttgart	1, 2, 3b, 4a
Twycross zoo	Luo	1	01-Dec-02	3	juvenile	parent	Diatou	Jasongo	Twycross	1, 2, 4a
Apenheul	Jasiri	2	06-Nov-02	4	juvenile	parent	Lomela	Mwindu	Apenheul	1, 2, 4a
Apenheul	*Jill	2	15-Jul-85	21	adult	parent			Yerkes	1, 2, 4a
Apenheul	Kumbuka	2	09-Jul-99	7	adolescent	parent			Apenheul	1, 2, 4a
Apenheul	Liboso	2	17-Jan-98	8	adolescent	parent	Zuani	n° 1006	Kinshasa	1, 2, 4a
Apenheul	Lingala	2	17-Jul-03	3	juvenile	parent	Jill	Mwindu	Apenheul	1, 2, 4a
Apenheul	Lomela 1	2	19-May-92	14	adult	parent			Frankfurt	1, 2, 4a
Apenheul	*Mobikisi*	1	1981	25	adult	parent			Wild Born	1, 4a
Apenheul	Mwindu	1	1985	21	adult	parent			Wild Born	1, 2
Apenheul	Nayembi	2	26-Apr-06	0	infant	parent	Liboso		Apenheul	
Apenheul	Zuani	2	1991	15	adult	parent			Wild Born	1, 2, 4a
lola enclos2	Api	1	Oct-00	7	adolescent	lola			Wild Born	1, 2
lola enclos1	*Bandundu*	2	May-97	11	adult	lola			Wild Born	4b
lola enclos1	Beni	1	Mar-98	10	adult	lola			Wild Born	1, 2, 4b
lola enclos3	Bili	1	Oct-01	6	juvenile	lola			Wild Born	1, 2, 4b
lola enclos2	Bisengo	1	Aug-05	3	infant	parent	Maya	unknown	Lola	1, 2, 4a
lola enclos3	Boende	1	2000	7	adolescent	lola			Wild Born	1, 2, 4b
lola enclos1	Bolobo	1	2003	5	juvenile	lola			Wild Born	1, 2, 4b
lola nursery	Boyoma	1	2004	4	juvenile	lola			Wild Born	2
lola enclos3	Dilolo	1	May-01	6	juvenile	lola			Wild Born	1, 2, 3a, 4a, 4b
lola nursery	Eleke	1	2003	5	juvenile	lola			Wild Born	2
lola enclos1	Elikya	2	Sep-05	3	infant	parent	Semendwa	unknown	Lola	1
lola enclos2	*Etumbe*	2	INRB		adult	lola			Wild Born	
lola enclos2	Fizi	1	May-00	7	adolescent	lola			Wild Born	1, 2
lola enclos1	Ilebo	1	2001	6	juvenile	lola			Wild Born	1, 2, 4b

table 4 continued	**name**	**sex**	**date of birth**	**age at the beginning of the study**	**age class**	**rearing**	**mother**	**father**	**origin (zoo of birth or wild born)**	**analyzed in studies:**
lola enclos2	Isiro	2	Jul-97	11	adult	lola			Wild Born	1, 2, 4b
lola enclos1	Kalina	2	Jan-98	10	adult	lola			Wild Born	1, 2
lola enclos1	Kasongo	1	May-02	6	juvenile	lola			Wild Born	1, 2
lola nursery	Katako	2	2004	4	juvenile	lola			Wild Born	2
lola enclos2	*Keza*	1	INRB		adult	lola			Wild Born	2
lola enclos3	Kikongo	1	Mar-01	7	adolescent	lola			Wild Born	1, 2, 4b
lola enclos1	*Kikwit*	1	Oct-97	11	adult	lola			Wild Born	4b
lola enclos1	*Kindu*	1	2001	6	juvenile	lola			Wild Born	
lola enclos1	*Kisantu*	2	Apr-98	10	adult	lola			Wild Born	
lola enclos3	Kubulu	1	2002	6	juvenile	lola			Wild Born	1, 2, 4b
lola enclos3	Likasi	2	Sep-01	6	juvenile	lola			Wild Born	1, 2, 3a, 4b
lola enclos2	Lisala	2	Sep-01	6	juvenile	lola			Wild Born	1, 2, 4b
lola enclos3	Lodja	2	Feb-03	5	juvenile	lola			Wild Born	1, 2, 4a
lola enclos2	*Lomami*	1	Feb-99	8	adolescent	lola			Wild Born	
lola nursery	Lomela 2	2	2003	5	juvenile	lola			Wild Born	2
lola enclos2	Lukaya	2	May-01	6	juvenile	lola			Wild Born	1, 2
lola enclos3	Luozi	1	2003	5	juvenile	lola			Wild Born	1, 2
lola enclos3	Mabali	1	2001	6	juvenile	lola			Wild Born	1, 2
lola enclos2	Makali	1	INRB		adult	lola			Wild Born	2
lola enclos1	Malaika	2	Apr-07	1	infant	parent	Kalina	unknown	Lola	4a
lola enclos3	Maluku	2	2002	6	juvenile	lola			Wild Born	1, 2
lola enclos3	Maniema	1	2001	6	juvenile	lola			Wild Born	1, 2
lola enclos1	Manono	1	Aug-94	14	adult	lola			Wild Born	1, 2
lola enclos1	Matadi	1	Apr-01	7	adolescent	lola			Wild Born	1, 2, 4b
lola enclos2	Max	1	May-86	22	adult	lola			Wild Born	1, 2
lola enclos2	Maya	2	Aug-93	15	adult	lola			Wild Born	1, 2, 4b
lola enclos2	Mbandaka	1	2001	6	juvenile	lola			Wild Born	1, 2, 4b
lola enclos2	Mbano	1	Mar-05	3	juvenile	parent	Etumbe	unknown	Lola	1, 2

table 4 continued	**name**	**sex**	**date of birth**	**age at the beginning of the study**	**age class**	**rearing**	**mother**	**father**	**origin (zoo of birth or wild born)**	**analyzed in studies:**
lola enclos1	Mimia	2	Oct-82	26	adult	lola			Wild Born	1, 2, 4b
lola enclos2	Mixa	1	Dec-98	9	adolescent	lola			Wild Born	1, 2, 4b
lola enclos3	Moyi	1	Aug-07	1	infant	parent	Tshilomba	unknown	Lola	4a
lola nursery	Muanda	2	2003	5	juvenile	lola			Wild Born	2
lola enclos1	Nioki	2	Dec-98	9	adolescent	lola			Wild Born	1, 2, 4b
lola enclos1	Opala	2	Jun-95	13	adult	lola			Wild Born	1, 2, 4b
lola enclos1	Pole	1	Apr-06	2	infant	parent	Opala	unknown	Lola	1, 4b
lola nursery	Sake	2	2005	3	infant	lola			Wild Born	2
lola enclos1	Salonga	2	Oct-97	11	adult	lola			Wild Born	1, 2
lola enclos1	Semendwa	2	Nov-96	12	adult	lola			Wild Born	1, 2, 4b
lola enclos1	Tatango	1	Nov-95	13	adult	lola			Wild Born	1, 2
lola enclos2	Tembo	1	Oct-97	11	adult	lola			Wild Born	1, 2, 4b
lola nursery	Tshilenge	2	2003	5	juvenile	lola			Wild Born	2
lola enclos3	Tshilomba	2	INRB		adult	lola			Wild Born	1, 2, 4b
lola nursery	Vanga	1	2004	4	juvenile	lola			Wild Born	2
lola enclos3	Yolo	1	2003	5	juvenile	lola			Wild Born	1, 2

1.3. Settings:

Table 5 summarizes the information about the different settings.

- Twycross zoo

At Twycross zoo, the cage for the 10 bonobos included a grassy outdoor enclosure (25 x 16m hexagon, surface 800m²) connected with an indoor part divided into two rooms (9.5 x 5.5m and 9.5 x 6m).

- Stuttgart zoo

At Stuttgart, the 16 bonobos were separated into two groups and the space available was very small. One group was housed in a room (9.32 x 5.25m) connected with a small outdoor area (6.5 x 4.75m). The other group was housed in a small room (4.12 x 2.75m) connected with an outdoor area (4 x 9.5m) and all had concrete floors.

- Apenheul zoo

At Apenheul, the 9 bonobos were housed on a large island with grass, bushes and trees (area: 4.670m^2). The island was connected with a large indoor part divided into four rooms (total area: 175.2m², biggest room: 77.3m² with a height of 8.2m).

- Lola Ya Bonobo sanctuary

At Lola Ya Bonobo sanctuary, the 58 bonobos were semi-free ranging. The enclosure was a 30 hectares area of rainforest. This area was divided into three separate enclosures (enclos1, enclos2, enclos3) that each hosted a group of about 15 bonobos (N=20 for enclos1, N=16 for enclos2, N=14 for enclos3). Each of these enclosures had a small enclosure that was used to isolate the individuals in the routine of the sanctuary, and a house where the bonobos slept at night. The infants that did not yet live in the enclosure (N=8) were in the nursery. This was a small area of forest that was not surrounded with wire netting.

- Food and objects available

A variety of objects were available for the bonobos to interact with and manipulate. All the zoo settings provided platforms on the walls, and ropes and wood structures within the area of the room. Moreover, at Twycross zoo, the bonobos occasionally received cardboard boxes, plastic objects and rags. At Stuttgart zoo, the bonobos were sometimes given leafy branches. At Apenheul, the bonobos had straw indoor, and natural objects on the island (though the trees were protected with wire netting to prevent them from climbing). At Lola Ya Bonobo, the bonobos benefited from the forest environment and water pond areas.

With regard to food, the bonobos received a variety of fresh fruit and vegetables at least twice a day. The food given was raw so the bonobos had to process it before eating (e.g. peeling). In the zoos, they sometimes received extra food as enrichment, which was given in designs that required complicated and time consuming manipulations before the food could be eaten (e.g. food hidden inside an object).

- Contact with humans

In Europe, zoos are the first visited places of a town and receive millions of visitors each year. The bonobos that lived in zoos were thus subjected to an important exposure to human visitors. The sanctuary in Africa was also open to visitors, but their number was tiny in comparison to European zoos.

The distance between the bonobos and the public was almost none for the indoor rooms in the zoos (as the public stood right behind the glass). At Apenheul, the bonobos were far from the public when outside on the island (as the public stood on the roof of the bonobo house), and this zoo was closed during winter.

Regarding interactions with the keepers, the bonobos had limited interactions with them at Twycross zoo. At the other places, the keepers interacted more with the bonobos. This depended on the zoo policy.

Therefore, the four study sites varied with regard to several factors, including: the amount of space available and the asymmetry of the living areas, the degree of interactions with humans (keepers and public) and the variety of external stimuli available.

Globally, the settings varied with a general gradient from very unnatural settings at Stuttgart and Twycross (small cages) to more natural at Apenheul (island), to natural-like at Lola Ya Bonobo (forest enclosure) (Table 5). Therefore, the subjects studied experienced very different living conditions.

Table 5: Information about the living conditions of the bonobos studied.
N total: number of subjects in the group, N tested: number of subjects tested/studied.

	N total	N tested	Description of the setting	Interaction with the keepers	visitors
Lola Ya Bonobo sanctuary (DR Congo)	58	48	The enclosure was a 30 hectares area of rainforest. It was divided into three separate enclosures (enclos1, enclos2, enclos3) that each hosted a group of about 15 bonobos	some interaction	very few. close distance to the bonobos
Twycross zoo, Twycross (England)	10	8	The cage included a grassy outdoor enclosure (25 x 16m hexagon, surface 800m²) connected with an indoor part divided into two rooms (9.5 x 5.5m and 9.5 x 6m)	very limited interaction	very numerous. close distance to the bonobos
Apenheul zoo, Apeldoorn (Holland)	9	8	The bonobos were housed on a large island with grass and bushes (area: 4.670m^2). The island was connected with a large indoor part divided into several rooms (total area: 175.2m², biggest room: 77.3m² with a height of 8.2m)	some interaction	very numerous. far from the bonobos (and the zoo closes during winter)
Wilhelma zoo, Stuttgart (Germany)	16	13	The bonobos were separated into two groups and the space available was very small. One group was housed in a room (9.32 x 5.25m) connected with a small outdoor area (6.5 x 4.75m); the other group was housed in a small room (4.12 x 2.75m) connected with an outdoor area (4 x 9.5m) (all concrete floor)	some interaction	very numerous. close distance to the bonobos

- Research policy of the study sites

The four study sites had strict regulations regarding research. In fact, at all these places, only observational work was allowed. It was not possible to engage in any experimental procedure that involved disturbing the subjects in any way. This restricted my work to that presented in this thesis. Moreover, it was not possible to isolate the subjects for testing.

1.4. Observations times:

The main study was preceded by a one month pilot study. This pilot study was necessary to enable me to test the methods, in order to choose the most appropriate techniques for data collection, coding and analysis. These preliminary observations also allowed for establishment of the behavioural list and familiarization with the methods used. The pilot study was carried out at Twycross zoo between the 15th of August and the 11th of September 2005 (28 days).

For the main study that followed the pilot, the observations included 188 days in total. These observations were conducted between March 2006 and December 2007.

- At Twycross, the observations were conducted between the 7th of March and the 11th of May 2006 (60 days).
- At Stuttgart, the space available was very small and the environment was not suitable for observing lateralized behaviour (especially social behaviours). Thus the length of observations was reduced to the minimum time required for performing the “tube task”. Observations were conducted between the 28th of May and the 17th of June 2006 (21 days).
- At Apenheul, the observations were conducted between the 19th of July and the 1st of October 2006 (65 days).
- At Lola Ya Bonobo, the observations were conducted between the 8th of November and the 20th of December 2007 (42 days). This length was the maximum time allowed by the funding that covered the research fees of the sanctuary (see acknowledgements).

1.5. Total data analyzed:

Table 6 presents the data analyzed in each study.

Table 6: Data analyzed in each of the four studies.
Total data analyzed, after removing the individuals that had not enough data points for analysis (n<6 or n<15 for the "tube task" see section II.3). "Behavioural patterns", "frequency", "bouts" and "bout length" are defined in the glossary.

	number of subjects included in the analyses	number of data points analyzed	mean number of data points per subject	bout length*
Study 1 Total (bouts)	71	11131	mean number of data points per subject: 156.775 (min: 11, max: 825, SD:175.157)	
Study 1 Per behaviour (bouts)			mean number of data points per subject per behaviour: 6.643 (min: 6, max: 359)	
Study 1 Per behavioural pattern (bouts)			mean number of data points per subject per behavioural pattern: 6.791 (min: 6, max: 359)	
Study 2 zoos (frequency)	29	7889	mean number of data points per subject: 272 (SD: 164,612) (min: 47, max: 656)	
Study 2 zoos (bouts)	29	1381	mean number of bouts per subject: 47.62 (SD: 20,455) (min: 15, max: 98)	mean number of data points per bout: 5.71 (min: 1, max: 44)
Study 2 lola (frequency)	48	7058	mean number of data points per subject: 147.042 (SD: 75,33) (min: 17, max: 332)	
Study 2 lola (bouts)	40	1186	mean number of bouts per subject: 29.65 (SD: 11.26) (min: 15, max: 56)	mean number of data points per bout: 5.51 (min: 1, max: 44)
Study 2 Lola + zoos (frequency)	77	14947	mean number of data points per subject: 194,1 (SD: 131,2) (min: 17, max: 656)	
Study 2 Lola + zoos (bouts)	69	2567	mean number of bouts per subject: 37,2 (SD: 18,02) (min: 15, max: 98)	
Study 3b data from videos (frequency)	7	2279	mean number of data points per subject: 325,571 (SD: 250.822) (min: 25, max: 784)	
Study 3b data from videos (bouts)	7	332	mean number of bouts per subject: 47,429 (SD: 27.27) (min: 6, max: 78)	mean number of data points per bout: 6.864 (min: 1, max: 71)
Study 3b data from videos + direct observations (bouts)	19	1005	mean number of bouts per subject: 52,895 (SD: 37.154) (min: 6, max: 131)	
Study 4a Total (bouts)	32	4013	mean number of data points per subject: 125,406 (min: 6)	
Study 4a Per behaviour (bouts)			mean number of data points per subject per action: 26,229 (min: 6, max: 167, s.e.: 0.205)	
Study 4a Per behavioural pattern (bouts)			mean number of data points per behavioural pattern: 119.784 (min: 6, max: 634, s.e.: 3.868)	
Study 4b (bouts)	24	348	mean number of data points per subject: 14.5 (SD: 6.058) (min: 6, max: 30)	

Chapter 2: Description of the procedures used in each study

Study 1: spontaneous daily actions

- Subjects included in study 1

The total sample studied included 94 bonobos from the four study sites. 71 individuals provided enough data for individual-level analysis (minimum of 6 data points) (Table 4). There were 31 bonobos from the zoos and 40 bonobos from the sanctuary. The sample comprised 37 males and 34 females. There were 31 young subjects (infants + juveniles), 12 adolescents and 28 adults.

- Data recorded

Behaviours: The behaviours studied were familiar actions that were part of the daily routine of the individuals. I recorded all the manual behaviours; as well as all other behaviours (e.g. posture) that could be performed asymmetrically. A behavioural list was made during preliminary observations (one month pilot study), and completed as the work progressed. This comprehensive list included 140 behaviours.Table 7 gives the list of all the behaviours considered. For the analysis, I only kept the behaviours for which at least one subject provided enough data, which rendered 32 behaviours.

Number of data points per subject: I set the minimum number of data points at 6, which is the minimum required for performing the Binomial test (Seagel and Castellan 1988) (see section II.3.4). Thus, for each action, only the individuals for whom I had at least 6 observations were kept in the analysis.

For each data point, I recorded: the individual's identity, the action performed, which hand was used to perform the action, the activity of the other hand (inactive, postural support, holding an object, holding a food item, holding a food item against the ground, social action) and the posture of the subject (seated, tripedal, supine, bipedal, lying on the belly, lying on the left/right side, extended tripedal), which are variables that have been recorded in several previous studies (Chapelain et al. 2006; Fletcher and Weghorst 2005; Harrison and Nystrom 2008; Hopkins and DeWaal 1995; Marchant and McGrew 1996; Marchant and McGrew 2007; McGrew and Marchant 2001). I also recorded information about the object that was manipulated (e.g. glass, bucket, yogurt pot, cardboard box, bottle, rag, straw, branch, twig, sand, stone), the body part that was touched (e.g. right side of the face, left shoulder, right leg, genitals) and the type of locomotion if moving (walk, quick walk, run). This detailed recording was to enable me to investigate and control for the effects of these possible influential factors.

I also recorded any possible source of bias that could affect hand use. For instance, I recorded whether there was a bias due to the position of the object relative to the hands (i.e. the object was located closer to the hand that was used) (Fagot et al. 1991; Marchant and Steklis 1986; Vauclair and Fagot 1987), a bias due to the posture of the subject (e.g. the bonobo was lying on the right side, which prevented right hand use) or a bias in the environment (e.g. there was a wall on the left side that prevented left hand use). In the analysis, I excluded all those cases when the hand used could have been influenced by such external factors.

In addition, I controlled for possible influence of different posture or activity of the other hand. Indeed, in cases when the other activity or posture could not be investigated because of a small sample, I removed the rare behavioural patterns to standardize the action (see Table 9). For instance, for "swinging", the other hand was generally inactive. It was only rarely used to hold an object or food item that may influence hand use. Therefore, the cases when the other hand was not inactive were removed from analysis, to standardize the action to "swinging with other hand inactive".

Analysis: I performed analyses on each behaviour separately. Furthermore, I split the behaviours into behavioural patterns, according to the posture and action of the other hand (whenever possible). Examples of behavioural patterns are: feeding while seated with the other hand in postural support, feeding while seated with the other hand inactive, feeding from a tripedal posture. I analyzed each behavioural pattern separately. This detailed level of analysis allowed for investigating and controling for the effects of the posture and activity of the other hand on laterality. I analyzed a total of 53 behavioural patterns.

Contrary to previous studies, we did not perform any analysis on pooled data ("overall limb use"). Indeed, analyzing each action separately is the most appropriate technique for investigating hand use because laterality depends on the action considered. Hand preference varies between tasks so examining overall limb use (merging different actions together) may hide significant effects for individual actions, mask the asymmetries and lead to false negative findings (Fagot and Vauclair 1991). Moreover, from a statistical point of view, analyzing pooled data is nonsensical unless we have the same number of events for each action and from each subject, which was not the case.

- Recording technique

I observed the bonobos during their spontaneous daily behaviour. The subjects were observed each day, between 4 and 5 hours a day, on successive days. The observations were spread over the day, between the zoo opening hour and its closure hour. The observations times varied between days to optimize the representativeness of the sample of data; with obligatory observations periods at feeding times, when the bonobos were the most active. Data collection was made by direct observation with recording of vocal comments on a Dictaphone. I used direct observation instead of video taping because when I tested video taping during the pilot study, this approach appeared inappropriate. Indeed, the field did not include the whole enclosure and could not allow following all individuals at the same time. Moreover, the image quality did not permit recognition of the individuals at a distance.

The sampling method chosen was based on the preliminary observations and tests done during the pilot study. I have tested "*Focal animal sampling*" (Altmann 1974), which is a formal recording technique in behavioural research. However, this technique appeared unsuitable during the pilot study. Indeed, focusing on one individual at a time entailed losing most of the information that could be recorded, i.e. all what happened in the rest of the group. Originally, the main focus of my study was social actions that are infrequent events (especially when considering dyad-level analysis). "*Focal animal sampling*" is not appropriate for recording rare events, so I instead used "*Ad libitum*" sampling (Altmann 1974), which is observing all the individuals of the group at the same time. I scanned the group continually and recorded all occurrences of the behaviours studied, whenever they occurred. This method was the best way to optimize data recording, especially regarding infrequent actions. When using this method, I assumed that "the likelihood that a behaviour would be observed and recorded does not depend on" laterality (Altmann 1974). It is indeed reasonable to think that the chance that a particular behaviour would be recorded does not depend on whether it is performed with the right or left hand.

Data independence: Every effort was made to ensure that the data points recorded were independent of each other (see section II.3.5). I recorded **bouts** instead of events (**frequency**) (Marchant and McGrew 1991; McGrew and Marchant 1996; McGrew and Marchant 1997a; Westergaard and Suomi 1996). Namely, when the actions occurred in a sequence, I counted only the first action of a sequence (each sequence was then counted as one bout). Two identical actions were considered independent only if they were separated by an intervening action (McGrew and Marchant 1997a), which is an action by which the subject could have changed its hand. For instance, a new bout was recorded after the individual had dropped the item.

Table 7: Behaviours that have been recorded in study 1.

bipedal movement dragging an object
bipedal movement holding a food item in one hand
bipedal movement holding an object in one hand
bipedal movement holding object/food item close with one arm
bipedal movement while drinking from the glass with one hand
bipedal movement while taking a food item to the mouth
break a piece from the food item
catch a flying insect
catch a food item in the air
clean food item in water
crack open nuts with a stone
dig
dip a finger into the hole (termite mound, log, fixed tubes)
dip the container into the water pond, fill it and take it out
dip the container into the water pond, fill it, but take it out with the other hand
dip the rag into the bucket which contains water
dip the twig into the hole (termite mound, log, fixed tube)
drag a branch
drink from a container that requires holding with both hands (watering can) (hand closer to mouth recorded)
drink with the hand
empty the glass
forage
forage in bushes
forage in straw
go forward and backward while pushing an object
groom itself
hang with one arm
hang with one arm and both feet
hold its own hand or foot with one hand
insert a finger into its anus
insert a finger into its genitals (cleaning)
insert a finger into its nose
insert hand in throat
jump and catch the rope
jump with one arm extended to reach the strap
leading limb in locomotion
make current in water
make lateral movements in water
manipulate parts of its face
massage itself with an object
move an object laterally on the floor
move straw or litter aside
move with one foot stuck against the floor
move with one hand stuck against the floor
pat its chest with one hand
pat its chest while arms are crossed
pat its side with one hand
pat its side while arms are crossed
peel the fruit
pick its teeth
pick over items held in the other hand
play with an object
pluck berries
pluck hair
pluck leaves
pull grass out
pull leaves out
pull the fixed object
pull the rope
pull water vegetation out
push an object while moving
push the hanging object
put its hand on its head as protection
put the glass full of water on the floor
put the item in the other hand before moving
put the item in the other hand before taking it to the mouth
put the item in the other hand before throwing it
put the object on its back
put the stone in the other hand before cracking open nuts with it
quadrupedal movement dragging an object
quadrupedal movement holding a food item in one hand
quadrupedal movement holding an object in one hand
quadrupedal movement holding the glass full of water in one hand
rake seeds on the floor

reach for an object
reach for big items
reach for small items (seeds)
reach for something in the water pond
reach in bushes
reach into the glass which is held by the other hand
reach into the glass/bucket which is on the floor
retrieve feces during excretion
rub its chest with both hands (hand above recorded)
rub its chest with one hand
rub its side with one hand
rub the floor with one hand
rub (clean) the floor or wall with a rag
scratch itself with an object
scratch itself with one finger
scratch itself with one hand
search in the hole underneath the tree
search under the door with a stick
shade its eyes with its hand
slap an object against the floor
slap grass laterally
slap in water
slap its back
slap on the food item which is on the floor
slap on the tube which is on the floor
slap the food item against the floor
stand on one foot
suck its thumb
sweep litter or floor
swing while hanging with one arm
take feces to the mouth
take food item from the other hand
take the container to the mouth and drink
take the food item to the mouth (feed)
take the glass full of water from the floor
take the object to the mouth
throw an object
touch a scary object
touch its face
touch/rub/scratch/explore its genitals
tripedal movement dragging an object
tripedal movement holding a food item in one hand
tripedal movement holding an object in one hand
tripedal movement holding object/food item close with one arm
tripedal movement holding the glass full of water in one hand
tripedal movement while drinking from the glass with one hand
tripedal movement while reaching for small items
tripedal movement while taking a food item to the mouth
tripedal movement while taking an object to the mouth
try to break the stick/tube by pushing in the middle with one foot
try to catch a flying insect
try to catch a food item in the air
try to reach for something in the water pond
turn the perche
turn while hanging at the end of the rope with one hand and both feet
use a stick to try to catch an item outside of the cage

Non-manual actions:

arm around neck (posture)
arms crossed (arm on top recorded) (includes arms crossed and hands crossed)
legs crossed (leg on top recorded) (includes legs crossed and feet crossed)
legs crossed with a foot on the knee
run in circles
seated with swollen genitals on one side
turning around an object (e.g. tree)
turning in the air while jumping
turning while standing
turning while supine

Grip types:
- lateral grip type: grasping the item between the pulp of the thumb and the side of the index finger (1p2mlat).
- dorsal grip type: grasping the item between the index and middle fingers (dorsal side of the hand).
- index dorsal grip type: grasping the item between the index dorsal side and the middle finger (2dd3t).
- one finger grip type: sticking the item on the pulp of the index finger.

Study 2: the "tube task"

- Subjects included in study 2

The total sample included 94 bonobos from the four study sites. 77 individuals provided enough data for individual-level analysis with frequency* (minimum of 15 data points. see below) (Table 4), which is the largest sample ever analyzed in bonobos. The 77 subjects were: 8 bonobos from Twycross zoo, 13 bonobos (separated in two groups) from Stuttgart zoo, 8 bonobos from Apenheul zoo and 48 bonobos (separated in four groups) from Lola Ya Bonobo sanctuary. There were 40 males and 37 females. The group included 29 adults, 12 adolescents, 32 juveniles and 4 infants (Badrian and Badrian 1984). Regarding rearing history, 23 bonobos were "mother-reared", 8 bonobos were "human hand-reared" and 46 bonobos were "Lola-reared".

- Experimental protocol

Hand preferences were assessed using the "tube task" (Hopkins 1995). This task was specifically chosen to allow comparisons with other studies. The methodology was based on that of previous studies (see Table 3 that reviews the previous studies). For the "tube task", the individual holds a tube with one hand while reaching for food inside with a finger of the other hand. The tubes were white plastic tubes (15cm in length, 32mm in diameter) baited with some sticky food (honey, peanut butter or syrup). The food was smeared on the inside edge at both ends of the tubes (10cm long, 3mm thick). The baited tubes were given to the group in the home cage. They were spread on the floor when the bonobos were away or thrown into the enclosure to the bonobos. At the sanctuary, the bonobos were tested in the small isolation enclosures and in the night houses, to allow the observations and avoid the loss of the tubes in the forest. The number of tubes was superior to the number of individuals, to avoid fights and to allow the low ranked individuals to have access to the tubes (Hopkins 1995; Vauclair et al. 2005; Westergaard and Suomi 1996).

10 to 12 test sessions were performed for each of the 8 bonobos groups; at the rate of one test session per day, on successive days. Thus, on average, each subject was tested on 9 different days in the zoos (min=4, max=11) and on 8 different days at Lola Ya Bonobo (min=3, max=12). This number of test sessions was higher than that of previous studies (Table 3). Testing on many sessions was to ensure a sufficiently large dataset for each individual.

The test sessions were videotaped. This approach could be used here because the animals were not moving around when using the tubes but seated, and because a test session only lasted between 15 and 60 minutes. Using a video camera greatly optimized data collection. It enabled me to get all the data simultaneously from all the individuals located in the field. Since all the individuals were using tubes at the same time, it was not possible to observe all the individuals simultaneously via direct observation and focusing on one individual at a time would have meant losing the information for the rest of the group. Using videos also allowed for detailed analysis of hand and finger use. Video analysis was done using Windows media player and "*Focal animal sampling*" (Altmann 1974) was used as sampling technique during video analysis. At Lola Ya Bonobo, filming was not possible because the experiment had to be done in dark sleeping houses when the bonobos came to sleep in the evening and the visibility was not good enough for filming. Thus, at this study site, the observations were done directly, with recording of vocal comments on a Dictaphone and focusing on one individual at a time.

- Data recorded

Behaviour: The behaviour studied was "dipping the finger into the tube" that was held by the opposite hand. During this bimanual coordination, the hand assuming the active role was the one extracting the food, and the hand holding the tube was considered as subordinate. The action analyzed was "inserting the finger into the tube, removing it and bringing it to the mouth". Incomplete movements were not taken into account (e.g. dipping without taking the finger to the mouth). This requirement was to standardize the data between trials and with the data of previous studies.

For each data point, I recorded: the individual's identity, which hand held the tube, which hand was used to extract food from the tube, which digit was used (index, middle finger, thumb, ring finger, index and middle fingers, middle and ring fingers, unknown/digit not visible), the number of tubes held by the subordinate hand (1 to 4), the number of tubes held by the active hand (if any), the posture of the subject (e.g. seated, bipedal, supine) and other information, including whether the tube was held by one foot or by another individual. This detailed recording was to enable me to investigate and control for the effects of these possible influential factors.

Analysis: For the analyses, I removed all cases when: the subject held more than one tube in the subordinate hand, held a tube in the active hand, held the tube with one foot and when the tube was held by another individual. These requirements were set to ensure that I analyzed only "bimanual coordinated actions", and that the action studied was standardized between trials and between individuals.

- Recording techniques

Two different recording techniques were used: "**frequency**" and "**bouts**".

Frequency: For the frequency, I counted every time that the subject "inserted its finger into the tube and brought it to the mouth". I recorded this variable because it has been used in most other "tube task" studies (Table 3). It was necessary for between-studies comparisons. However, this method has been criticized on the grounds of lack of data independence (McGrew and Marchant 1997a; Palmer 2003). Indeed, the use of one hand could influence the following use of this hand in the subsequent trials of the sequence. The data points that are in a sequence of actions would not be independent of each other. Recording every trial in a sequence may thus introduce biases in the sample and is disputed (Byrne and Byrne 1991; Lehman 1993; Marchant and McGrew 1991; McGrew and Marchant 1997a; Palmer 2002; Palmer 2003).

Bouts: To ensure that the data points were strictly independent of each other, I recorded bouts for the action "inserting the finger into the tube and bringing it to the mouth". Bouts are specifically designed to record independent data points, as explained below (Byrne and Byrne 1991; Marchant and McGrew 1991; McGrew and Marchant 1997a). I counted one bout for one sequence of identical actions, by recording only the first pattern of a sequence (Marchant and McGrew 1991; McGrew and Marchant 1996; McGrew and Marchant 1997a; Westergaard and Suomi 1996). A sequence was considered terminated when the subject dropped the tube, changed the hand holding the tube or manipulated the tube with both hands (an action by which the subject could have changed its hand) (locomotion with the tube in one hand was not considered as a separating event). After such an intervening action, the hand used in the next bout was considered independent of the one used previously (McGrew and Marchant 1997a). These high requirements were set to ensure strict independence of the data points recorded (McGrew and Marchant 1997a).

Some have argued that recording bouts could raise issues because of the differences in bout lengths (Hopkins et al. 2001c). Indeed, I counted one bout for one sequence of identical actions, but the sequences varied in length (i.e. the number of data points per bout varied). To investigate this issue, I analyzed bout length to examine possible asymmetries in bout length.

The debate over the use of frequency or bouts is an ongoing discussion. Some researchers try to demonstrate that frequency and bouts would provide similar results (Hopkins et al. 2001c; Hopkins and Cantalupo 2003; Hopkins et al. 2004; Hopkins and Cantalupo 2005; Hopkins et al. 2005a; Palmer 2002; Palmer 2003; Westergaard and Suomi 1996). In this study, I investigated this hypothesis by comparing the data obtained with frequency and with bouts.

<u>50 frequency data points</u>: It has been proposed that the difference between the findings obtained with frequency and with bouts may come from a difference of sample size (Hopkins et al. 2001c). Indeed, when recording frequency, the sample of data obtained is much larger than that for bouts. In fact, recording frequency is suspected to artificially inflate the sample size of data (McGrew and Marchant 1997a) and bias the findings toward false-positive effects (Byrne and Byrne 1991; Lehman 1993; Marchant and McGrew 1991; McGrew and Marchant 1992; McGrew and Marchant 1997a; Palmer 2002; Palmer 2003). Inflating the sample size might create significant preferences because significant biases are more likely to appear with big than small samples (Hopkins 2006; Hopkins et al. 2001c; Hopkins et al. 2005a; McGrew and Marchant 1997a). I tested the effect of sample size difference in the study in zoos. The mean number of data points per subject was 272 for frequency and 48 for bouts. I modified the data for the frequency to obtain a new variable that included only 50 data points, which was used to compare frequency and bouts on similar sample sizes (mean=50). Namely, I cut out the data points over 50, keeping only the first 50 data

points. It should be noted that these 50 points were not necessarily the first 50 trials for the individual on the task, as it could have used the tube before, without being recorded (i.e. individual outside of the camera field).

Number of data points per subject: For this experimental study that focused on one behaviour, I obtained a larger sample of data than in my other studies. In fact, I had enough data for all the subjects that performed the task. It was thus possible to set a stricter inclusion criterion than in my other studies (see section II.3.4). Thus for this study, I analyzed only the individuals that had a minimum of 15 data points.

Observations Times: The "tube task" experiment was conducted from 1st to 11th September 2005 at Twycross zoo, from 2nd to 17th June 2006 at Stuttgart zoo, from 2nd to 29th September 2006 at Apenheul zoo and between 9th November and 20th December 2007 at Lola Ya Bonobo sanctuary.

Study 3: tool-use

3A. spontaneous actions:

- Subjects included in study 3a

The total sample studied included 94 bonobos from the four study sites. However, tool-use is a rare behaviour and few individuals performed these actions, so only 4 individuals provided enough data for individual-level analysis (minimum of 6 data points) (Table 4).

- Data recorded

Behaviours: I examined tool-use actions that occurred in the daily activities. The behaviours were qualified as tool-use according to the following definition: "use of an object to alter more efficiently the form, position or condition of another object, individual or oneself" (Harrison and Nystrom 2008). The studied behaviours included: using a stone to crack open nuts on an anvil, using a container to take water in the pond, using a container to drink, using a stick to scratch itself, using a rag to clean the wall or ground, using a stick as a rake to get out-of-reach items.

The methodology was the same as that used for study 1 (see section II.2.1). Indeed the actions were part of the spontaneous behaviours observed, so hand use for tool-use was recorded along with the other spontaneous daily actions and using the same methodology. For the recording, tool-use was given the top priority over the other actions studied, because of its low frequency of occurrence.

3B. the “termite fishing” task:

- Subjects included in study 3b

The sample studied included 26 bonobos from Twycross zoo and Stuttgart zoo where this enrichment was given. 19 individuals provided enough data for individual-level analysis (minimum of 6 data points). There were 8 males and 11 females; 5 young subjects (infants + juveniles), 3 adolescents and 11 adults.

- Data recorded

Behaviour: I assessed hand use during an enrichment procedure that involved using sticks as probes. For this enrichment, the caretakers put honey or yogurt inside the holes of the artificial termite mound or other designs (logs, tubes fixed onto the perches). They also provided branches and twigs that the bonobos used to dip into the holes to extract the food. The task was similar to the “termite-fishing” task that is known in wild chimpanzees (Wrangham et al. 1994), although it has not been observed in wild bonobos so far (McGrew et al. 2007a).

The behaviour studied was “dipping the stick into the hole, removing it and holding it to the mouth” with one hand (no coordination). Incomplete movements were not taken into account (e.g. dipping without taking the stick out of the hole, dipping and taking out without eating). This requirement was to standardize the data between trials and with the data previously collected in chimpanzees (Fletcher and Weghorst 2005; Lonsdorf and Hopkins 2005; Marchant and McGrew 1996; McGrew and Marchant 1992; McGrew and Marchant 1999; Nishida and Hiraiwa 1982).

At Twycross zoo, the sessions were videotaped. This approach could be used because the animals were not moving around but used fixed designs, and because a test session lasted less than 2 hours and was scheduled in advance. Using videos greatly optimized data collection. This enabled me to get all the data simultaneously from all the individuals located in the field. The use of videos also allowed for detailed analysis of hand use. Video analysis was done using Windows media player and “*Focal animal sampling*” (Altmann 1974) was used as sampling technique during video analysis. At

Stuttgart, filming was not necessary because the number of holes stocked with food was small. In fact, only one or two bonobos could access the design simultaneously. This allowed recording by direct observation with recording of vocal comments on a Dictaphone, using "*Focal animal sampling*" (Altmann 1974).

For each data point, I recorded: the individual's identity, which hand was used to perform the action, the activity of the other hand (inactive, postural support, holding an object, holding a food item, holding a food item against the ground, social action), the posture of the subject (seated, tripedal, bipedal, lying on the belly, hanging with the right arm, hanging with the left arm).

Analysis: For the analyses, I removed the few cases when the subject held an object or food item in the other hand, to standardize the action between trials and individuals. All postures were kept in the analysis because the behaviour occurred in a variety of postures.

- Recording techniques

Two different recording techniques were used: "frequency" and "bouts" (see section II.2.2 for a discussion on these two techniques).

Frequency: For the frequency, I counted every time that the subject "dipped the stick into the hole and brought it to the mouth". This technique was used for the videos only, because direct observations did not allow such detailed recording.

Bouts: To ensure that the data points were strictly independent of each other, I recorded bouts for the action "dipping the stick into the hole and bringing it to the mouth". I counted one bout for one sequence of identical actions (Marchant and McGrew 1991; McGrew and Marchant 1996; McGrew and Marchant 1997a; Westergaard and Suomi 1996). A sequence was considered terminated when the subject dropped the stick, changed the hand holding the stick or manipulated the stick with both hands (an action by which the subject could have changed its hand) (locomotion with the stick in one hand was not considered as a separating event). After such an intervening action, the hand used in the next bout was considered independent of the one used previously

(McGrew and Marchant 1997a). This technique was used for both videos and direct observations.

Number of data points per subject: I set the minimum number of data points at 6, which is the minimum required for performing the Binomial test (Seagel and Castellan 1988) (see section II.3.4). Thus, only the individuals for whom I had at least 6 observations were kept in the analysis.

Observations Times: At Twycross, the data were collected in September 2005 (19th and 21st), March 2006 (16th, 20th, 21st, 23rd and 31st) and April 2006 (12th) (8 days in total). At Stuttgart, the data were collected in May 2006 (28th, 29th, 30th, 31st) and June 2006 (each day from 1st to 17th) (21 days in total).

Study 4: social actions and gestures

4A. spontaneous actions:

- Subjects included in study 4a

The total sample studied included 94 bonobos from the zoos and the sanctuary. Among this sample, 32 individuals provided enough data for individual-level analysis (minimum of 6 data points) (Table 4). There were 14 males and 18 females; 9 infants, 5 juveniles, 5 adolescents and 13 adults. Most of these individuals were from the zoos. Indeed, at the sanctuary the number of subjects per group (N≈15) and the relatively limited observation time, made detailed observations (dyad-level) on social actions difficult. The study at the sanctuary was thus focused on non-social actions that were more frequent (study 1), and only the most frequent social actions were included (i.e. “suckling at mother’s breast”).

- Data recorded

Behaviours: The behaviours studied were actions that occurred spontaneously in the daily social interactions between bonobos. I also examined actions that occurred during spontaneous inter-specific interactions, i.e. the actions directed toward humans. I recorded all the manual behaviours; as well as other behaviours (e.g. “suckling at mother’s breast”) that were social, that is, all the actions that were directed toward another individual (bonobo or human). A behavioural list was made during preliminary observations (one month pilot study), and completed as the work progressed. This comprehensive list included 66 behaviours. Table 8 lists the behaviours considered. For the analysis, I only kept the behaviours for which at least one subject provided enough data, which rendered 41 behavioural patterns.

Among social actions, I was particularly interested in the actions that could be considered as gestures, i.e. when the hand was used for communicative purposes towards another individual (bonobo or human) from a distance. Such actions included: hand clapping (Fletcher 2006), arm held towards the other (invitation), arm held towards the other (begging), slapping the floor with one hand (Meguerditchian and Vauclair 2005; Meguerditchian and Vauclair 2006), stamping the floor with one foot and banging the glass with one hand.

Number of data points per subject: I set the minimum number of data points at 6, which is the minimum required for performing the Binomial test (Seagel and Castellan 1988) (see section II.3.4). Thus, for each action, only the individuals for whom I had at least 6 observations were kept in the analysis.

For each data point, I recorded: the individual's identity, the action performed, which hand was used to perform the action, the activity of the other hand (inactive, postural support, holding an object, holding a food item) (Chapelain et al. 2006; Hopkins and De Waal 1995), the posture of the subject (seated, tripedal, supine, bipedal, lying on the belly, lying on the left/right side) (Chapelain et al. 2006; Harrison and Nystrom 2008), the body part involved. In addition, for these social actions, the following variables were recorded: the identity of the recipient, the context of the interaction (e.g. play, grooming, aggression, food related excitement, reassurance), the meaning of the gesture (e.g. invitation, rejection, begging), the emotional valence of the gesture (on a 7 levels scale from very positive to very negative), the degree of violence (on a scale including: soft, neutral, violent 1, violent 2, violent 3 and violent 4), the facial expressions of the individuals involved (e.g. silent teeth-baring, play face, pout face (De Waal 1988)), the distance between the two individuals (contact, within arm length, further than arm length, more than 5m). This detailed recording was to enable me to investigate and control for the effects of these possible influential factors.

I also recorded any possible source of bias that could affect hand use (see methods for study 1). In the analysis, I excluded all those cases when the hand used could have been influenced by external factors.

Analysis: I recorded and analyzed each behaviour separately. This is the most detailed and appropriate technique for investigating hand use since laterality may depend on the type of gesture (see data in chimpanzees: (Hopkins and Leavens 1998; Hopkins and Wesley 2002; Leavens et al. 1996)). Previous bonobos studies have only considered "gestures" as a category gathering different kinds of gestures together (see section I.4.2). I chose a different and more detailed approach, to allow examination of laterality for each action; as well as investigation of the variability between actions. Secondly, I grouped some actions into relevant categories to enlarge the sample size, for the behaviours of particular interest (e.g. inviting related behaviours). I analyzed a total of 40 behavioural patterns.

Our objective was to analyze the social actions at the dyad-level to investigate the effects of: the identity of the emitter, the identity of the recipient, the relationship between the two subjects (e.g. subordinate/dominant, friends, kins, mother-infant).

- Recording technique

The methodology used here was the same as that used for study 1 (see section II.2.1) because these actions were part of the spontaneous behaviours observed. Laterality in social actions was recorded along with the other spontaneous daily actions and using the same methodology. For the recording, the social actions were given priority over the other actions studied, because of their relatively low frequency of occurrence.

Table 8: Behaviours that have been recorded in study 4
based on the following ethograms: (DeWaal 1988; Pika et al. 2005).

arm held towards the other (invitation)
arm held towards the other who has an item (begging)
arm open with hand on the floor (invitation)
arm up (arm lifted) (invitation)
banging the glass with one hand
bipedal branch shaking display (walk or run bipedal while shaking a branch)
catching the other
crossed arms around the other during ventro-ventral mount (arm on top recorded)
dragging the other
fending off the other with one arm/hand
following with hand on the other's body (bodypart recorded)
hand clapping
helping the infant to cling under belly
hitting the other

holding the arm of the other (preventing it from doing something)
holding the hand or foot of the other in its hand
holding the mountee partner during ventro-dorsal mount (including mount walk)
holding the other during grooming
holding the other during ventro-ventral mount
holding the other during ventro-ventral mount with both arms (arm above recorded)
holding the other off
hunching over the other (gentle)
hunching over the other (not gentle)
incomplete retrieving infant movement (touch only)
kicking the other
lateral embrace (embracing the other with one arm, side by side)
moving with arm around the other
opening its arms (invitation for the infant to come)
patting the floor with one hand
patting the other's body (with the palm or back of the hand)
playing with the other
plucking the other's hair
pretending to catch the other
pretending to hit the other (arm movement without touching it)
pulling the other in close contact
punching the other
pushing away the approacher
pushing the other
pushing the other aside
putting arm around the mounting partner during ventro-dorsal mount
putting arm around the other
putting hand on the other
retrieving the infant with one arm
shaking hand towards the other
sitting holding the infant with one arm
sitting with arm around the other (side by side)
sitting with crossed arms around the infant
slapping the floor with one fist
slapping the floor with one hand
slapping the other during grooming
stamping the floor with one foot
standing and placing the infant under belly
standing tripedal holding the infant under belly with one arm
stroking the other with one hand
suckling at mother's breast
taking the food item from the other
taking the object from the other
touching the genitals of the other
touching the other's body (bodypart recorded) (genitals excluded)
tripedal movement holding the infant under belly with one arm
trying to catch the other
trying to hit the other
turning the other around itself holding its hand
ventral embrace (embrace the other, face to face)
waist thrusting while holding infant under belly in tripedal posture

4B. induced gestures:

- Subjects included in study 4b

The sample studied included 58 bonobos housed at Lola Ya Bonobo sanctuary. This experiment was not allowed in the zoos. Among this sample, 24 individuals provided enough data for individual-level analysis (minimum of 6 data points) (Table 4). There were 15 males and 9 females; 11 young subjects (infants + juveniles), 4 adolescents and 9 adults.

- Experimental protocol

To induce gesturing, I presented the bonobos with food that was in their sight, but out-of-reach. Namely, the experimenter stood next to the enclosure, holding bananas in her hands and the bonobos gestured toward her to request the food. This methodology was inspired by the one used in previous studies (Hopkins and Leavens 1998; Hopkins and Wesley 2002; Hopkins et al. 2005b). At the onset of a test session, the experimenter approached the enclosure holding a bunch of bananas in her hands. The bananas were held 0.6m above the ground, at the experimenter’s midline. She positioned herself 1.5 to 2 meters from the wire netting, in the midline of the subject. These precautions were to avoid possible biases linked to the position of the experimenter relative to the subject (Hopkins and Wesley 2002).

In previous research, several studies findings could have been biased by an effect of positive reinforcement. For instance, in (Hopkins and Leavens 1998; Hopkins and Wesley 2002), if the subjects gestured “they were immediately given the banana”. This may be problematic because if the subject receives food after begging with the left hand (for instance), it may establish an association between the reward received and the action performed and hand used. This could encourage the later use of this hand, i.e. make the occurrence of left hand begging higher in the following trials and artificially create a preference (Deuel and Dunlop 1980; Warren 1980). Within the same vein, in several studies the experimenter encouraged gestural communication with greetings and vocal comments (Meguerditchian pers. com.; VOCOID conference 2007). Such encouragements can be viewed as positive reinforcement (Milinski 1997).

In my study, I strived to avoid rewarding and selective positive reinforcement. The experimenter did not encourage gestural communication; she simply stood, still, quiet and neutral. In addition, she gave no food to the subjects during the experiment. When the test session was finished, she left the area and gave the bananas to the caretaker. Then the caretaker threw the bananas randomly into the enclosure to avoid frustration and fights in the bonobo group. This feeding session happened after a few minutes and did not involve the experimenter.

The bonobos were tested in their home enclosure. The infants were tested in their night cages because of the absence of wire netting at the nursery (which was necessary to hold them off the experimenter). It would have been appropriate to isolate the subject tested to avoid any possible bias due to the presence of congeners (Chapelain et al. 2006; Hook-Costigan and Rogers 1998). Unfortunately, isolation was not allowed at the sanctuary because of the disturbance and stress that it caused to the bonobos. Within the same line, each test session had to be limited to a few minutes, to limit the disturbance on the bonobos (excitement and frustration). Each subject was tested on a minimum of 4 test sessions (maximum 10). The number of trials per subject per day ranged from 1 to 12.

- Data recorded

Behaviours: I aimed to measure hand preference for an induced inter-specific begging gesture, i.e. a gesture directed toward a human experimenter. This has never been done in bonobos, while there have been several such studies in chimpanzees (Hopkins and Leavens 1998; Hopkins and Wesley 2002; Hopkins and Cantero 2003; Hopkins et al. 2005b; VOCOID conference 2007). The behaviour recorded was the begging gesture defined as follows: “begging by stretching its arm toward the experimenter, extended arm with the hand facing up and in a cupped position” (as used in the chimpanzees studies). This action belongs to the natural repertoire of the species as wild bonobos beg to a conspecific that have food to request food sharing (DeWaal 1988; Pika et al. 2005).

The gestures recorded may be considered as intentional and referential communicative gestures. Indeed, the begging gestures were sometimes accompanied by gaze alternation between the food requested and the observer (Hopkins and Leavens 1998; Hostetter et al. 2001; Leavens et al. 1996; Leavens 2007). The bonobos were oriented toward the recipient and monitored her attentional status (Hostetter et al. 2001; Leavens et al. 1996). When she did not attend, they often exhibited attention getting behaviours to try to attract her attention and response. Some bonobos threw sand to her, others noisily clapped their hands or vocalized (behaviours that have also been reported in chimpanzees (Fletcher 2006; Hopkins and Cantero 2003; Hostetter et al. 2001; Leavens et al. 1996)). This indicates the communicative value of the gestures (Meguerditchian and Vauclair 2005). Therefore the begging gestures could be considered as intentional (convey an intention to the other) and referential (refer to something) actions, different from emotional communication (Hostetter et al. 2001; Meguerditchian and Vauclair 2005). Thus, they could be viewed and studied as a form of communicative language (Hopkins et al. 2005b; Meguerditchian and Vauclair 2006).

Number of data points per subject: I set the minimum number of data points at 6, which is the minimum required for performing the Binomial test (Seagel and Castellan 1988) (see section II.3.4). Therefore, only the individuals for whom I had at least 6 observations were kept in the analysis.

For each data point, I recorded: the individual's identity, the hand used to do the begging gesture, the activity of the other hand and the posture of the subject (seated, tripedal, supine, bipedal) (Chapelain et al. 2006; Harrison and Nystrom 2008). I also recorded the behaviours that were associated with gesturing, including vocalizations, hand clapping and sand throwing.

To avoid possible influence of different posture or activity of the other hand, I removed the few cases when there could have been a bias related to posture and when the other hand was holding an item, to standardize the action studied (see methods for study 1).

- Recording technique

Data collection was made by direct observation with recording of vocal comments on a dictaphone. Video taping was not necessary because the action recorded was not a rapid movement but lasted several seconds. Moreover, only one individual at a time performed the action, so I did not need to observe several individuals simultaneously. Indeed, the bonobos were observed in the group (because isolation was not possible), but only the individual that had the attention and gaze of the observer begged. The test sessions were restricted to 5-15 minutes in order to limit frustration, excitation and tension in the bonobo group.

Data independence: I recorded “bouts” in order to ensure data independence (Marchant and McGrew 1991; McGrew and Marchant 1996; McGrew and Marchant 1997a; Westergaard and Suomi 1996) (see section II.3.5). Two identical actions were considered independent only if they were separated by an intervening action; i.e. an action by which the subject could have changed its hand (e.g. after the individual had put its hand back on the ground) (Marchant and McGrew 1991; McGrew and Marchant 1996; McGrew and Marchant 1997a).

Observations times: The experiment on gestures was carried out from 9th November to 20th December 2007.

Chapter 3: Presentation of the statistics used for studies 1 - 4

The aim of this study was to investigate manual laterality in bonobos. Laterality can be examined at different levels. The first level of analysis is the individual-level, which is determining whether each individual is right-handed, left-handed or unlateralized. The second level of analysis is the group-level, which is determining whether the group is biased regarding the proportion of right-handed and left-handed subjects. Group-level laterality is defined as “a significant majority of individuals display the same preference” (based on the Binomial test. see below). These are the levels of analyses that are usually considered.

In laterality research, the main focus is the search for group-level biases. Indeed, it has long been thought that only group-level biases could stem from natural selection, while individual preferences could be related to other factors (e.g. sex, age, history, experience) (Vauclair and Fagot 1987). Only recently have other views and approaches started to develop (Rogers and Andrew 2002). There are many degrees in laterality, both at the individual-level (from no preference to exclusive preference) and at the group-level (from a small proportion of lateralized subjects to all subjects lateralized and with different degrees of bias in the proportion of left-handers and right-handers). In this study, I considered laterality on a continuum, on which each individual could vary from being unlateralized to being exclusively lateralized, and the group could vary from all individuals unlateralized to all individuals exclusively lateralized and from unskewed to exclusively skewed distribution of lateralized individuals toward one side (Fletcher and Weghorst 2005; McGrew and Marchant 1997a).

Within laterality research, there is no consensus regarding the statistics used. In fact, a variety of methods have been used, which is very problematic for between studies comparisons.

In this study, I aimed to use methods that were the most appropriate for my analyses and that allowed for reliable comparisons with other studies. In this chapter, I present the statistical analyses performed in this study.

For all analyses, lateral biases were considered significant for $p<0.05$ two-tailed, which is the most appropriate α level and matches other studies methods (McGrew and Marchant 1997a). Trends were considered when the p value was between 0.05 and 0.10. All analyses were carried out using Excel and SPSS 16.

3.1. Individual-level analysis:

This level of analysis determines whether the individual displays a significant preference for using one hand over the other or whether it shows no preference, i.e. random hand use (50:50) (McGrew and Marchant 1997a). In the literature, there are great differences regarding classification of the individuals into categories (McNeilage et al. 1987). For instance, some authors classified their subjects as left-handed or right-handed when the percentage of use of one hand was over 50%, while others only did so when it was over 70% (e.g. Boesch 1991). Also, some authors classified their subjects as right-handed if they made 2 right hand responses among 3 trials (e.g. Hopkins and Fernandez-Carriba 2000). These methodological inconsistencies between studies are very disturbing because subjects that would be classified as lateralized by some authors, would be classified as unlateralized by others. Thus, great attention should be paid to this issue when considering the database. This is why, in my review of previous data in bonobos, I have reanalyzed the original data using the same method, for all studies and my own study, to allow reliable comparisons.

Nowadays, most researchers perform statistical tests to classify the subjects as lateralized or unlateralized. The Binomial test (Seagel and Castellan 1988) is used by most authors, to compare the numbers of right and left hand responses. If the difference is statistically significant, the subject is classified as lateralized. If the difference is not significant, the subject is classified as unlateralized. I chose to use this test in my study, because it would be the most appropriate test (Seagel and Castellan 1988) and it has been used in the majority of previous studies, hereby allowing comparisons.

Laterality research mainly focuses on whether the preferences are significant or not. However, hand preference is not an all-or-nothing phenomenon. There are degrees in the preference, along a continuum from exclusive right hand preference to exclusive left hand preference, via no preference. To characterize hand preference along this continuum, I used a commonly used handedness index: **HI**. This handedness index is calculated for each subject using the following formula: (R-L)/(R+L), where R and L are the numbers of times that the right and left hands are used. HI gives the direction of preference from -1.0 to +1.0. Negative values indicate a left hand bias and positive values indicate a right hand bias. This index is informative of hand use and does not tell whether the subject is lateralized or not. The absolute value of HI: **ABSHI** gives the strength of preference from 0.0 to 1.0. I used this index to define hand use for each individual. I also calculated the mean HI and ABSHI for the bonobo group to characterize laterality for each action (for actions with $N \geq 6$). These mean HI and ABSHI values were used to compare the actions to each other. This method of analysis has been used in the majority of recent studies, which allows for comparisons. The mean HI value is interesting because it provides a general idea of the bias in hand use for the group. However, it must be interpreted with caution because a mean HI of zero can indicate that the subjects are unlateralized or that there are extreme left–handers and extreme right-handers that mask the effect.

We chose to use two different approaches for measuring individual preferences - HI and categorization into categories - because both are important measures. Categorizing the subjects as right-handed, left-handed and unlateralized is the key point in research on laterality, and is essential for assessing group-level biases and for comparing with the data in humans. However, laterality cannot be restricted to “being significantly lateralized or not”, so considering it on a continuum is sensible. Thus, the HI and ABSHI values provide another interesting view of the phenomenon.

Within the same line, I calculated the percentage of use of the preferred hand to examine the degree of preference of lateralized subjects, i.e. from a weak preference to an exclusive preference (100% use of the preferred hand).

3.2. Group-level analysis:

In the literature, there are several views and tests to investigate whether there is a bias in the group considered. First, I investigated the group-level bias in the proportion of right-handers versus left-handers. I wanted to know whether there was a greater proportion of right-handers compared to left-handers in bonobos, as predicted by the hypotheses (see section I.2). I calculated the percentage of right-handed and left-handed individuals to compare with the pattern of laterality observed in humans (90% of right-handers). I also used statistics to test whether the group-level bias was significant or not. Namely, the Binomial test (Seagel and Castellan 1988) was performed on the number of right-handed and left-handed individuals (for actions with at least 6 lateralized subjects). This is the method used in many recent studies and it would be the most appropriate method to assess group-level bias in the proportion of individuals (McGrew and Marchant 1997a). However, one issue with this method is that the unlateralized subjects are excluded. Indeed, when comparing the numbers of right-handers and left-handers, we consider only the lateralized subjects. Whether the group include no unlateralized subjects (e.g. 10 right-handers, 8 left-handers, 0 unlateralized) or a high proportion of unlateralized subjects (e.g. 10 right-handers, 8 left-handers, 20 unlateralized) is not taken into account, while this is a crucial point. To deal with this issue, I always mentioned the proportion of unlateralized subjects in the group. I also systematically examined the proportion of unlateralized subjects. I calculated the percentage of lateralized and unlateralized individuals in the group, and I compared the number of lateralized and unlateralized subjects using the Binomial test (Seagel and Castellan 1988).

I did not restrict my analyses to demonstrating the presence of absence of group-level bias. Laterality was considered on a continuum and the HI values were used to provide information on the general bias in hand use. Many authors have assessed group-level bias in hand use by performing one sample T-test (T) (Seagel and Castellan 1988) on the HI values of the group (e.g. Hopkins et al. 2000a; Hopkins et al. 2004; Scweitzer et al. 2007; Vauclair et al. 2005; Westergaard et al. 1997a). Also, the T-test is a parametric test and using it on such data (see below) could be debatable (McGrew and Marchant 1997a). I used this test here to allow comparisons with previous studies.

3.3. Test of the effects of possible influential factors:

As seen in the introduction, several factors have been suggested or shown to influence laterality. In this study, I investigated the effects of several factors. The first variables tested were individual related factors, including: sex, age, rearing history and living conditions. Then I examined factors that are related to the task. Namely, I compared the different actions to each other and the different behavioural patterns to each other in order to test the effect of the action, of the posture and of the activity of the other hand. I used the following statistical tests: Mann-Whitney (MW) and Kruskall-Wallis (KW) tests (Seagel and Castellan 1988) performed on the HI and ABSHI values, to compare the categories of individuals (e.g. males versus females) and the behavioural patterns (e.g. reaching for small items versus reaching for big items).

If several individuals were present in the two samples that were compared, not all the individuals were present in both samples. Therefore, the data could not be analyzed as related samples and I treated these mixed data as unrelated samples. Only for the analysis on the effect of posture and other hand activity for “feeding” and “reaching for small items”, I had data for the same subjects within the different conditions, so I used tests for related samples: Friedman (F) and Wilcoxon (W) tests (Seagel and Castellan 1988).

To avoid analyzing small samples that could yield unreliable findings, I limited my analyses to the cases when at least 10 individuals were available in each category (7 individuals in a few exceptional cases).

Non-parametric tests were used, because they are the most suitable tests for analysing behavioural data. Indeed, these data seldom meet the strict criteria for using parametric statistics, so non-parametric tests should be preferred (McGrew and Marchant 1997a). Specifically, I had small sample sizes (N ≤ 30 in most cases). Moreover, the normal distributions and homoscedasticity of variances could not be assumed (Seagel and Castellan 1988). Normality was tested using graphic representations of the data (histogram with Normal curve) and Kolmogorov-Smirnov test. Homogeneity of variance was tested using Levene test. The results of these tests, in addition to the small samples, implied that the data could not be analyzed using parametric statistics.

3.4. Number of data points per subject:

In the literature, the number of data points per subject greatly varies: from 1 (e.g. (Hopkins and Leavens 1998) to 500 (e.g. Peters and Rogers 2008). There is no consensus on the ideal number and the issue is matter of controversy (Fagot and Vauclair 1993; Hopkins 1993; Marchant and McGrew 1991; McGrew and Marchant 1996; McGrew and Marchant 1997a).

In fact, regarding the number of data points necessary, the key point is representativeness: the sample analyzed must be representative of the pattern studied. Some researchers think that the proportion of right and left hand responses may remain constant over trials repetition. In that case, hand preference could be deduced from the first trials that would be predictive of further hand use (De Vleeschouwer et al. 1995). Following this reasoning, very few trials would be necessary to reliably assess laterality. There is no evidence that demonstrates this hypothesis in non-human primates, which makes this assumption hazardous. I endorse the cautious conservative idea that analyzing large samples is a better approach, as they are always more representative of the pattern studied.

Moreover, large samples are preferable in terms of statistical power, because it can be difficult to reveal significant biases in small samples (see section I.3.3 and II.1.2) (Hopkins et al. 2001c; Hopkins et al. 2005a; Hopkins 2006; McGrew and Marchant 1997a).

What minimum sample would be considered large enough for allowing reliable assessment of laterality? This question is matter of debate and inquiry. Some have suggested that findings calculated on fewer than 25 data points would not be reliable (Palmer 2002) and others proposed that even a sample of 50 trials may be too small to reveal laterality (Marchant and McGrew 1991). Some researchers have examined the effect of sample size on laterality (Hopkins and Cantalupo 2003; Hopkins et al. 2004; Marchant and McGrew 1991; McGrew and Marchant 1997a; Palmer 2002). For instance, Palmer (Palmer 2002) has reanalyzed published Hopkins' chimpanzee data. He found that ambilaterality increased with the number of observations, and showed a disappearance of right-handedness when removing all individuals who had fewer than 25 data points. However, some other studies found no significant effect of the number of data points on hand preferences (e.g. "tube task" studies (Hopkins 1995; Vauclair et al. 2005; Westergaard and Suomi 1996; Westergaard et al. 1997a)). Thus, while most researchers think that the sample has to be large enough for allowing reliable assessment of hand preference (Marchant and McGrew 1991; McGrew and Marchant 1996; McGrew and Marchant 1997a), the most appropriate number of data points per individual remains matter of controversy (Fagot and Vauclair 1993; Hopkins 1993; Marchant and McGrew 1991; McGrew and Marchant 1996; McGrew and Marchant 1997a).

In research on non-human primates, the data are often very limited, especially when observing spontaneously occurring actions in a large group of subjects. Therefore, researchers have to deal with very small samples and they can only decide on what minimum sample is acceptable. In the literature, the authors have set the minimum number of data points required at different levels. Some researchers have accepted only 1-3 data points per subject (Hopkins and Leavens 1998; Hopkins and Wesley 2002), while others have excluded all subjects that had fewer than 20 data points (Marchant and McGrew 1996).

From a statistical point of view, the minimum number of observations has to be large enough to allow performance of statistical tests (Hopkins and Cantalupo 2005). The minimum number of data point permitting statistical testing with the Binomial test is n=6. Therefore, most authors have set the minimum number of data points accepted at 6, which is the minimum required for performing Binomial tests (e.g. Chapelain et al. 2006; Fletcher 2006; Meguerditchian and Vauclair 2006).
This is the criterion that I chose to use in my study. Namely, an individual had to exhibit a given behaviour at least 6 times to be included in the analyses. I acknowledge that 6 is a small number, which may raise issues in terms of representativeness and statistical power. However, the data available only enabled me to restrict analyses to this level. Using a more strict criteria (e.g. minimum n=20 per subject) would have meant losing too much information. The inclusion criterion was raised to n=15 for the "tube task" for which the larger sample of data allowed it. This number has often been used in previous studies (e.g. Bennett et al. 2008; Westergaard and Suomi 1993).

Another issue related to the number of data points is the variability between individuals (Palmer 2002; Papademetriou et al. 2005). In my research, the number of data points per subject varied between 6 and 359 for spontaneous non-social actions, between 6 and 167 for spontaneous social actions, between 6 and 131 for the "termite fishing" task, between 6 and 30 for the begging experiment and between 15 and 98 for the "tube task", with bouts. With frequency, the number of data points was higher than with bouts, so the variability was greater (ranging from 6 to 784 for the "termite fishing" task and from 15 to 656 for the "tube task"). Between subjects differences in the number of data points is a recurrent issue in laterality research (e.g. Hopkins 1995; Hopkins and Cantalupo 2005; Vauclair et al. 2005). This problem has been discussed because it may influence laterality and introduce sampling biases (Hopkins and Cantalupo 2003; Hopkins and Cantalupo 2005; McGrew and Marchant 1997a; Palmer 2002; Palmer 2003).

Standardizing all subjects to the same sample size (e.g. the minimum number: 6 data points) was not possible, because this would mean the loss of too much information and dramatically weakening the analyses. I am aware of this possible issue and I investigated it. I examined whether the number of data points could influence laterality.

Namely, I performed tests throughout all the analyses to assess the possible effect of the number of data points on the results. I ran Spearman tests (Seagel and Castellan 1988) to assess the relationship between the number of data points and laterality (HI and ABSHI values). I built scatter plots to visualize possible effects. I also compared the number of data points between lateralized and unlateralized subjects, using Mann-Whitney (MW) tests (Seagel and Castellan 1988). Finally, I modified the data to compare variables that had similar sample sizes (see analysis on the 50 frequency data points in study 2).

3.5. Data independence:

Independence of the data points is a formal requirement in laterality research (Byrne and Byrne 1991; Marchant and McGrew 1991; McGrew and Marchant 1997a). Specifically, “the occurrence of an event must not bias the chances of occurrence of another equivalent event” (McGrew and Marchant 1997a). For instance, when actions occur in a sequence, the use of one hand may influence the following use of this hand in the subsequent trials of the sequence. The data points are not independent of each other, and recording every consecutive action in a behavioural sequence (“frequency”) may bias the findings (Byrne and Byrne 1991; Lehman 1993; Marchant and McGrew 1991; McGrew and Marchant 1997a; McGrew and Marchant 1992; Palmer 2002; Palmer 2003).

Different techniques have been used to ensure independence of the data points (e.g. time delay, intervening event). The best criteria would be the occurrence of an intervening event (McGrew and Marchant 1997a), which is: “when a different behavioral pattern performed by the same hand intervenes between two instances of the same pattern” (McGrew and Marchant 1997a). This means that two data points are considered independent of each other only if they are separated by an intervening action (Marchant and McGrew 1991; McGrew and Marchant 1996; McGrew and Marchant 1997a).

In this study, I used strict criteria to ensure data independence. I recorded "bouts" by counting only the first action of a sequence; so that each sequence of identical actions was counted as one event (one bout) (Marchant and McGrew 1991; McGrew and Marchant 1996; McGrew and Marchant 1997a; Westergaard and Suomi 1996). This is what has been done in the majority of previous studies (except for the "tube task" studies) (Table 3). I used the criterion of an "intervening event" to separate the different bouts, so I counted two different bouts only if they were separated by an intervening action, i.e. an action by which the subject could have changed its hand (e.g. after the individual had dropped the item). "Frequency" has been recorded along with bouts in study 2 and 3b, to provide another view of the laterality and to compare the results obtained with the two recording techniques.

In sum, the data analyses used in this thesis were conservative. I employed the most appropriate analyses for the kind of data available. I made the analyses plan similar to that of previous studies to enable between studies comparisons. Data collection and analysis were designed in order to avoid or test any possible bias due to small sample sizes, differences of sample size and interdependency of the data points.

Section III :

Results

Chapter 1: Results of study 1: Spontaneous non-social actions

In this chapter, I present the results of the study on hand use in spontaneous daily activities. I analyse lola and the zoos combined (when I say "the group", I refer to the combined sample lola + zoos).

The general summary table (Table 9), gives the data and the descriptive statistics for each sample: lola, zoos, lola + zoos.
The results of analyses on the effect of the number of data points, sex, age, settings and rearing history are presented in tables (Table 7app and 8app in appendix), and are discussed at the end of this chapter.

Data analyzed

Table 6 in the methods section gives the number of data analyzed in total, for the behaviours and for the behavioural patterns. I analyzed 32 behaviours and 53 behavioural patterns. Behaviours are the main actions (whatever the posture and action of the other hand), behavioural patterns are the behaviours split according to the posture and action of the other hand.

Table 9: Results for each spontaneous behaviour and behavioural pattern (non-social actions) (study 1).
condition: posture, activity of the other hand (e.g. "seated, holding food" means: posture: seated, activity of the other hand: holding a food item), when no precision is given it means: all postures and other hand activities (general). n: number of data points collected (total*); N total: total number of subjects from which I had data; N analyzed: number of subjects analyzed (subjects with min n=6 or n=15 for the "tube task"); Left-handed, Nlat and right-handed: number of subjects that were classified as left-handed, unlateralized and right-handed based on the Binomial test; (n.b. for "turning": left-handed means anticlockwise and right-handed means clockwise); sum lat: number of subjects that were classified as lateralized; B test: p value of the Binomial test performed on the number of right-handed versus left-handed subjects (for actions with at least 6 lateralized subjects); % Right handed: proportion of right-handed subjects in the group. % Nlat: proportion of unlateralized subjects in the group. B test lat vs unlat: p value of the Binomial test performed on the number of lateralized versus unlateralized subjects; mean HI: mean value for the group (for actions with N ≥ 6); T test: p value of the T test performed on the individual HI values (for actions with N ≥ 6); mean ABSHI: mean ABSHI value for the group (for actions with N ≥ 6).

	action	**condition**	**n**	**N total**	**N analyzed**	**Left handed**	**Nlat**	**Right handed**	**sum lat**	**B test**	**% Right handed**	**% Left handed**	**% Nlat**	**B test lat vs unlat**	**mean HI**	**T test**	**mean ABSHI**
zoos	feeding	general	2197	30	25	3	18	4	7	1	16	12	72	0.043	0.021	0.812	0.329
lola	feeding	general	2366	40	40	3	29	8	11	0.227	20	7,5	72.5	0.006	0.094	0.046	0.233
lola +zoos	feeding	general	4563	70	65	6	47	12	18	0.238	18.46	9,231	72.308	4E-04	0.066	0.14	0.27
zoos	feeding	triped, postural support	430	16	11	2	5	4	6	0.688	36.36	18,18	45.455	1	0.121	0.443	0.406
lola	feeding	triped, postural support	389	36	22	2	15	5	7	0.453	22.73	9,091	68.182	0.134	0.07	0.537	0.42
lola +zoos	feeding	triped, postural support	819	52	33	4	20	9	13	0.267	27.27	12,12	60.606	0.296	0.087	0.334	0.415
zoos	feeding	seated, postural support	569	24	14	1	11	2	3		14.29	7,143	78.571	0.057	0.148	0.093	0.2
lola	feeding	seated, postural support	688	38	35	0	29	6	6	0.031	17.14	0	82.857	1E-04	0.135	0.045	0.318
lola +zoos	feeding	seated, postural support	1257	62	49	1	40	8	9	0.039	16.33	2,041	81.633	9E-06	0.139	0.01	0.284

table 9 continued	**action**	**condition**	**n**	**N total**	**N analyzed**	**Left handed**	**Nlat**	**Right handed**	**sum lat**	**B test**	**% Right handed**	**% Left handed**	**% Nlat**	**B test lat vs unlat**	**mean HI**	**T test**	**mean ABSHI**
zoos	feeding	seated, inactive	679	29	19	4	11	4	8	1.273	21.05	21,05	57.895	0.648	0.069	0.59	0.452
lola	feeding	seated, inactive	660	40	35	3	27	5	8	0.727	14.29	8,571	77.143	0.002	0.144	0.027	0.314
lola +zoos	feeding	seated, inactive	1339	69	54	7	38	9	16	0.804	16.67	12,96	70.37	0.004	0.117	0.053	0.363
zoos	feeding	seated, holding food	411	21	11	1	8	2	3		18.18	9,091	72.727	0.227	-0.09	0.525	0.401
lola	feeding	seated, holding food	490	40	30	0	29	1	1		3.333	0	96.667	6E-08	0.058	0.32	0.247
lola +zoos	feeding	seated, holding food	901	61	41	1	37	3	4		7.317	2,439	90.244	1E-07	0.017	0.762	0.288
zoos	pulling grass out	general	169	16	11	2	5	4	6	0.688	36.36	18,18	45.455	1	0.113	0.648	0.706
zoos	pulling grass out	triped, postural support	*59*	*13*	*2*	*0*	*1*	*1*	*1*								
zoos	pulling grass out	seated, postural support	*50*	*14*	*2*	*1*	*0*	*1*	*2*								
zoos	pulling grass out	seated, inactive	*45*	*8*	*3*	*1*	*1*	*1*	*2*								
zoos	swinging	other hand inactive	442	19	7	2	5	0	2		0	28,57	71.429	0.453	-0.21	0.134	0.29
zoos	hanging	other hand: inactive	671	23	11	1	10	0	1		0	9,091	90.909	0.012	-0.21	0.025	0.209
zoos	swinging+hanging	other hand: inactive	1113	25	13	3	10	0	3		0	23,08	76.923	0.092	-0.29	0.005	0.294
lola	swinging+hanging	other hand: inactive	29	9	2	0	2	0	0								
lola +zoos	swinging+hanging	other hand: inactive	1142	34	15	3	12	0	3		0	20	80	0.035	-0.29	0.001	0.299
zoos	quadrupedal movement holding food/object in one hand	other hand: postural support	423	20	10	2	4	4	6	0.688	40	20	40	0.754	0.17	0.371	0.481

table 9 continued	**action**	**condition**	**n**	**N total**	**N analyzed**	**Left handed**	**Nlat**	**Right handed**	**sum lat**	**B test**	**% Right handed**	**% Left handed**	**% Nlat**	**B test lat vs unlat**	**mean HI**	**T test**	**mean ABSHI**
lola	quadrupedal movement holding food/object in one hand	other hand: postural support	278	38	22	1	21	0	1		0	4,545	95.455	1E-05	9E-04	0.993	0.445
lola +zoos	quadrupedal movement holding food/object in one hand	other hand: postural support	701	58	32	3	25	4	7	1	12.5	9,375	78.125	0.002	0.054	0.567	0.456
zoos	tripedal movement holding food/object in one hand	other hand: postural support	188	26	13	3	7	3	6	1.313	23.08	23,08	53.846	1	0.076	0.695	0.563
lola	tripedal movement holding food/object in one hand	other hand: postural support	91	31	4	1	3	0	1								
lola +zoos	tripedal movement holding food/object in one hand	other hand: postural support	279	57	17	4	10	3	7	1	17.65	23,53	58.824	0.629	0.009	0.956	0.55
zoos	tripedal movement while feeding	other hand: postural support		9	4	0	3	1	1								
lola	tripedal movement while feeding	other hand: postural support	124	32	6	3	2	1	4		16.67	50	33.333	0.688	-0.31	0.377	0.685
lola +zoos	tripedal movement while feeding	other hand: postural support	124	41	10	3	5	2	5		20	30	50	1.246	-0.05	0.847	0.567
zoos	tripedal movement holding food/object in one hand + while feeding	other hand: postural support	267	26	15	3	9	3	6		20	20	60	0.607	0.103	0.527	0.496
lola	tripedal movement holding food/object in one hand + while feeding	other hand: postural support	215	38	12	3	8	1	4		8.333	25	66.667	0.388	-0.08	0.656	0.443
lola +zoos	tripedal movement holding food/object in one hand + while feeding	other hand: postural support	482	64	27	6	17	4	10		14.81	22,22	62.963	0.248	0.022	0.851	0.473

table 9 continued	action	condition	n	N total	N analyzed	Left handed	Nlat	Right handed	sum lat	B test	% Right handed	% Left handed	% Nlat	B test lat vs unlat	mean HI	T test	mean ABSHI
zoos	reaching for big items	general	313	21	13	2	6	5	7	0.453	38.46	15,38	46.154	1	0.075	0.65	0.499
lola	reaching for big items	general	156	35	13	0	13	0	0		0	0	100	2E-04	0.082	0.554	0.404
lola +zoos	reaching for big items	general	469	56	26	2	19	5	7	0.453	19.23	7,692	73.077	0.029	0.078	0.453	0.452
zoos	reaching for big items	triped, postural support	247	15	11	1	7	3	4		27.27	9,091	63.636	0.549	0.115	0.514	0.482
lola	reaching for big items	triped, postural support	142	35	10	0	10	0	0		0	0	100	0.002	0.09	0.601	0.442
lola +zoos	reaching for big items	triped, postural support	389	50	21	1	17	3	4		14.29	4,762	80.952	0.007	0.103	0.385	0.463
zoos	reaching for small items (seeds)	general	2078	30	28	4	14	10	14	0.18	35.71	14,29	50	1.149	0.171	0.08	0.428
lola	reaching for small items (seeds)	general	82	20	5	1	4	0	1								
lola +zoos	reaching for small items (seeds)	general	2160	50	33	5	18	10	15	0.302	30.3	15,15	54.545	0.728	0.14	0.118	0.43
zoos	reaching for small items (seeds)	triped, postural support	776	26	17	2	9	6	8	0.289	35.29	11,76	52.941	1	0.23	0.071	0.431
lola	reaching for small items (seeds)	triped, postural support	35	16	1	0	1	0	0								
lola +zoos	reaching for small items (seeds)	triped, postural support	811	42	18	2	10	6	8	0.289	33.33	11,11	55.556	0.815	0.259	0.039	0.448
zoos	reaching for small items (seeds)	seated, postural support	758	28	24	3	14	7	10	0.344	29.17	12,5	58.333	0.541	0.186	0.129	0.505
lola	reaching for small items (seeds)	seated, postural support	33	10	3	0	3	0	0								
lola+zoos	reaching for small items (seeds)	seated, postural support	791	38	27	3	17	7	10	0.344	25.93	11,11	62.963	0.248	0.155	0.171	0.492

table 9 continued	**action**	**condition**	**n**	**N total**	**N analyzed**	**Left handed**	**Nlat**	**Right handed**	**sum lat**	**B test**	**% Right handed**	**% Left handed**	**% Nlat**	**B test lat vs unlat**	**mean HI**	**T test**	**mean ABSHI**
zoos	reaching for small items (seeds)	seated, inactive	369	28	22	3	15	4	7	1	18.18	13,64	68.182	0.134	0.086	0.451	0.433
zoos	reaching for small items (seeds)	lying on the belly, inactive	86	6	2	0	1	1	1								
zoos	reaching for small items (seeds)	grip type: lateral grip (1p2mlat)	1165	21	17	1	10	6	7	0.125	35.29	5,882	58.824	0.629	0.312	0.015	0.464
zoos	reaching for small items (seeds)	grip type: one finger	81	7	5	2	1	2	4								
zoos	reaching for small items (seeds)	grip type: dorsal grip	228	9	3	3	0	0	3								
zoos	pushing an object	other hand: postural support	232	13	6	2	2	2	4		33.33	33,33	33.333	0.688	0.128	0.651	0.555
lola	pushing an object	other hand: postural support	66	14	4	1	0	3	4								
lola +zoos	pushing an object	other hand: postural support	298	27	10	3	2	5	8	0.727	50	30	20	0.109	0.281	0.25	0.693
zoos	dragging an object	other hand: postural support	148	21	5	1	4	0	1								
lola	dragging an object	other hand: postural support	101	24	6	1	2	3	4		50	16,67	33.333	0.688	0.154	0.669	0.75
lola +zoos	dragging an object	other hand: postural support	249	45	11	2	6	3	5		27.27	18,18	54.545	1	0.107	0.578	0.485
lola	breaking a piece from the food item	other hand: holding the food item	18	6	1	1	0	0	1								
lola	throwing		50	9	3	1	1	1	2								
lola	peeling the fruit	other hand: holding the food item	84	29	4	1	3	0	1								
lola	chest rubbing (two hands)		12	1	1	1	0	0	1								
lola	nut cracking				2	2	0	0	2								

table 9 continued	**action**	**condition**	**n**	**N total**	**N analyzed**	**Left handed**	**Nlat**	**Right handed**	**sum lat**	**B test**	**% Right handed**	**% Left handed**	**% Nlat**	**B test lat vs unlat**	**mean HI**	**T test**	**mean ABSHI**
zoos	pulling water vegetation out	general	69	7	4	1	3	0	1								
zoos	pulling water vegetation out	triped, postural support	57	6	4	1	2	1	2								
zoos	pulling leaves out	other hand: holding the food item	40	10	3	0	2	1	1								
zoos	behaviours related to genitals	general	113	11	2	0	1	1	1								
zoos	inserting a finger (self-directed)		126	17	6	2	2	2	4		33.33	33,33	33.333	0.688	0.093	0.77	0.599
zoos	inserting hand in throat		84	7	3	0	3	0	0								
zoos	raking seeds on the floor	general	421	12	7	1	1	5	6	0.219	71.43	14,29	14.286	0.125	0.502	0.124	0.787
zoos	raking seeds on the floor	triped, postural support	180	10	5	0	1	4	4								
zoos	raking seeds on the floor	posture: seated	241	12	6	1	2	3	4		50	16,67	33.333	0.688	0.403	0.255	0.736
zoos	reaching in the object (dipping) (bimanual)	other hand: holding the object	56	13	5	1	3	1	2								
zoos	reaching in water pond		90	18	6	1	4	1	2		16.67	16,67	66.667	0.688	-0.03	0.934	0.569
zoos	chest rubbing (unimanual)		66	4	2	1	1	0	1								
zoos	arm put around the neck		64	2	1	0	0	1	1								
zoos	reaching in the fixed object (dipping) (unimanual)		137	14	8	0	8	0	0		0	0	100	0.008	0.138	0.341	0.335
zoos	catching		22	5	1	0	0	1	1								
zoos	self-scratching with a stick		28	2	1	1	0	0	1								
zoos	cleaning with a rag		16	4	1	0	1	0	0								
zoos	drinking with a container		19	6	1	0	1	0	0								

Table 9 continued	**action**	**condition**	**n**	**N total**	**N analyzed**	**Left handed**	**Nlat**	**Right handed**	**sum lat**	**B test**	**% Right handed**	**% Left handed**	**% Nlat**	**B test lat vs unlat**	**mean HI**	**T test**	**mean ABSHI**
zoos	fœtus position		915	21	18	1	15	2	3		11.11	5,556	83.333		0.146	0.028	0.242
zoos	turning (supine)		45	4	3	0	2	1	1								
zoos	side of the sexual swellings when seated		205	4	3	0	1	2	2								
zoos	crossing arms		1718	23	18	6	5	7	13	1	38.89	33,33	27.778	0.096	-0.06	0.669	0.448
zoos	turning (standing)		217	19	7	0	5	2	2		28.57	0	71.429	0.453	0.181	0.335	0.343
lola	turning (standing)		51	19	2	1	1	0	1								
lola +zoos	turning (standing)		268	38	9	1	6	2	3		22.22	11,11	66.667	0.508	0.03	0.877	0.378
zoos	crossing legs		68	10	4	0	3	1	1								
lola	crossing legs		148	28	9	0	8	1	1		11.11	0	88.889	0.039	-0.14	0.485	0.513
lola +zoos	crossing legs		216	38	13	0	11	2	2		15.38	0	84.615	0.022	-0.01	0.956	0.532

1.1. Analysis for each behaviour and behavioural pattern:

Table 9 gives the data for each behaviour and each behavioural pattern for the group.
In the next paragraphs, I first examine each action separately. Then, I compare and group the actions in categories to examine the effect of different factors that may affect laterality.

- Proportion of unlateralized subjects:

Each of the behaviours and behavioural patterns induced significant individual preferences (with the exception of 2 cases for which there was no lateralized individual).

- I calculated the proportion of unlateralized subjects in the group for each manual action (for actions with N ≥ 6) (non-manual behaviours are excluded because I wanted to calculate the mean for all manual actions). (Table 9). For the 13 manual behaviours analyzed, the average percentage of unlateralized subjects was 57.782 (min=14.286, max=100, SD=24.673). For the 27 behavioural patterns analyzed, the average percentage of unlateralized subjects was 62.56 (min=14.286, max=100, SD=20.685). Therefore, on average, there was a high proportion of unlateralized subjects in the group, which shows the small number of lateralized subjects (below 40%).
- I compared the numbers of lateralized and unlateralized subjects (for actions with N ≥ 6) (non-manual behaviours are included because I did not calculate the mean). (Table 9). For the 17 behaviours tested, there was significantly more unlateralized subjects than lateralized subjects in 6 cases. For the 30 behavioural patterns tested, there were significantly more unlateralized subjects than lateralized subjects in 11 cases. In no case was the number of lateralized subjects significantly greater than the number of unlateralized subjects (though there was a trend for “crossing arms”). This further shows that many individuals were unlateralized and relatively few individuals were lateralized.

- Group-level biases:

- I examined group-level biases in the proportion of right-handed and left-handed subjects. I compared the numbers of right-handed and left-handed subjects, whenever possible (for actions with at least 6 lateralized subjects) (Table 9). There was no group-level bias for the 9 behaviours tested (B $p \geq 0.219$). There was no group-level bias for 16 of the 17 behavioural patterns tested (B $p \geq 0.125$). A significant group-level right bias appeared in one case: for feeding in a seated posture with other hand in postural support (B p=0.039). However, this bias was weak (8R versus 1L and 40Nlat). Therefore, the bonobos did not exhibit group-level laterality for any of the studied actions (with one exception).

- I examined the percentage of right-handers in the group (for actions with $N \geq 6$) (non-manual behaviours excluded). For the 13 manual behaviours analyzed, the average percentage of right-handers in the group was 25.631 (min=0, max=71.43, SD=19.607). For the 27 behavioural patterns analyzed, the average percentage of right-handers in the group was 22.69 (min=0, max=71.43, SD=16.73). When considering only the lateralized subjects, the percentage of right-handers was 64.658 (min=42.86, max=83.33, SD=11.607) for the 8 manual behaviours analyzed and 67.966 (min=42.86, max=88.89, SD=12.227) for the 15 behavioural patterns analyzed.

- I also tested biases in the HI values (for actions with $N \geq 6$), which reflects biases toward the use of one hand (Table 9). Among the 18 behaviours tested, the HI values were significantly skewed toward one side in 2 cases: for “foetus position” and for “swinging + hanging”. Among the 31 behavioural patterns tested, the HI values were significantly skewed toward one side in 5 cases: feeding while seated with other hand in postural support, “foetus position”, “swinging + hanging”, reaching for small items (seeds) in tripedal posture, reaching for small items (seeds) with lateral grip type (1p2mlat) (and in 1 case as a trend, for feeding seated with other hand inactive). Therefore, there was no bias toward the use of one particular hand in most actions. However, several significant biases appeared; and they were all toward the right hand; except for hanging related behaviours.

1.2. Effect of task-related factors:

I now investigate whether the laterality varied between the different actions studied.

Direction of laterality:

- As seen above, there was no significant group-level bias for any of the actions studied (except in one case). However, I consider laterality on a continuum and use here the HI values to examine the general trend in the direction of laterality.
Considering all the behaviours and behavioural patterns (for actions with $N \geq 6$) (non-manual behaviours excluded), the HI values ranged from -0.315 to 0.502. The median was 0.093 (SD=0.152) indicating a slight right bias. Moreover, almost all (83%) of the behaviours and behavioural patterns displayed positive HI values. Therefore, whatever the action, posture, other hand activity and other possible influential factors, the bonobos' hand use was rather toward the right hand (not significant preference; with the exception of the cases described above). In fact, the HI values were frankly negative only for "swinging + hanging" (significant left hand bias) and for "tripedal movement while feeding with one hand".

- Ranking: To visualize the pattern of laterality across actions, I ranked the behaviours and behavioural patterns according to their HI values (Table 3app in appendix). Only the top 6 actions could be considered relatively right skewed, with $HI \geq 0.15$. These include: reaching for small items (seeds) related behaviours, pushing an object and raking seeds on the floor related behaviours. Only the bottom 3 actions could be considered relatively left skewed, with $HI \leq -0.15$. These were hanging related behaviours.

- Below, I focus the analysis on the 13 main manual behaviours and compare them to each other (actions with $N \geq 6$). Figure 2 shows the mean HI values for these 13 behaviours.

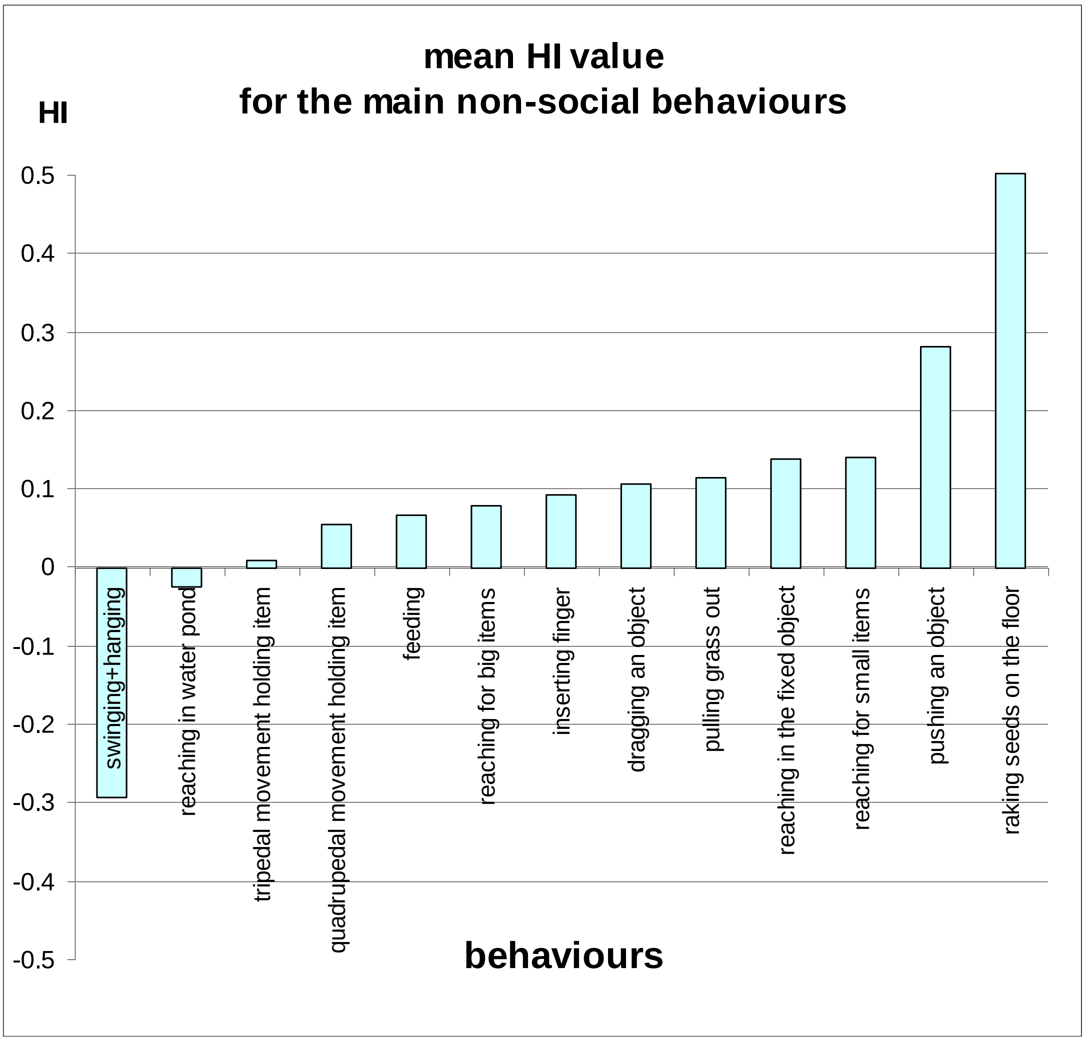

Figure 2: Mean HI values for the 13 main non-social manual behaviours.

Global analysis showed that the HI values did not significantly vary according to the behaviour (KW, df=12, p=0.121) (the number of data points also varied KW df=12, p<0.001). However, I performed further analyses, with paired comparisons, to test my hypotheses regarding specific behaviours of interest (Winer, 1971). Table 4app in appendix presents the results of the MW tests.

- Testing predictions 4: I investigated whether one hand was particularly preferred for postural support. Namely, I examined the behaviours that involved one hand to support the body weight (with various degrees of support).
- The arboreal action “swinging + hanging”, that implied one hand for supporting the whole body-weight, was the only behaviour to be skewed toward the left hand, and

paired comparisons showed that its HI values were significantly lower than that of several other behaviours (MW $p \leq 0.05$) (Table 4app, Figure 2).

- On the ground, one hand was used for support during the movements: “quadrupedal movement holding food/object in one hand”, “tripedal movement holding food/object in one hand”, “dragging an object” and “pushing an object”. These behaviours showed positive HI values and their HI values did not differ from the other behaviours (MW $p>0.05$)*. These movements presented different degrees of postural demands; but when I compared these four actions to each other, no difference appeared in the HI values (MW $p>0.05$).

- Testing predictions 6’’: I investigated whether the right hand was particularly preferred for precise actions. The following behaviours could be considered as precise: “inserting a finger (self directed)”, “reaching in the fixed object (dipping) (unimanual)” and “reaching for small items (seeds)”. These behaviours showed positive HI values and their HI values did not differ from the other behaviours (MW $p>0.05$)*.

* the non-significant results exclude comparisons with the outliers behaviours (i.e. “swinging + hanging” and “raking seeds on the floor”).

Strength of laterality:

- I consider laterality on a continuum and use the ABSHI values to examine the general pattern of laterality. Considering all the behaviours and behavioural patterns (for actions with $N \geq 6$) (non-manual behaviours excluded), the ABSHI values ranged from 0.20 to 0.787. The median was 0.445 (SD=0.139), indicating a not strong laterality.

- Ranking: To visualize the pattern of laterality across actions, I ranked the behaviours and behavioural patterns according to their ABSHI values (Table 5app in appendix). The top 11 actions could be considered relatively strongly lateralized, displaying ABSHI ≥ 0.485 (close to 0.5). These include: “dragging an object”, “reaching for small items (seeds)”, “crossing legs”, tripedal movement related behaviours, “reaching in the water pond”, “inserting a finger (self directed)”, “pushing an object”, “pulling grass out" and raking seeds on the floor related behaviours. The bottom 7 actions could be considered relatively weakly lateralized, with ABSHI ≤ 0.3. These included: feeding related behaviours, foetus position, hanging related behaviours.

- Below, I focus the analysis on the 13 main manual behaviours and compare them to each other (actions with N ≥ 6). Figure 3 shows the mean ABSHI values for these 13 behaviours.

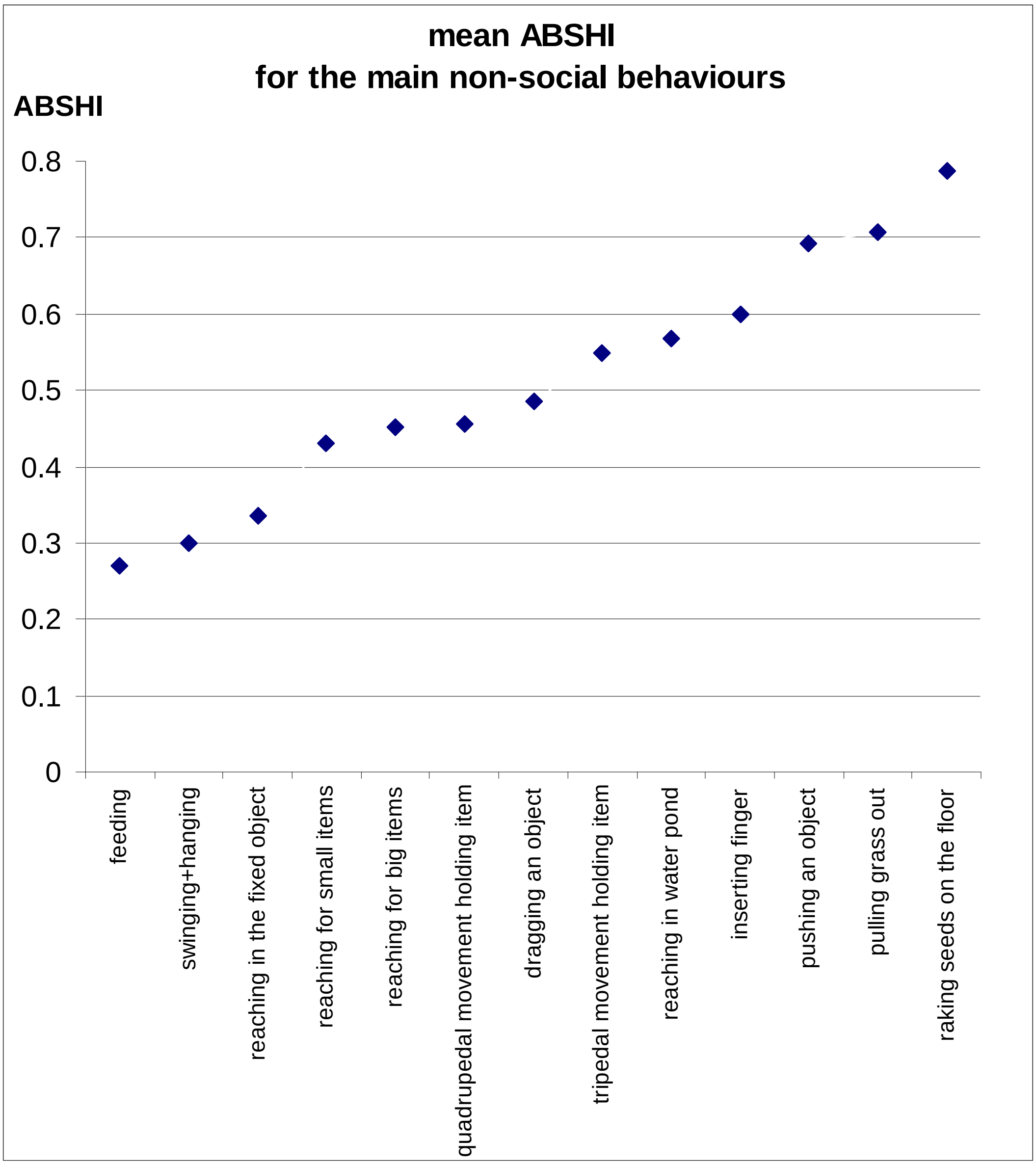

Figure 3: Mean ABSHI values for the 13 main non-social manual behaviours.

Global analysis showed that the ABSHI values significantly varied according to the behaviour (KW df=12, p<0.001) (the number of data points also varied KW df=12, p<0.001). Post-Hoc analyses with paired comparisons showed that several behaviours stood out, having values significantly different from the other behaviours. On the one hand there were "feeding", "swinging + hanging" and "reaching in the fixed object" with very low ABSHI values; and on the other hand there were "raking seeds on the floor", "pushing an object" and "pulling grass out" with very high ABSHI values.

- Testing predictions 6: I investigated whether the laterality was stronger in complex compared to simple tasks. The following behaviours could be considered the most complex (notably in terms of precision or postural demands): "reaching in the fixed object (dipping) (unimanual)", "reaching for small items (seeds)", "inserting a finger (self directed)", "pushing an object", "reaching in the water pond", "swinging + hanging" and "tripedal movement holding food/object in one hand". When I compared the ABSHI values of these behaviours with that of the other behaviours, only "pushing an object" showed a significantly stronger laterality than simpler actions (Table 4app). On the graphic (Figure 3), "pushing an object", "inserting a finger (self directed)", "reaching in the water pond" and "tripedal movement holding food/object in one hand" were amongst the most lateralized actions, which supports the hypothesis. However, "swinging + hanging", "reaching in the fixed object (dipping) (unimanual)" and "reaching for small items (seeds)" were amongst the least lateralized actions, which is opposite to the prediction.

- Testing predictions 5: I investigated whether having one hand used for postural support could affect laterality. I examined the behaviours that involved one hand to support the body weight (with various degrees of support).
- The arboreal action "swinging + hanging", was weakly lateralized and its ABSHI values were significantly lower than those of several other behaviours (Table 4app, Figure 3). Moreover, the proportion of unlateralized subjects was one of the highest of all the actions studied in this PhD research (Table 9).
- On the ground, the movements ("quadrupedal movement holding food/object in one hand", "tripedal movement holding food/object in one hand", "dragging and object" and "pushing an object") did not differ from the other behaviours regarding the ABSHI values (MW p>0.05)*. When I compared these four actions to each other, there was no

difference in the ABSHI values (MW p>0.05), except in one case: the ABSHI values were significantly higher for “pushing an object” compared to “quadrupedal movement holding food/object in one hand” (Table 4app).

* the non-significant results exclude comparisons with the outliers behaviours (i.e. “swinging + hanging” and “feeding”; “raking seeds on the floor”, “pushing” and “pulling grass out”).

1.3. Effect of the posture and activity of the other hand:

I examined whether the posture and activity of the other hand affected laterality, hereby testing predictions 2, 4, 5 and 6. I analyzed the behaviours separately.

Descriptive analysis:

- tripedal posture:

* direction:

- I individually examined the actions performed in the tripedal still posture (e.g. tripedal feeding, tripedal reaching for big items). There was no group-level bias for any of these behavioural patterns. Regarding the HI values, there was no bias, except in one case: for reaching for small items in tripedal posture (right skewed HI values) (T t(17)=2.237, p=0.039), indicating a bias toward using the right hand for reaching (while the left hand was used for support). Interestingly, this significant bias appeared only in the tripedal posture, not in the other conditions.

At the individual-level, Manono exhibited a right hand preference for feeding when tripedal and a left hand preference for feeding when seated with the other hand inactive (Table 10app in appendix).

- I then considered the actions performed when the animal was moving in the environment. There was no group-level bias in these movements: “quadrupedal

movement holding food/object in one hand", "tripedal movement holding food/object in one hand", "dragging an object" and "pushing an object" (Table 9).
Regarding the HI values, no bias appeared in these actions, though "pushing an object" showed relatively high values, indicating a trend for right hand use for pushing the object (with the left hand used for locomotion). When I compared these actions to the other (non-locomotion) actions, the HI values showed no differences (see above) (Table 4app).
* strength:
Regarding the strength of laterality, I observed a notable effect of posture. The actions performed in tripedal posture were very strongly lateralized. They stood in the top 12 of the most lateralized actions (Table 5app). The tripedal actions, especially the movements, showed a marked laterality. In particular, "reaching in the water pond" which was amongst the most lateralized actions; and "pushing an object", which was very strongly lateralized and significantly more lateralized than several other actions.

<u>- seated posture:</u>
* direction:
- I examined the actions performed in a seated posture individually (e.g. pulling grass out when seated with other hand inactive). There was no group-level bias for any of these seated behavioural patterns; with the exception of feeding seated with other hand as postural support (see above).
* strength:
Regarding the strength of laterality, no effect of the posture and other hand activity were observed.

At the individual-level, I examined consistency of hand preference between postures. The lateralized subjects did not change hand preference direction between the two postures within a given behaviour (with one exception, Manono. see above).

At the individual-level, the lateralized subjects displayed consistency of hand preference between the three categories of other hand activity. They did not change hand preference direction between categories within a given behaviour (with one exception, Lomela 1) (Tables 15, 16, 17 and 9app, 10app,11app).

Statistical analysis:

I now examine and compare laterality between postural conditions (different postures and different activities of the other hand) within a given behaviour. Only “feeding” and “reaching for small items” provided enough data for this detailed analysis. I had data for the same subjects within the different postural patterns, so I could here use statistical tests for related samples. The results of the tests are presented in Table 6app.

- “feeding”:

When I examined the different postural patterns separately (Figure 4), several significant biases occurred. There was a group-level right bias in “feeding with other hand as postural support” (B test p=0.039), indicating a greater number of right-handers. Regarding the HI values, I observed a right bias for “feeding with other hand as postural support” (T test, t(48)=2.702, p=0.01) and a right trend for “feeding with other hand inactive” (T test, t(53)=1.982, p=0.053). This suggests a trend toward right hand use for feeding. However, no bias occurred for feeding in tripedal posture or seated with the other hand holding a food item.

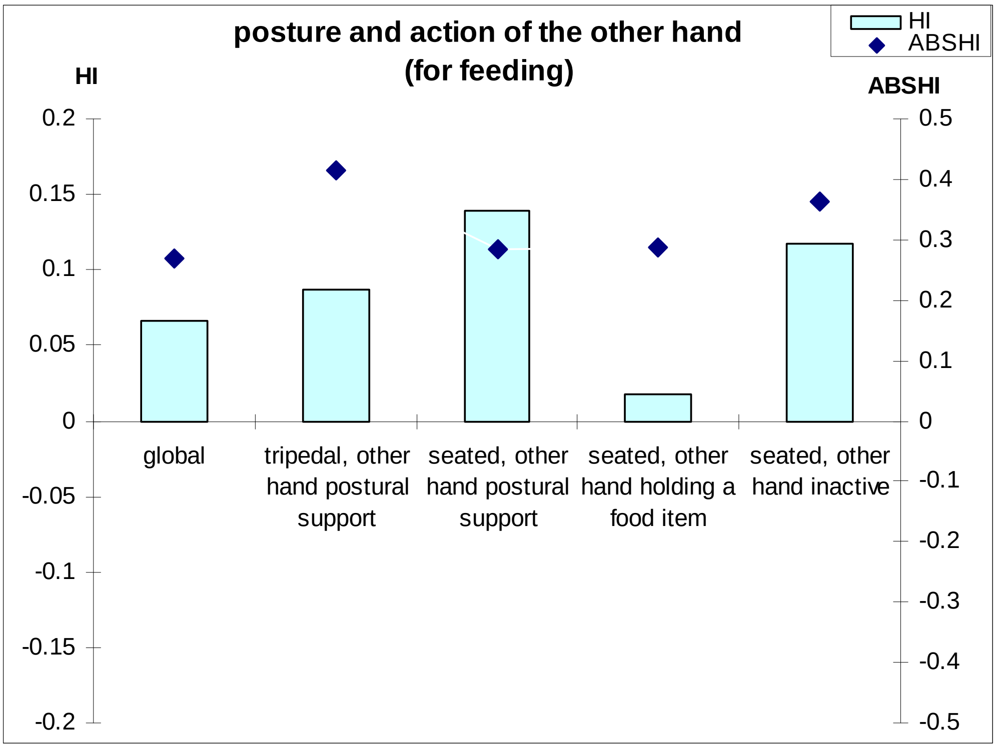

Figure 4: Mean HI and ABSHI values for each posture and action of the other hand for “feeding”.

Global analysis showed that there was no significant effect of the posture and action of the other hand on the HI or ABSHI values (F *N=27, df=3*, p=0.608 for HI, p=0.222 for ABSHI). However, I performed further analyses to test my hypotheses (Winer, 1971). The same paired comparisons as done above are performed for "feeding".

- I found no effect of posture on the HI values (W p>0.05). However, the ABSHI values varied, with significantly higher ABSHI values in tripedal compared to seated posture when the other hand was used as postural support (W, N=30, z=-2.541, p=0.011 for ABSHI). In that case, there was also a difference in the number of data points per subject, with more data points for seated compared to tripedal (W, N=30, z=-2.489, p=0.013). The other comparisons were not significant (W p>0.05).

At the individual-level, Manono, exhibited a right hand preference for feeding when tripedal, but a left hand preference for feeding when seated with the other hand inactive (Table 10app).

- I found no effect of the activity of the other hand on the HI values (W p>0.05). Nevertheless, the ABSHI values were influenced. They were significantly higher when the other hand was inactive compared to not-inactive (active, all activities merged together) (W, N=50, z=-2.375, p=0.018 for ABSHI). In that case, the number of data points per subject also differed, with more data points for "active" than inactive (W, N=50, z=-5.016, p<0.001). The other comparisons were not significant.

At the individual-level, Lomela 1 exhibited a right hand preference for feeding when the other hand was holding a food item, but a left hand preference for feeding when the other hand was inactive (Table 17).

Therefore, when analysing feeding alone, both the posture and activity of the other hand showed no effect on the direction of laterality, but influenced the strength of laterality.

- "reaching for small items":

The data available only allowed one comparison. I compared the data in tripedal posture and in seated posture with other hand in postural support. No difference appeared regarding both the HI and ABSHI values (W N=17, z=-0.17, p=0.865 for HI, z=-0.284, p=0.776 for ABSHI).

1.4. Effect of the size of the item:

Testing predictions 6, 6’’ and 6’’’: I investigated whether the size of the item to grasp (big or small item, meaning unprecise or precise grasping) and whether the specific grip type used (shape of the hand and fingers used) influenced laterality.

- “Reaching for small items (seeds)” versus “reaching for big items”

I first compared reaching for big items and reaching for small items. The results are presented in Table 10.

*direction:

There was a bias toward right hand use with small items (in tripedal posture) that was absent with big items (Table 9). Moreover, the HI values were slightly higher with small compared to big items (but the difference was not significant) (Table 10). Thus, the data suggest a slightly greater right hand use with small items.

* strength:

There was no difference in the ABSHI values between the two item sizes. However, the proportion of unlateralized subjects appeared higher with big than small items, suggesting a stronger laterality with small items.

Table 10: Results of tests on the effect of the size of the item (study 1).
Results of comparison between “reaching for big items” and “reaching for small items (seeds)” (general and in tripedal posture).

	MW on total	**MW on HI values**	**MW on ABSHI values**
general N1=33, N2=26	U=168.5 **p<0.001**	U=406.5 p=0.731	U=408.5 p=0.754
tripedal posture N1=18, N2=21	U=114 **p=0.034**	U=164.5 p=0.49	U=177 p=0.735

- Grip type

I collected data for different grip types (Table 7), for the action of reaching for seeds. I examined the effect of the grip type on laterality, first at the group-level (Table 9) and then at the individual-level (Tables 15, 16, 17).

- With the lateral grip type (1p2mlat), most lateralized subjects were right-handed (6R versus 1L), and there was a significant right bias in the HI values (T test, t(16)=2.71, p=0.015). This suggests that the lateral grip type (1p2mlat) elicited right hand use.
- For the one finger grip type, the sample was very small (N=5) and there were: 2L, 2R and 1Nlat.
- With the dorsal grip type, the sample was very small but an effect appeared: all three subjects were left-handed. This suggests that the dorsal grip type elicited left hand use.
- When considering the individual-level (Tables 15, 16, 17), I also observed a marked effect of the grip type on laterality. Namely, several individuals changed hand preference according to the grip type used. Daniela showed a right hand preference for the lateral grip type (1p2mlat) and a left hand preference for the one finger grip type. Jill showed a right hand preference for most (7) reaching actions, but changed toward a left hand preference when using the dorsal grip type. Similarly, Lomela 1 showed a right hand preference for several reaching actions (3) and changed for a left hand preference when using the dorsal grip type. These observations support the findings observed at the group-level.

Therefore, the results suggest a relationship between the grip type used and hand preference.

1.5. Effect of possible influential factors:

In the next paragraphs, I investigate the effects of several possible influential factors including: living conditions (settings), sex, age, rearing history (testing predictions 7, 15 and 16) and the number of data points.

Table 7app in appendix presents the data for each group considered.

I examined each individual behaviour separately. Only the behaviours with a large sample of subjects (N close to 30) were considered in these analyses: feeding ("feeding, general") with N=65, reaching for small items ("reaching for small items (seeds), general") with N=33, quadrupedal movement ("quadrupedal movement holding food/object in one hand") with N=32, reaching for big items ("reaching for big items, global") with N=26, tripedal movement ("tripedal movement holding food/object in one hand + while feeding with one hand") with N=27. This was to avoid performing tests on categories that had less than 10 subjects.

Effect of the settings:

I compared the data between the two settings: zoos versus Lola for each behaviour. I found no significant difference regarding the HI and ABSHI values (MW p>0.05), which suggests no significant effect of the settings on laterality.

Effect of sex:

- I first examined each sex group separately, for each behaviour. I found no group-level bias in males, nor in females (in the number of individuals (B test p>0.05) and in the HI values (T test p>0.05) (Table 7app). For "feeding", there was a right trend in HI values in males (mean HI=0.116, t(35)=1.915, p=0.064).
- I then compared the data between males and females, for each behaviour. I found no difference in the HI and ABSHI values (MW p>0.05), which suggests no significant effect of sex on laterality

Effect of age:

- I first examined each age group separately, for each behaviour. I found no significant group-level bias (in the number of individuals (B test p>0.05) and in the HI values (T test p>0.05) (Table 7app); except for two behaviours. For "feeding", there was a group-level right bias in the number of individuals (B test p=0.016), and a right bias in the HI values (t(25)=2.695, p=0.012), in the youngest age group (infants + juveniles). Moreover, there was a right bias in HI values (t(37)=2.055, p=0.047) in the category gathering infants, juveniles and adolescents. For "reaching for small items", there was a right bias in HI values in the youngest age group (infants + juveniles) (t(5)=3.101, p=0.027). These results could suggest some effect of age.
- I then compared the data between the different age groups, for each behaviour. In a global analysis, I compared the data between the three age categories (infants + juveniles, adolescents, adults) (whenever possible, i.e. when I had at least 10 subjects per category). I found no difference in HI and ABSHI values (MW p>0.05), which suggests no significant effect of age on laterality.

I performed further analyses on combined age categories, to test the hypothesis that immature subjects may exhibit a different laterality than other individuals (combining also allowed testing the behaviours for which I had few subjects per category). I first compared the youngest individuals (infants + juveniles) with the other older bonobos (adolescents + adults) and found no difference in the HI and ABSHI values (MW p>0.05). I then compared the adults to the other bonobos (infants + juveniles + adolescents) and again found no difference in HI and ABSHI values (MW p>0.05). These results suggest no effect of age on laterality.

Effect of rearing:

- I first examined each category of individuals ("parent-reared", "human hand-reared", "lola-reared") separately, for each behaviour. I found no significant bias (in the number of individuals (B test p>0.05) and in the HI values (T test p>0.05) (Table 7app); except in one case. For "reaching for small items", there was a group-level right trend (B test p=0.065) and a right bias in HI values in "parent-reared" bonobos (t(20)=2.725, p=0.013).
- I then compared the data between rearing groups, for each behaviour. Because of the small number of "human hand-reared" bonobos, I combined "human hand-reared" and "lola-reared" individuals into a category of bonobos that have been in contact with humans during infancy. I compared the data between "parent-reared" and "human hand-reared + lola-reared" bonobos and found no significant difference regarding HI and ABSHI values (MW p>0.05). These results suggest no significant effect of rearing history on laterality.

Effect of the number of data points:

I tested the possible effect of the number of data points on laterality in two ways.

- First, I assessed the correlation between the number of data points per subject and the HI and ABSHI values, for each behaviour (for actions with $N \geq 6$). The number of data points was not correlated to the HI or ABSHI values (Spearman p>0.05) (Table 8app); with the exception of the following three cases.
- Regarding HI values, for "tripedal movement holding food/object in one hand" and "tripedal movement while feeding with one hand", there was a significant positive

correlation between the number of data points and the HI values (Spearman N=17 rho=0.606, p=0.010 and N=10 rho=0.710, p=0.021 respectively), indicating that the HI values increased (right hand use) with the number of data points. However, when observing the graphs (Figure 5 and 6), it seemed that the effects could be due to outliers. Indeed, when I removed the outliers, the effect disappeared (Spearman rho=0.420, p=0.119 with N=15 and rho=0.641, p=0.063 with N=9 respectively).

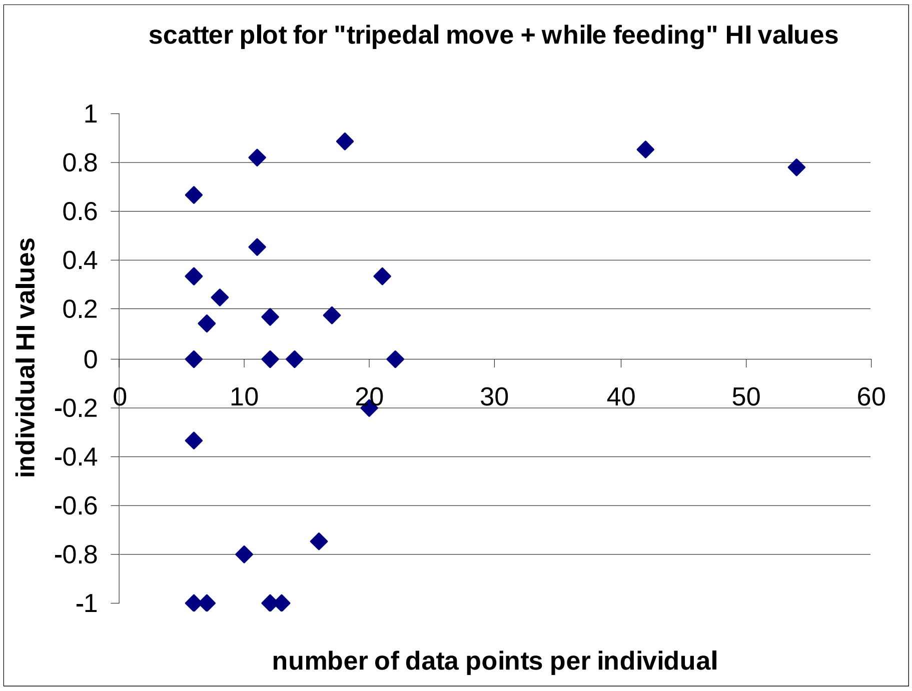

Figure 5: Scatter plot showing the distribution of HI values with increasing number of data points for “tripedal movement holding food/object in one hand while feeding”.

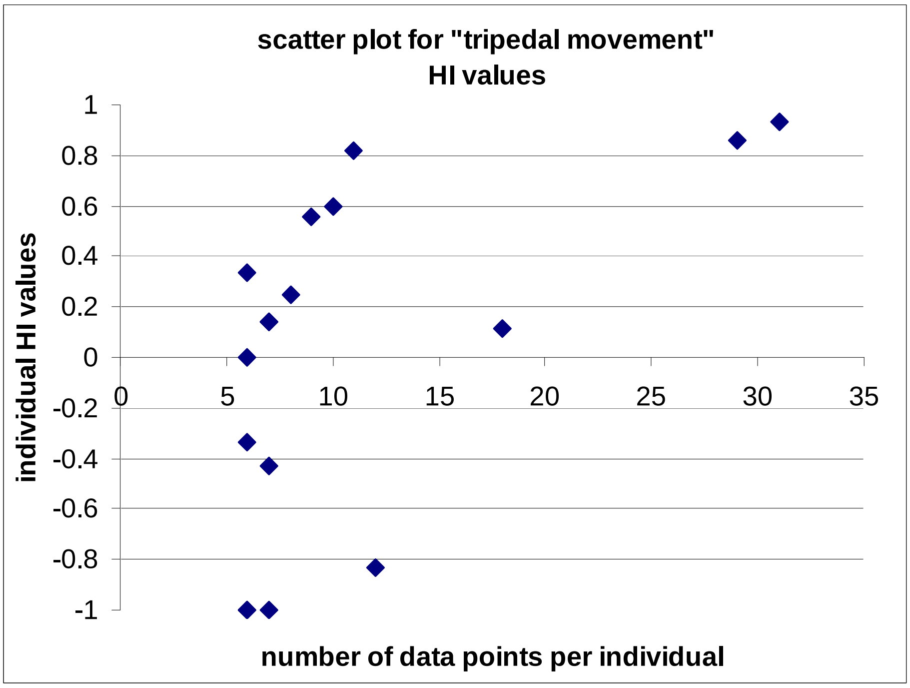

Figure 6: Scatter plot showing the distribution of HI values with increasing number of data points for “tripedal movement holding food/object in one hand”.

- Regarding ABSHI values, for feeding (“feeding, general”), there was a significant negative correlation between the number of data points and the ABSHI values (Spearman N=65 rho=-0.294, p=0.017), indicating that the strength of laterality decreased as the number of data points increased (Figure 7). This effect remained when I removed the outliers (Spearman rho=-0.276 p=0.030 with N=62). The same effect appeared as a trend in “tripedal movement while feeding with one hand” (Spearman N=10 rho=-0.586, p=0.075).

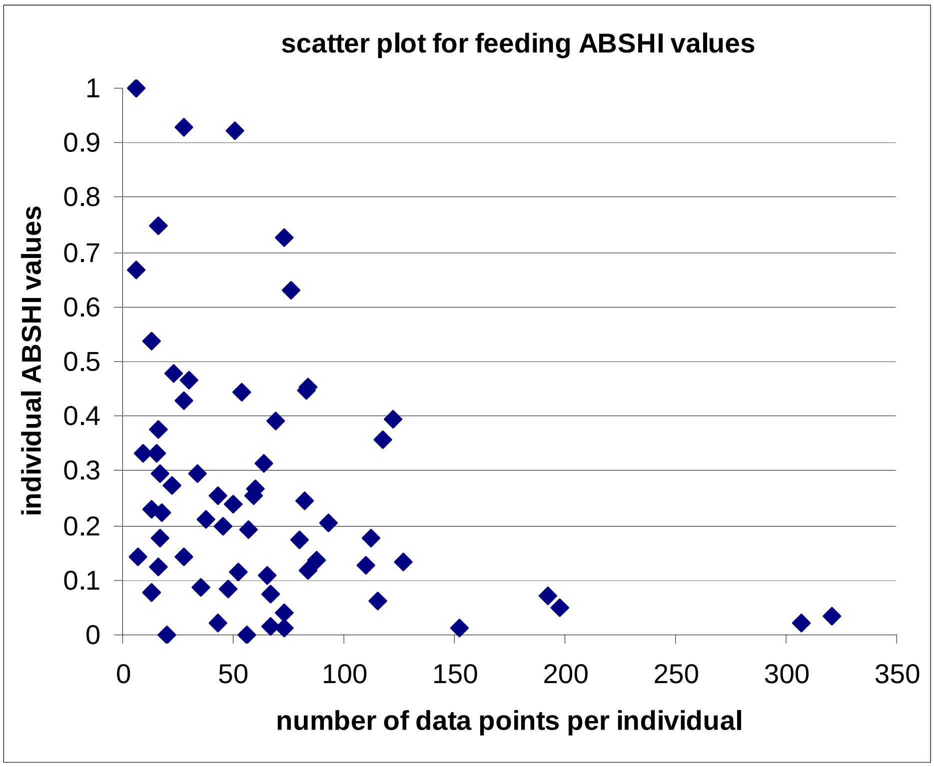

Figure 7: Scatter plot showing the distribution of ABSHI values with increasing number of data points for “feeding”.

To conclude, on the correlations the data generally show no effect of the sample size on laterality (direction and strength). However, there was a notable caveat with the effect observed for “feeding”.

- To further assess the possible influence of the sample size on laterality, I compared the number of data points in lateralized versus unlateralized individuals. When considering each behaviour separately (actions with N ≥ 6), there were more data points in lateralized than unlateralized subjects in many cases: significant difference in 8 cases, non-significant trend in 2 cases, no difference in 8 cases (Table 8app). This suggests that, in many cases, the laterality was weaker in the individuals with few data points.

- When considering the particular case of “feeding”, this was the behaviour with the greatest number of subjects and the largest number of data points per subject (significantly more data points per subject for feeding than for other behaviours in most cases). Interestingly, this action exhibited a weak laterality and its ABSHI values were significantly lower than that of most other behaviours (MW $p \leq 0.05$) (Table 4app, Figure 3).

In conclusion, to summarize the findings on the effect of the number of data points: whilst the correlations yielded mainly negative findings (no effect), the analysis on "feeding" and the analyses comparing lateralized and unlateralized subjects show that the number of data points may influence the strength of laterality.

1.6. Other analyses:

Tables 15, 16, 17 at the end of this chapter present the laterality of each individual, i.e. the classification of each subject as right-handed, left-handed or unlateralized, for each behaviour.

Laterality appeared to be strongly related to the individual. For a given action some individuals exhibited right hand preference, while other individuals showed left hand preference and others were unlateralized.

Consistency of hand preference between actions:

I investigated intra-individual consistency across manual actions, i.e. whether the individuals changed hand preference between the different actions. Only the individuals that had data for at least 3 actions were included in this analysis. The individuals lateralized for at least 2 actions were tested for consistency across lateralized actions. The other individuals were classified as "always unlateralized", if they had no lateralized action, and "almost always unlateralized", if they had only one lateralized action. The results are presented in Table 11.

Table 11: Within-subject consistency of hand preference across actions (study 1).

			individuals with fewer than two lateralized behaviours		individuals with at least two lateralized behaviours	
		number of bonobos tested	always unlateralized	almost always unlateralized	same preference across actions	different preference between actions
Behaviours (n=26)	Lola	23	9	9	3	2
	zoos	26	2	6	9	9
	Lola + zoos	49	11	15	12	11
Behavioural patterns (n=42)	Lola	38	14	10	9	5
	zoos	28	2	5	10	11
	Lola + zoos	66	16	15	19	16

Therefore, the data show that: a) most bonobos showed no preference in the majority of the actions studied (especially at Lola), b) a number of bonobos changed hand preference between the different actions, c) a number of bonobos exhibited the same hand preference between the different actions. Namely, there was a consistency of preference in half of the bonobos analyzed, while the others showed changes of preference across behaviours or behavioural patterns.

Effect of kinship:

I considered the question of heritability of hand preference (predictions 7 and 17). This was the first time that this issue was addressed in bonobos. I examined laterality in pairs of related individuals. I compared the preference: a) R, L, Nlat, b) R, L only, excluding Nlat, between related subjects. The results are presented in Tables 12 and 13.

Table 12: Effect of kinship (mother).
For each action, the table gives the number of pairs tested, the number of pairs showing a matched laterality (R, L, Nlat) between the mother and its infant, or between siblings (same mother), and the number of pairs showing a different laterality. The numbers in brackets are the numbers based on analysis with L and R only, excluding Nlat.

		Pairs tested	**Pairs with matched laterality**	**Pairs with different laterality**
mother-infant pairs	feeding	12	8 (1)	4 (0)
	reaching for small items	11	5 (2)	6 (1)
	quadrupedal movement	3	1 (1)	2 (1)
	reach for big items	3	1 (1)	2 (0)
	tripedal movement + while feeding	5	0 (0)	5 (0)
	swinging + hanging	1	1 (1)	0 (0)
	the ''tube task''	14	3 (3)	11 (9)
	''termite fishing'' task	9	3 (2)	6 (1)
	play category	5	5 (0)	0 (0)
siblings pairs (same mother)	feeding	3	2 (0)	1 (0)
	reaching for small items	3	0 (0)	3 (0)
	swinging + hanging	2	2 (0)	0 (0)
	the ''tube task''	6	3 (3)	3 (3)
	''termite fishing'' task	4	1 (0)	3 (1)
	play category	2	2 (0)	2 (0)

For the actions of study 1, I found more pairs with different than matched preferences among mother-infant pairs, but this did not appear when I removed unlateralized subjects from the analysis. Regarding siblings pairs, there were about identical numbers of pairs with matched laterality and pairs with different laterality. These results suggest no particular relationship between the laterality of related individuals.

Table 13: Effect of kinship (father).
For each action, the table gives the number of pairs tested, the number of pairs showing a matched laterality (R, L, Nlat) between the father and its infant, or between siblings (same father), and the number of pairs showing a different laterality. The numbers in brackets are the numbers based on analysis with L and R only, excluding Nlat.

		Pairs tested	**Pairs with matched laterality**	**Pairs with different laterality**
father-infant pairs	feeding	5	2 (1)	3 (0)
	reaching for small items	7	1 (0)	6 (1)
	quadrupedal movement	2	0 (0)	2 (0)
	reach for big items	2	1 (1)	1 (0)
	tripedal movement + while feeding	2	2 (0)	0 (0)
	swinging + hanging	2	1 (0)	1 (0)
	the ’’tube task’’	9	0 (0)	9 (8)
	’’termite fishing’’ task	1	0 (0)	1 (0)
	play category	2	2 (0)	0 (0)
siblings pairs (same father)	feeding	2	1 (0)	1 (0)
	reaching for small items	4	3 (0)	1 (0)
	swinging + hanging	1	0 (0)	1 (0)
	the ’’tube task’’	5	3 (3)	2 (0)

For the actions of study 1, I found more pairs with different than matched laterality among father-infant pairs, but this did not appear when I removed unlateralized subjects from the analysis. Regarding siblings pairs, there were slightly more pairs with matched than different preferences. These results suggest no particular relationship between the laterality of related individuals.

Consistency of hand preference over time:

I investigated the issue of consistency of hand preference over time (predictions 7). This was the first time that this question was addressed in bonobos. I compared my data with data collected in the same subjects several years before my study (May to November 2000 by Harrison and Nystrom (2008) N=14 and June to August 1992 by Hopkins et al. (1993) N=1. These previously published data were reanalyzed with my statistical method to allow reliable comparison. I compared the classification (L, R, Nlat) of each individual for the behaviours that were comparable. The results are presented in Table 14.

Table 14: Consistency of hand preference over time for spontaneous non-social actions (study 1).
This table presents the results of Harrison and Nystrom (2008) and of Hopkins et al. (1993) compared to my results on the same individuals. Individuals in bold are those that are lateralized and consistent in direction between the studies.

behaviour	**individuals**	**Harrison and Nystrom 2008**	**This study**
carrying	**Daniela**	**R**	**R**
	Diatou	Nlat	Nlat
	Diwani	Nlat	Nlat
	Kakowet	Nlat	Nlat
	Kichele	/	L
	Louisoko	**L**	**L**
feeding	*Banya*	*L*	*R*
	Chipita	R	Nlat
	Daniela	R	Nlat
	Diatou	Nlat	L
	Diwani	L	Nlat
	Jasongo	Nlat	Nlat
	Kakowet	R	Nlat
	Keke	R	Nlat
	Kichele	Nlat	L
	Kirembo	**R**	**R**
	Lina	L	Nlat
	Louisoko	L	Nlat
	Zorba	**L**	**L**
gestures	Diwani	Nlat	Nlat
	Keke	Nlat	Nlat
		Hopkins *et al.* 1993	This study
carrying	Jill	Nlat	R
reaching	Jill	Nlat	R

- For the carrying behaviour, defined in my study as “tripedal movement holding food/object in one hand”, we could approximately compare it with the behaviour defined as “Carry and object manipulation: transport an object for at least 3 consecutive steps. manoeuvre an object for some purpose other than feeding or tool-use” of Harrison and Nystrom (2008), keeping in mind that these authors gathered carry and manipulation. I found that all the 5 subjects available were classified in the same category in both studies (3 of them were unlateralized).
- For the carrying behaviour, defined in my study as “tripedal movement holding food/object in one hand”, we could approximately compare with the behaviour defined as “Carrying: animal uses one or both hands to grasp an object, infant, or a food item and physically carry it to a different location in the cage. A minimum of 3 strides must occur for carrying to be recorded” of Hopkins et al. (1993), keeping in mind that these authors have gathered carrying object and carrying infant (see section I.4). I found that Jill was right-handed in my study while she was classified as unlateralized in Hopkins’ study.
- For the reaching behaviour, defined in my study as “reaching for big items”, we could approximately compare with the behaviour defined as “animal uses one hand to grasp a food item” (sliced fruits) of Hopkins et al. (1993). When I compared the data, I found that Jill was right-handed in my study while she was classified as unlateralized in Hopkins’ study.
- For the feeding behaviour, defined in my study as “feeding: place an item of food into the mouth”, we could compare with the behaviour defined as “feed: place an item of food in the mouth of Harrison and Nystrom (2008). Among the 13 subjects available, 10 were classified in different categories in the two studies (Banja was even placed in opposite categories) and 3 were classified in the same categories in the two studies (1 of them was unlateralized).

Therefore, in many cases, I found no consistency between my results and the previously published findings. However, these inconsistencies concerned only classification as lateralized or unlateralized. In only one case, there was a preference in the opposite direction between my study and the previous data. Importantly, in several cases, I observed the same laterality in my study and in the previous studies, suggesting consistency of hand preference over years.

Table 15: Data per subject for spontaneous non-social actions (study 1) and for studies 2, 3b, 4b for comparison. Apenheul zoo. (study 1).

	Jasiri	**Jill**	**Kumbuka**	**Liboso**	**Lingala**	**Lomela 1**	**Mobikisi**	**Mwindu**	**Zuani**
swinging	Nlat		Nlat		L				
hanging	Nlat	Nlat	Nlat		L				Nlat
swinging+hanging	Nlat	L	Nlat		L				Nlat
feeding, general	R	Nlat	Nlat	Nlat	Nlat	Nlat	Nlat	R	Nlat
feeding, tripedal	Nlat	R	Nlat	R	Nlat	Nlat	Nlat	R	L
feeding, seated, other hand in postural support	R	Nlat	L	Nlat	Nlat	Nlat	Nlat	Nlat	Nlat
feeding, seated, other hand holding a food item	Nlat	L	Nlat	Nlat	Nlat	R	Nlat	R	Nlat
feeding, seated, other hand inactive	R	Nlat	Nlat	Nlat	Nlat	L	L	R	Nlat
pulling grass out, general	Nlat	R		R		Nlat		Nlat	Nlat
pulling grass out, tripedal		R							Nlat
pulling grass out, seated, other hand in postural support									
pulling grass out, seated, other hand inactive		Nlat							
quadrupedal movement holding item	R	R	Nlat	R	R	L	L	Nlat	Nlat
tripedal movement holding item	Nlat	R	Nlat	R	Nlat	L			Nlat
tripedal movement while feeding		R	Nlat	Nlat	Nlat				
reaching for big items, general	R	R	Nlat	R	Nlat	Nlat	Nlat	R	Nlat
reaching for big items, tripedal	Nlat	R	Nlat	Nlat	Nlat	Nlat	Nlat	R	Nlat
reaching for small items, general	R	R	L	Nlat	Nlat	R	Nlat	Nlat	Nlat
reaching for small items, tripedal	R	R	L	Nlat	Nlat	R	Nlat	R	Nlat
reaching for small items, seated, other hand in postural support	R	R	L	Nlat	Nlat	Nlat	Nlat	Nlat	Nlat
reaching for small items, seated, other hand inactive	Nlat	Nlat	L	Nlat	Nlat	Nlat		Nlat	Nlat
reaching for small items, lying on the belly		R						Nlat	
reaching for small items with lateral grip type	R	R	L	Nlat	Nlat	R	Nlat	Nlat	Nlat
reaching for small items with one finger grip type									
reaching for small items with dorsal grip type		L		L		L			
pushing an object							Nlat		

table 15 continued	**Jasiri**	**Jill**	**Kumbuka**	**Liboso**	**Lingala**	**Lomela 1**	**Mobikisi**	**Mwindu**	**Zuani**
dragging an object							Nlat		
pulling water vegetation out, general	Nlat	Nlat				L			Nlat
pulling water vegetation out, tripedal	Nlat	R				L			Nlat
pulling leaves out (bimanual)		Nlat				R			Nlat
behaviours related to genitals, general									
behaviours related to genitals, tripedal									
inserting a finger (self-directed)			R	Nlat		L			
inserting hand in throat		Nlat				Nlat			Nlat
raking seeds on the floor									
reaching in water pond	Nlat	Nlat	L			Nlat			
chest rubbing								Nlat	
reaching in the fixed object (unimanual)									
reaching in the object (bimanual)									
catching		R							
nut cracking									
arm around neck posture									
foetus position		Nlat	Nlat	Nlat		Nlat	Nlat	Nlat	Nlat
turning (standing)	Nlat		R		Nlat				
turning (supine)					R				
crossing legs				Nlat		R	Nlat		Nlat
side of the sexual swellings when seated									
crossing arms		R	Nlat			L	Nlat	R	R
breaking a piece from the food item									
throwing									
peeling the fruit									
begging experiment									
"termite fishing" task (bouts)									
"tube task" (bouts)	L	R	L	R	L	L		Not lat	L
"tube task" (frequency)	L	R	L	R	L	L		R	L

Table 16: Data per subject for spontaneous non-social actions (study 1) and for studies 2, 3b, 4b for comparison. Stuttgart zoo. (study 1)

	Banbo	**Chipita**	**Daniela**	**David**	**Diwani**	**Khaya**	**Kirembo**	**Kombote**	**Lina**	**Louisoko**	**Lucuma**	**Mixi**	**Zorba**
swinging											Nlat		
hanging						Nlat					Nlat		
swinging+hanging						Nlat					Nlat		
feeding, general		Nlat	Nlat	Nlat	Nlat		R		Nlat	Nlat	Nlat		L
feeding, tripedal													
feeding, seated, other hand in postural support		Nlat			Nlat								
feeding, seated, other hand holding a food item				Nlat					Nlat				
feeding, seated, other hand inactive					Nlat		Nlat		Nlat	Nlat			
pulling grass out, general													
pulling grass out, tripedal													
pulling grass out, seated, other hand in postural support													
pulling grass out, seated, other hand inactive													
quadrupedal movement holding item													
tripedal movement holding item			R		Nlat					L			
tripedal movement while feeding													
reaching for big items, general													
reaching for big items, tripedal													
reaching for small items, general	Nlat	Nlat	Nlat	Nlat	L		R	Nlat	R	R	Nlat	Nlat	Nlat
reaching for small items, tripedal			Nlat				Nlat		Nlat				
reaching for small items, seated, other hand in postural support		Nlat	Nlat	Nlat	Nlat		R		Nlat	Nlat			Nlat
reaching for small items, seated, other hand inactive		Nlat	Nlat	Nlat	L		R	Nlat	R	R	Nlat		Nlat
reaching for small items, lying on the belly													

table 16 continued	**Banbo**	**Chipita**	**Daniela**	**David**	**Diwani**	**Khaya**	**Kirembo**	**Kombote**	**Lina**	**Louisoko**	**Lucuma**	**Mixi**	**Zorba**
reaching for small items with lateral grip type		Nlat	R	R			Nlat	Nlat	R			Nlat	Nlat
reaching for small items with one finger grip type			L		L		R		Nlat	R			
reaching for small items with dorsal grip type													
pushing an object				R									
dragging an object													
pulling water vegetation out, general													
pulling water vegetation out, tripedal													
pulling leaves out (bimanual)													
behaviours related to genitals, general													
behaviours related to genitals, tripedal													
inserting a finger (self-directed)		L							Nlat				
inserting hand in throat													
raking seeds on the floor			Nlat	R	L		R		R	R	R		
reaching in water pond													
chest rubbing													
reaching in the fixed object (unimanual)				Nlat									
reaching in the object (bimanual)				L									
catching													
nut cracking													
arm around neck posture													
foetus position			Nlat				Nlat		Nlat				Nlat
turning (standing)													
turning (supine)													
crossing legs													
side of the sexual swellings when seated													
crossing arms					L		Nlat		R	L			Nlat
breaking a piece from the food item													
throwing													

table 16 continued	**Banbo**	**Chipita**	**Daniela**	**David**	**Diwani**	**Khaya**	**Kirembo**	**Kombote**	**Lina**	**Louisoko**	**Lucuma**	**Mixi**	**Zorba**
peeling the fruit													
begging experiment													
"termite fishing" task (bouts)	L	Nlat	R	Nlat	Nlat	R	R	R	L	L	Nlat	R	
"tube task" (bouts)	L	Not lat	R	L	L	Not lat (L trend)	R	Not lat	Not lat (L trend)	R	Not lat (L trend)	Not lat	R
"tube task" (frequency)	L	L	R	L	L	L	R	L	L	R	L	Not lat	R

Table 17: Data per subject for spontaneous non-social actions (study 1) and for studies 2, 3b, 4b for comparison. Twycross zoo. (study 1).

	Banya	Bokela	Cheka	Diatou	Jasongo	Kakowet Ii	Keke	Kichele	Luo
swinging		L					Nlat		Nlat
hanging		Nlat	Nlat					Nlat	Nlat
swinging+hanging		L	Nlat		Nlat		Nlat	Nlat	Nlat
feeding, general	R		Nlat	L	Nlat	Nlat	Nlat	L	
feeding, tripedal	R			L					
feeding, seated, other hand in postural support	R						Nlat	Nlat	
feeding, seated, other hand holding a food item									
feeding, seated, other hand inactive	R			L	Nlat	Nlat	R	L	
pulling grass out, general	L		Nlat		R		R	L	
pulling grass out, tripedal									
pulling grass out, seated, other hand in postural support							R	L	
pulling grass out, seated, other hand inactive	L						R		
quadrupedal movement holding item							Nlat		
tripedal movement holding item				Nlat		Nlat		L	
tripedal movement while feeding									
reaching for big items, general	R			L	Nlat			L	
reaching for big items, tripedal	R			L					
reaching for small items, general	R		R	L	R	L	R	Nlat	
reaching for small items, tripedal	R		Nlat	L	R			Nlat	
reaching for small items, seated, other hand in postural support	R		R	L	R	L	R	Nlat	
reaching for small items, seated, other hand inactive	R		Nlat		Nlat	L			
reaching for small items, lying on the belly									
reaching for small items with lateral grip type									
reaching for small items with one finger grip type									
reaching for small items with dorsal grip type									
pushing an object				Nlat	R	L	L		
dragging an object	Nlat		Nlat			Nlat		L	

table 17 continued	**Banya**	**Bokela**	**Cheka**	**Diatou**	**Jasongo**	**Kakowet Ii**	**Keke**	**Kichele**	**Luo**
pulling water vegetation out, general									
pulling water vegetation out, tripedal									
pulling leaves out (bimanual)									
behaviours related to genitals, general	R							Nlat	
behaviours related to genitals, tripedal									
inserting a finger (self-directed)	R								
inserting hand in throat									
raking seeds on the floor									
reaching in water pond							R	Nlat	
chest rubbing						L			
reaching in the fixed object (unimanual)	Nlat	Nlat	Nlat	Nlat		Nlat		Nlat	Nlat
reaching in the object (bimanual)			Nlat			R		Nlat	Nlat
catching									
nut cracking									
arm around neck posture				R					
foetus position	Nlat		L	R	Nlat	Nlat	Nlat	R	
turning (standing)		Nlat	Nlat		R				Nlat
turning (supine)		Nlat							Nlat
crossing legs									
side of the sexual swellings when seated	R			R				Nlat	
crossing arms	R		L	R	Nlat	L	L	R	
breaking a piece from the food item									
throwing									
peeling the fruit									
begging experiment									
"termite fishing" task (bouts)	L		R	Nlat	Nlat	Nlat	Nlat	R	
"tube task" (bouts)	Not lat		Not lat	L	R	Not lat (L trend)	R	Not lat	Not lat
"tube task" (frequency)	R		Not lat	L	R	Not lat	R	R	L

The data for Lola ya bonobo are presented in Tables 9app, 10app, 11app in appendix.

Chapter 2: Results of study 2: the "Tube task" experiment

The "tube task" was the major piece of research of this PhD thesis (see section I.4.3.3). The findings have been published in :

- CHAPELAIN A. & E. HOGERVORST. 2009. Hand preferences for bimanual coordination in 29 bonobos (*Pan paniscus*). Behavioural Brain Research, 196: 15-29.
- CHAPELAIN A., HOGERVORST E., MBONZO P. & WD. HOPKINS (in press). Hand preferences for bimanual coordination in 77 bonobos (*Pan paniscus*): replication and extension. International Journal of Primatology.

I here investigated hypotheses related to manipulation and bimanual coordination (predictions 4, 6, 6' and 6'').

The results of the "tube task" study are presented in this chapter.
Because of the large sample of subjects and data, I could here perform more detailed investigation than in my other studies. First, I present a summary of the data from the zoos and from the sanctuary separately. Then, I present analyses for the combined dataset (lola + zoos). As the sample of data was large enough, I could restrict analysis to the individuals that had at least 15 data points.

Table 6 in the methods section gives the number of data analyzed.
The raw data for each individual are presented in Table 12app in appendix.
The descriptive statistics for each sample are presented in Table 18.
The results of analyses on the effect of the number of data points, sex, age, settings, rearing history are presented in tables (Tables 20, 21 and 13app, 14app, 15app) and are discussed at the end of this chapter.

Table 18: Descriptive statistics of laterality for the “tube task”, for frequency and for bouts, for each sample (study 2).
N: number of subjects included in the analyses (individuals with n ≥ 15). The columns give the number of subjects that were classified as unlateralized, right-handed or left-handed based on Binomial tests. % preference: mean percentage of use of the preferred hand.

		N	number of data points	not lateralized	right-handed	left-handed	mean ABSHI	% preference	mean HI
Lola Ya Bonobo	frequency	48	total: 7058 mean: 147.04 SD=75.33, range=17 to 332	6 (12.5%)	22	20	0.458 SD=0.27	75.41% SD=12.72, N=42, range=58.2 to 100	0.043 SD=0.54
	bouts	40	total: 1186 mean: 29.65 SD=11.26, range=15 to 56	29 (72.5%)	6	5	0.335 SD=0.26	85.72% SD=7.68, N=11, range=76 to 100	0.026 SD=0.43
Zoos (Twycross Stuttgart Apenheul)	frequency	29	total: 7889 mean: 272 SD=164.61, range=47 to 656	3 (10.34%)	11	15	0.569 SD=0.32	81.18% SD=14.14, N=26, range=57.84 to 100	0.02 SD=0.66
	bouts	29	total: 1381 mean: 47.62 SD=20.46, range=15 to 98	12 (41.38%)	8	9	0.492 SD=0.3	83.98% SD=11.94, N=17, range=64.62 to 100	0.026 SD=0.58
Lola Ya Bonobo + Zoos	frequency	77	total: 14947 mean: 194.12 SD=131.18, range=17 to 656	9 (11.69%)	33	35	0.499 SD=0.29	77.62% SD=13.48, N=68, range=57.84 to 100	0.034 SD=0.58
	bouts	69	total: 2567 mean: 37.20 SD=18.02, range=15 to 98	41 (59.42%)	14	14	0.401 SD=0.3	84.66% SD=10.35, N=28, range=64.62 to 100	0.026 SD=0.5

2.1. Zoos:

Frequency (number of responses per subject):

The number of lateralized subjects was greater than the number of unlateralized individuals (B p<0.001) (Table 18). The mean HI value was not significantly different from 0, the value expected by chance (T t(28)=0.160, p=0.874), indicating no bias toward the use of one particular hand. There was no group-level bias regarding the numbers of right-handed and left-handed subjects (B p=0.557).

Bouts (number of bouts per subject):

The numbers of lateralized subjects and unlateralized subjects did not differ (B p=0.458) (Table 18). The mean HI value for the group was not significantly different from the value expected by chance (T t(28)=0.239, p=0.813). Thus, there was no bias toward the use of one particular hand. There was no group-level bias regarding the numbers of right-handed and left-handed subjects (B p=1).

Comparison between frequency and bouts:

I compared the two recording techniques to assess any possible difference. There were significantly more lateralized subjects with frequency than with bouts (B p=0.035). Moreover, the ABSHI values were higher with frequency (mean=0.568) than with bouts (mean=0.492) (W z=-3.234, p=0.001). This indicates that the laterality was stronger with frequency. The HI values were similar with the two measures (W z=-0.296, p=0.767), suggesting that the results for the direction of laterality were not influenced by the measure. The HI values with frequency and bouts were correlated (Spearman rho=0.972, p<0.001) and so were the ABSHI values (Spearman rho=0.936, p<0.001).

50 frequency data points:

Frequency and bouts differed regarding the number of data points per subject (mean=272 with frequency, around 50 (47.62) with bouts). Actually, there was almost 6 times more data points with frequency than with bouts. To investigate the possible effect of this sample size difference, I considered only 50 frequency data points per subject, to compare measures that had similar sample sizes.

With the 50 frequency data points, 22 (75.86%) bonobos were significantly lateralized (B $p \leq 0.049$) and 7 (24.14%) had no preference (B $p \geq 0.119$). There were significantly more lateralized than unlateralized bonobos (B p=0.008). The mean ABSHI was 0.583 (SD=0.348) and the mean percentage of use of the preferred hand was 86.724 (SD=11.506, N= 22), indicating a very strong laterality. The mean HI value was -0.056 (SD=0.696), which was not significantly different from 0 (T t(28)=-0.441, p=0.663). Thus, there was no bias toward the use of one particular hand. 9 bonobos were classified as right-handed and 13 were left-handed, so there was no group-level bias in the proportion of right-handed and left-handed subjects (B p=0.523).

<u>- Comparison between 50 frequency data points and bouts:</u> The HI values with bouts were significantly higher than that with 50 frequency data points (W z=-2.054, p=0.04). The ABSHI values were significantly higher with 50 frequency data points than with bouts (W z=-2.174, p=0.03). Therefore, both the HI and ABSHI values differed between bouts and frequency when compared on similar sample sizes. This suggests that the recording method affected laterality, and the effect was not just related to a sample size difference.

<u>- Comparison between 50 frequency data points and frequency:</u> To examine the effect of sample size alone, I compared the data with 50 frequency data points and with frequency. The HI values with frequency were higher than that with 50 frequency data points (W z=-2.095, p=0.036). The ABSHI values were similar with the two measures (W z=-0.615, p=0.539). This indicates that the sample size affected the direction, but not the strength of laterality.

Bout length:

Bout length is the number of frequency data points per bout. This third measure can provide complementary information on laterality. I compared the mean bout length between the right and left hands for each individual. The mean length of bouts with the right hand (8.525) was greater than that with the left hand (4.619) (W z=-2.8, p=0.005) in right-handed subjects. Similarly, the mean length of left hand bouts (5.56) was greater than that of right hand bouts (3.84) (W z=-2.726, p=0.006) in left-handed individuals. There was no difference between the right hand (4.531) and the left hand (4.18) (W z=0, p=1) in unlateralized individuals (N=3). These findings indicate that the individuals performed longer bouts with their preferred hand.

2.2. Lola ya bonobo:

Frequency (number of responses per subject):

There were significantly more lateralized than unlateralized bonobos (B $p<0.001$) (Table 18). The mean HI value was not significantly different from 0 (T $t(47)=0.559$, $p=0.579$), indicating no bias toward the use of one particular hand. There was no group-level bias regarding the numbers of right-handed and left-handed subjects (B $p=0.878$).

Bouts (number of bouts per subject):

The individuals that had less than 15 bouts were excluded, which rendered 40 individuals for this analysis. There were significantly more unlateralized than lateralized subjects (B $p=0.006$) (Table 18). The mean HI value was not significantly different from the value expected by chance (T $t(39)=0.382$, $p=0.704$). Thus, there was no bias toward the use of one particular hand. There was no group-level bias regarding the number of right-handed and left-handed subjects (B $p=1$).

Comparison between frequency and bouts:

I compared the results of the two recording techniques (excluding individuals with less than 15 bouts). There were significantly more lateralized subjects with frequency than with bouts (B $p<0.001$). Moreover, the ABSHI values were higher with frequency than with bouts (W $z=-4.577$, $p<0.001$). This indicates that the laterality was stronger with frequency. The HI values were similar with the two measures (W $z=0.516$, $p=0.606$), which suggests that the results for the direction of laterality were not influenced by the measure. The HI values with frequency and bouts were correlated (Spearman $rho=0.936$, $p<0.001$, $N=40$) and so were the ABSHI values (Spearman $rho=0.851$, $p<0.001$, $N=40$).

Bout length:

I compared the bout length between the right and left hands for each individual. Among the 11 lateralized individuals tested only one subject exhibited a significant asymmetry in bout length (Mimia showed longer bouts with her preferred compared to her non-preferred hand (B test $p=0.012$)).

2.3. Lola ya bonobo + zoos:

Frequency (number of responses per subject):

Amongst the 77 bonobos, 68 (88.312%) were significantly lateralized (B $p \leq 0.032$) and only 9 (11.688%) showed no preference (B $p \geq 0.111$) (Table 18). There were significantly more lateralized than unlateralized bonobos (B $p<0.001$). The mean ABSHI was 0.499 (SD=0.293), which indicates a strong laterality. When considering lateralized subjects, the mean percentage of use of the preferred hand was 77.619% (min=57.84, max=100, SD=13.478, N=68), indicating quite strong preferences.

The mean HI value was 0.034 (SD=0.581), which was not significantly different from 0, the value expected by chance (T $t(76)=0.519$, $p=0.605$). Thus, there was no bias toward the use of one particular hand. 33 bonobos were classified as right-handed and 35 were left-handed. These numbers were not significantly different (B $p=0.904$), so there was no group-level bias.

The percentage of right-handers in the group was 42.857%. When excluding unlateralized subjects, the proportion of right-handers amongst lateralized subjects was 48.529%.

Bouts (number of bouts per subject):

Amongst the 69 bonobos kept for analysis on bouts (individuals with $n \geq 15$), 28 (40.58%) were significantly lateralized (B $p \leq 0.035$) and 41 (59.42%) showed no preference (B $p \geq 0.053$) (Table 18). The numbers of lateralized and unlateralized subjects were similar (B $p=0.148$). The mean ABSHI was 0.401 (SD=0.288), indicating a rather weak laterality. When considering lateralized individuals, the mean percentage of use of the preferred hand was 84.662 (min=64.62, max=100, SD=10.348, N=28), which indicates strong preferences.

The mean HI value was 0.026 (SD=0.495), which was not significantly different from the value expected by chance (T $t(68)=0.434$, $p=0.665$). Thus, there was no bias toward the use of one particular hand. 14 bonobos were classified as right-handed and 14 were left-handed, indicating no group-level bias (B $p=1.149$).

The percentage of right-handers in the group was 20.29%. When excluding unlateralized subjects, the proportion of right-handers amongst lateralized subjects was 50%.

Comparison between frequency and bouts:

I compared the results of the two recording techniques (excluding individuals with less than 15 bouts). There were significantly more lateralized subjects with frequency than with bouts (B $p<0.001$). Moreover, the ABSHI values were higher with frequency than with bouts (W $z=-5.585$, $p<0.001$). This indicates that laterality was stronger with frequency. The HI values were similar with the two measures (W $z=-0.2$, $p=0.842$), suggesting that the results for the direction of laterality were not influenced by the measure. The HI values with frequency and bouts were correlated (Spearman $rho=0.958$, $p<0.001$, $N=69$) and so were the ABSHI values (Spearman $rho=0.878$, $p<0.001$, $N=69$).

2.4. Comparison between the "tube task" and the other actions:

I compared the data for the "tube task" with the data for the 13 main spontaneous non-social actions, for bimanual feeding specifically and with data for tool-use (study 3), to test whether the laterality for this experimental task was more marked than that of spontaneous actions (predictions 7). This analysis is based on bouts as only bouts were recorded for the spontaneous actions. The individuals with less than 15 bouts were included for the "tube task" in order to have the same inclusion criterion as that used for spontaneous actions ($n \geq 6$). The results of the MW tests are presented in Table 19.

Table 19: Comparisons between the “tube task” and the other actions (study 2). Results of the MW test, p values for HI, ABSHI and total (number of data points per subject) comparisons between the “tube task” and other actions. Significant p values are in bold.

“Tube task” (bouts) (N=77) versus :	**MW on total**	**MW on HI values**	**MW on ABSHI values**
“reaching for big items, general” N=26	U=299 **p<0.001**	U=926 p=0.569	U=845.5 p=0.238
“reaching for small items (seeds), general” N=33	U=1173.5 p=0.527	U=1049.5 p=0.149	U=1169 p=0.508
“reaching in the fixed object (dipping) (unimanual)” N=8	U=100 **p=0.002**	U=258 p=0.452	U=289 p=0.775
“feeding, general” N=65	U=1679.5 **p=0.001**	U=2273.5 p=0.348	U=1814.5 **p=0.005**
“quadrupedal movement holding food/object in one hand” N=32	U=511 **p<0.001**	U=1230 p=0.989	U=1033 p=0.185
“tripedal movement holding food/object in one hand + while feeding” N=27	U=256.5 **p<0.001**	U=988.5 p=0.705	U=942 p=0.470
“pushing an object” N=10	U=202.5 **p=0.015**	U=292.5 p=0.218	U=201 **p=0.014**
“dragging an object” N=11	U=143.5 **p<0.001**	U=403.5 p=0.801	U=368.5 p=0.488
“swinging + hanging” N=15	U=407.5 p=0.072	U=348 **p=0.015**	U=449 p=0.174
“pulling grass out” N=11	U=114.5 **p<0.001**	U=405.5 p=0.820	U=206 **p=0.006**
“inserting a finger (self directed)” N=6	U=85.5 **p=0.010**	U=214 p=0.765	U=151.5 p=0.162
“raking seeds on the floor” N=7	U=153.5 p=0.060	U=139 **p=0.035**	U=113 **p=0.011**
“reaching in the water pond” N=6	U=15 **p=0.0001**	U=222.5 p=0.881	U=156.5 p=0.190
“feeding bimanual (seated with other hand holding a food item) N=41	U=764.5 **p<0.001**	U=1568 p=0.953	U=1237 *p=0.054*
“termite fishing” task N=19	U=539 p=0.077	U=629.5 p=0.348	U=639.5 p=0.397

- Regarding the HI values, the “tube task” was similar to most spontaneous actions (Table 19). The HI values for the ‘’tube task’’ were significantly lower than that for “raking seeds on the floor” and significantly higher than that for “swinging + hanging”, which are outliers behaviours among spontaneous non-social actions. Thus, the results suggest that the HI values for the “tube task” stood in the range of that for spontaneous non-social actions.

- Regarding the ABSHI values, the “tube task” data were similar to that of 9 spontaneous actions (Table 19), but differed significantly from that of 4 actions. The

ABSHI values for the “tube task” were significantly higher than that for “feeding”, and significantly lower than that for “pushing an object”, “pulling grass out” and “raking seeds on the floor”, which were outliers among spontaneous actions.

- However, it should be noted that the difference in the number of data points was always significant or close to significant (except for “reaching for small items”) (Table 19). In all cases (except feeding), there were more data points per subject for the “tube task” than for spontaneous actions, which may hinder the comparisons. In the case of feeding, the difference was in the opposite direction (more data points for feeding compared to the “tube task”). However, both actions had reasonable sample size and the laterality was stronger for the “tube task” compared to feeding.

- At the individual-level, the subjects generally showed the same preference for the “tube task” and the general trend for spontaneous actions, though several subjects showed opposite preferences (Table 15, 16, 17 and 9app, 10app, 11app) (when analyzing lateralized subjects, excluding unlateralized).

2.5. Effect of possible influential factors:

In the next paragraphs, I investigate the effects of several possible influential factors including: living conditions (settings), sex, age, rearing history (testing predictions 7, 15 and 16) and the number of data points, for each sample and for the combined sample.

Table 20 presents the HI and ABSHI and total means for each group considered.
The values of the tests are presented in Table 21.

Effect of the settings:

- When considering each setting separately no group-level bias occurred (in the number of individuals (B test p>0.05) and in the HI values (T test p>0.05). I then investigated the possible effect of the settings in two steps.

- First, I compared the data between the three zoos: Twycross, Stuttgart and Apenheul that were samples of similar size (around 10 subjects) (Table 5). I found no effect of the zoo on the HI values (KW p>0.05 for frequency and bouts) or ABSHI values (KW p>0.05) (Table 21). Regarding the number of data points per subject, there was a non-significant trend (KW frequency: p=0.07, bouts: p=0.097). Paired comparisons showed that there were more data points per subject at Apenheul compared to Stuttgart (MW frequency: p=0.033, bouts: p=0.039) (frequency: mean=387.75 for Apenheul, 198.615 for Stuttgart; bouts: mean=57.125 for Apenheul, 39.308 for Stuttgart).

- Secondly, I compared the data between Lola Ya Bonobo and the three zoos combined in a "zoos" group (Table 21). I found no significant effect of the settings on the HI values (MW p>0.05). Regarding the ABSHI values, there was no effect of the settings with frequency (MW p>0.05), but there was an effect with bouts: the ABSHI values were significantly higher in zoos compared to Lola with bouts (MW p=0.022). The number of data points per subject also differed, being significantly higher in zoos compared to Lola (MW frequency and bouts: p<0.001).

Therefore, the settings did not influence the direction of laterality. Regarding the strength, I observed a difference in ASBHI values in one case, but there was also a difference of sample size, which may hinder this comparison.

Table 20: Laterality data for each category of subjects based on age and sex (study 2). N: number of subjects included in the analyses. Asterixes indicate significant biases based on T tests.

		infants + juveniles	adolescents	adults	males	females
zoos - Frequency	N	8	5	16	11	18
	mean HI	-0.451* SD=0.327	-0.003 SD=0.821	0.262 SD=0.631	0.21 SD=0.787	-0.096 SD=0.558
	mean ABSHI	0.486 SD=0.264	0.669 SD=0.337	0.579 SD=0.339	0.71 SD=0.338	0.482 SD=0.274
	mean total	142.75 SD=100.92	269 SD=117.614	337.625 SD=169.213	209.546 SD=113.512	310.222 SD=181.6
zoos - Bouts	N	8	5	16	11	18
	mean HI	-0.398* SD=0.298	0.049 SD=0.682	0.231 SD=0.572	0.177 SD=0.731	-0.066 SD=0.471
	mean ABSHI	0.44 SD=0.221	0.551 SD=0.297	0.499 SD=0.344	0.646 SD=0.331	0.398 SD=0.242
	mean total	45 SD=21.213	50.8 SD=20.017	47.938 SD=21.377	35.818 SD=17.679	54.833 SD=18.974
Lola Ya Bonobo - Frequency	N	28	7	13	29	19
	mean HI	0.035 SD=0.571	-0.124 SD=0.542	0.152 SD=0.463	0.073 SD=0.551	-0.002 SD=0.523
	mean ABSHI	0.482 SD=0.294	0.425 SD=0.317	0.422 SD=0.216	0.466 SD=0.289	0.444 SD=0.256
	mean total	124.286 SD=61.406	153.286 SD=79.569	192.692 SD=84.187	143.517 SD=85.455	152.421 SD=58.371
Lola Ya Bonobo - Bouts	N	24	5	11	23	17
	mean HI	0.063 SD=0.507	-0.156* SD=0.121	0.027 SD=0.315	0.119 SD=0.456	-0.10 SD=0.362
	mean ABSHI	0.399 SD=0.307	0.173 SD=0.087	0.267 SD=0.147	0.358 SD=0.299	0.304 SD=0.21
	mean total	31.75 SD=12.467	26.8 SD=11.212	26.364 SD=7.775	30.13 SD=11.371	29 SD=11.429
Lola Ya Bonobo + zoos - Frequency	N	36	12	29	40	37
	mean HI	-0.073 SD=0.561	-0.074 SD=0.639	0.212* SD=0.556	0.110 SD=0.617	-0.048 SD=0.535
	mean ABSHI	0.483 SD=0.284	0.527 SD=0.335	0.508 SD=0.296	0.533 SD=0.319	0.463 SD=0.262
	mean total	128.389 SD=70.756	201.5 SD=109.699	272.655 SD=154.134	161.675 SD=97.15	229.189 SD=153.854
Lola Ya Bonobo + zoos - Bouts	N	32	10	27	34	35
	mean HI	-0.052 SD=0.502	-0.053 SD=0.474	0.148 SD=0.487	0.138 SD=0.549	-0.083 SD=0.416
	mean ABSHI	0.41 SD=0.285	0.362 SD=0.287	0.405 SD=0.3	0.451 SD=0.334	0.352 SD=0.228
	mean total	35.063 SD=15.84	38.8 SD=19.848	39.148 SD=20.09	31.971 SD=13.719	42.286 SD=20.325

Table 21: Results of tests on the effects of sex, age, settings and rearing (study 2). Results of tests on the HI values, ABSHI values and total (number of data points per subject). Effect of sex: MW test on males versus females. Effect of age: KW test on "infants + juveniles", "adolescents", "adults" and MW paired comparisons on grouped categories (regpt1, regpt2 see methods section II.1). Effect of the settings: KW on Twycross, Stuttgart, Apenheul and MW on zoos versus Lola ya bonobo. Effect of rearing history: KW test on "mother-reared", "human hand-reared", "Lola reared" and MW on "mother-reared" versus "human hand-reared + "Lola reared" (for zoos: MW on "mother-reared" versus "human hand-reared").

		analyses on HI values	**analyses on ABSHI values**	**analyses on the number of data points**
Zoos - Frequency	effect of sex	MW test, U=76, p=0.301, N1=11, N2=18	MW test, U=60, p=0.08, N1=11, N2=18 Trend for higher ABSHI values in males than females	MW test, U=66.5, p=0.144, N1=11, N2=18
	effect of age	KW test, H=6.339, p=0.042 Higher HI values in adults compared to "juveniles + infants" MW test, U=23, p=0.012 N1=8, N2=16	KW test, H=1.142, p=0.565 MW test, p>0.05	KW test, H=9.814, p=0.007 Fewer data points in youngs compared to adolescents MW test, U=5, p=0.028 N1=8, N2=5 and adults MW test, U=16, p=0.003 N1=8, N2=16
	effect of the settings	KW test, H=1.394, p=0.498	KW test, H=1.62, p=0.445	KW test, H=5.308, p=0.07 More data points at Apenheul than Stuttgart MW test, U=22.5, p=0,033 N1=8, N2=13
	effect of rearing history	MW test, U=78, p=0.77, N1=8, N2=21	MW test, U=69, p=0.464, N1=8, N2=21	MW test, U=68, p=0.435, N1=8, N2=21
Zoos - Bouts	effect of sex	MW test, U=84, p=0.50, N1=11, N2=18	MW test, U=56, p=0.053, N1=11, N2=18 Trend for higher ABSHI values in males than females	MW test, U=46.5, p=0.018, N1=11, N2=18 Fewer data points per subject in males
	effect of age	KW test, H=6.786, p=0.034 Higher HI values in adults compared to "juveniles + infants" MW test, U=20.5, p=0.008 N1=8, N2=16	KW test, H=0.322, p=0.851 MW test, p>0.05	KW test, H=0.687, p=0.709 MW test, p>0.05
	effect of the settings	KW test, H=1.352, p=0.51	KW test, H=1.372, p=0.5	KW test, H=4.659, p=0.09 More data points at Apenheul than Stuttgart MW test, U=23.5, p=0,039 N1=8, N2=13
	effect of rearing history	MW test, U=81 p=0.884, N1=8, N2=21	MW test, U=83, p=0.961 N1=8, N2=21	MW test, U=84, p=1 N1=8, N2=21

table 21 continued	**analyses on HI values**	**analyses on ABSHI values**	**analyses on the number of data points**	**analyses on HI values**
Lola Ya Bonobo - Frequency	effect of sex	MW test, U=247.5, p=0.555, N1=29, N2=19	MW test, U=274, p=0.975, N1=29, N2=19	MW test, U=239.5, p=0.448, N1=29, N2=19
	effect of age	KW test, H=1.665, p=0.435 MW test, p>0.05	KW test, H=0.17, p=0.919 MW test, p>0.05	KW test, H=6.083, p=0.048 Fewer data points in “juveniles + infants” than adults MW test, U=93, p=0.013 N1=28, N2=13
Lola Ya Bonobo - Bouts	effect of sex	MW test, U=130.5, p=0.075, N1=23, N2=17 Trend for higher HI values in males than females	MW test, U=190.5, p=0.891, N1=23, N2=17	MW test, U=184, p=0.753, N1=23, N2=17
	effect of age	KW test, H=2.358, p=0.308 MW test, p>0.05	KW test, H=2.193, p=0.334 MW test, p>0.05	KW test, H=1.627, p=0.443 MW test, p>0.05
Lola Ya Bonobo + Zoos – Frequency	effect of sex	MW test, U=622, p=0.229 N1=40, N2=37	MW test, U=652.5, p=0.372 N1=40, N2=37	MW test, U=539, p=0.040, N1=40, N2=37 Fewer data points per subject in males
	effect of age	KW test, H=4.469, p=0.107 Higher HI values in adults compared to “infants + juveniles” MW test, U=370.5, p=0.046, N1=36, N2=29. Higher HI values in adults compared to “infants + juveniles + adolescents” MW test, U=495, p=0.035, N1=48, N2=29	KW test, H=0.247, p=0.884 MW test, p>0.05	KW test, H=23.022, p<0.001 Fewer data points in ”juveniles + infants” than adolescents MW test, U=127, p=0.034 N1=36, N2=12 and adults MW test, U=163.5, p<0.001 N1=36, N2=29
	effect of the settings	MW test on lola versus zoos, U=657, p=0.682, N1=48, N2=29	MW test on lola versus zoos U=554.5, p=0.137, N1=48, N2=29	MW test on lola versus zoos U=339, p<0.001, N1=48, N2=29 More data points in zoos compared to lola
	effect of rearing history	KW test, H=0.299, p=0.861 MW test, U=572, p=0.586, N1=23, N2=54	KW test, H=1.465, p=0.481 MW test, U=514, p=0.234, N1=23, N2=54	KW test, H=8.776, p=0.012 MW test, U=415.5, p=0.022 N1=54, N2=23
Lola Ya Bonobo + Zoos - Bouts	effect of sex	MW test, U=429.5, p=0.047, N1=34, N2=35 Higher HI values in males	MW test, U=525.5, p=0.404, N1=34, N2=35	MW test, U=418.5, p=0.034, N1=34, N2=35 Fewer data points per subject in males than females
	effect of age	KW test, H=2.117, p=0.347 MW test, p>0.05	KW test, H=0.298, p=0.861 MW test, p>0.05	KW test, H=0.413, p=0.813 MW test, p>0.05
	effect of the settings	MW test on lola versus zoos, U=514.5, p=0.426, N1=40, N2=29	MW test, U=391, p=0.022, N1=40, N2=29 Higher ABSHI in zoos than lola	MW test, U=278, p<0.001 N1=40, N2=29 More data points in zoos compared to lola
	effect of rearing history	KW test, H=0.736, p=0.692 MW test, U=472, p=0.676, N1=21, N2=48	KW test, H=5.292, p=0.071 MW test, U=372.5, p=0.086, N1=21, N2=48	KW test, H=14.0, p=0.001 MW test, U=319.5, p=0.016, N1=21, N2=48

Effect of sex:

I tested the effect of sex in each sample (zoos, lola, lola+zoos).

- I first examined each sex group separately, and found no group-level bias in males, nor in females (in the number of individuals (B test p>0.05) and in the HI values (T test p>0.05) (Table 20, Table 13app, Table 14app).
- I compared the data for males and females. Regarding HI values, there was no significant difference between the two sexes (MW p ≥ 0.229), except in one case (Table 21): in the combined sample with bouts, the HI values were significantly higher in males than females (MW p=0.047), indicating a greater right hand use in males. In that case, there was also a significant difference of sample size (MW frequency p=0.04, bouts p=0.034), with fewer data points per subject in males than females. In the lola sample with bouts, there were also higher HI values in males than females (trend MW p=0.075). Regarding ABSHI values, there was no significant sex difference (MW p ≥ 0.372) (Table 21). However, there was a trend for males to be more strongly lateralized (higher ABSHI values) than females in the zoos sample (MW frequency: p=0.08, bouts: p=0.053). In that case, there was also a difference in the number of data points (MW N1=11, N2=18, U=46.5, p=0.018), with fewer data points per subject in males than females (Table 21).

Therefore, sex did not significantly influence laterality in most cases. I observed several significant effects or trends (but there might have been a confounding effect of sample size in these cases).

Effect of age:

I tested the effect of age in each sample (zoos, lola, lola + zoos).

- When considering each age group separately, significant biases occurred in several cases (Table 20, Table 13app, Table 14app). In zoos with frequency, there was a group-level left bias in the number of individuals in young subjects (infants + juveniles) (B p=0.016). Moreover, with frequency and with bouts (in zoos), there was a bias toward left hand use (skewed HI values) (frequency: mean HI: -0.451, T t(8)=-3.891 p=0.006, bouts: mean HI: -0.398, T t(8)=-3.777, p=0.007) in these young subjects. Finally, in the combined sample (lola + zoos) with frequency, there was a significant bias toward right hand use (skewed HI values) (*t*(28)=2.059, p=0.049) in adults.

- I compared the data between the three age groups (infants + juveniles, adolescents, adults) represented in (Figure 8, Table 20). I found no significant difference in the ABSHI values (KW p>0.05) (Table 21). However, I performed further analyses to test the hypothesis suggesting that immature subjects may differ from others. I compared each age group to each other group and to combined categories, using paired comparisons. No difference appeared regarding ABSHI values (MW p>0.05) (Table 21), which indicates no age difference in the strength of laterality. Regarding HI values, I found significant differences between age categories (Table 21). In zoos with frequency and bouts, the HI values were significantly lower in young subjects compared to others, indicating greater left hand use in young individuals. In the combined sample (lola + zoos) with frequency, adults displayed significantly higher HI values than the infants + juveniles group (MW test, U=370.5, p=0.046, N1=36, N2=29) and than the non-adults category (infants + juveniles + adolescents) (MW test, U=495, p=0.035, N1=48, N2=29), reflecting a greater right hand use in adults. The number of data points per subject also differed between age categories (Table 21). With frequency, at lola, at the zoos and at lola + zoos, there were more data points in older compared to young individuals, which may hinder the comparisons.

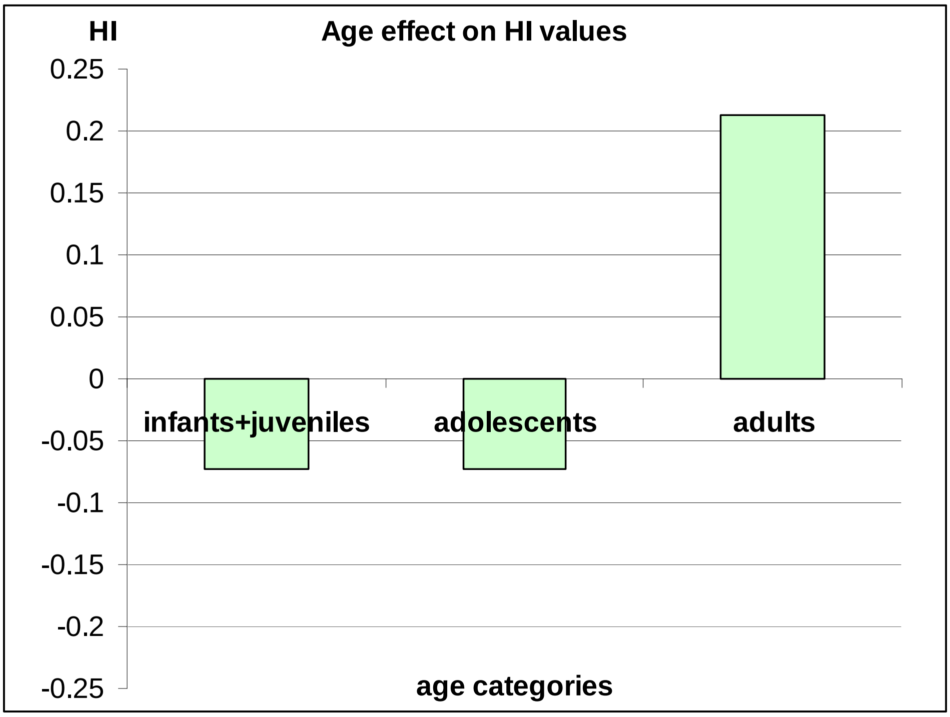

Figure 8: HI values according to age for the "tube task".
Mean HI value for each age category (with frequency) (for the sample lola + zoos).
The right bias in HI values in adults was statistically significant (see text).

Effect of rearing:

- When considering each rearing group separately, no group-level bias occurred in any of the groups (in the number of individuals (B test p>0.05) and in the HI values (T test p>0.05) (Table 13app, 14app).

- To test whether rearing by humans affected laterality, I compared individuals that had different rearing histories (Table 21). In the zoos sample, I compared “parent-reared” and “human hand-reared” bonobos. I found no difference regarding the HI values, ABSHI values and the number of data points per subject. In the combined sample (Lola + zoos), I compared the three categories of rearing history (“parent-reared”, “human-hand reared”, “lola-reared”). I found no difference between the groups regarding the HI values and ABSHI values. However, there was a trend for a difference in ABSHI values with bouts (KW chi2=5.292, df=2, p=0.071). Paired comparisons showed that the ABSHI values were higher in “parent-reared” (mean=0.492) compared to “lola-reared” bonobos (mean=0.335) with bouts (MW N1=21, N2=40, U=287.5, p=0.044). There was also a significant difference in the number of data points per subject in that case (KW chi2=14, df=2, p=0.001), with more data points per subject in “parent-reared” (mean=47.191) compared to “lola-reared” bonobos (mean=29.65) with bouts (MW N1=21, N2=40, U=235.5, p=0.005).

Finally, I compared “mother-reared” bonobos to the other bonobos that have been in close contact with humans during infancy (“human-hand reared” + “lola-reared”). I found no difference regarding the HI values and the ABSHI values. Therefore, the results indicate that the rearing history had no significant effect on the strength or direction of laterality.

Effect of the number of data points:

I tested the possible effect of the number of data points on laterality in two ways.

- I assessed the correlation between the number of data points per subject and the HI and ABSHI values (Table 15app in appendix). There was no significant correlation in the combined sample (lola + zoos) (Figures 9-12) and at the zoos. However, at lola with bouts, there was a significant negative correlation between the number of data points and the ABSHI values (Spearman, rho=-0.529, p=0.0004, N=40) (Figure 13). This correlation remained when I removed the outliers (2 removed, Spearman, rho=-0.455, p=0.004, N=38; 5 removed, Spearman, rho=-0.373, p=0.027, N=35). Figures 9-13 present the scatter plots for the HI and ABSHI values.

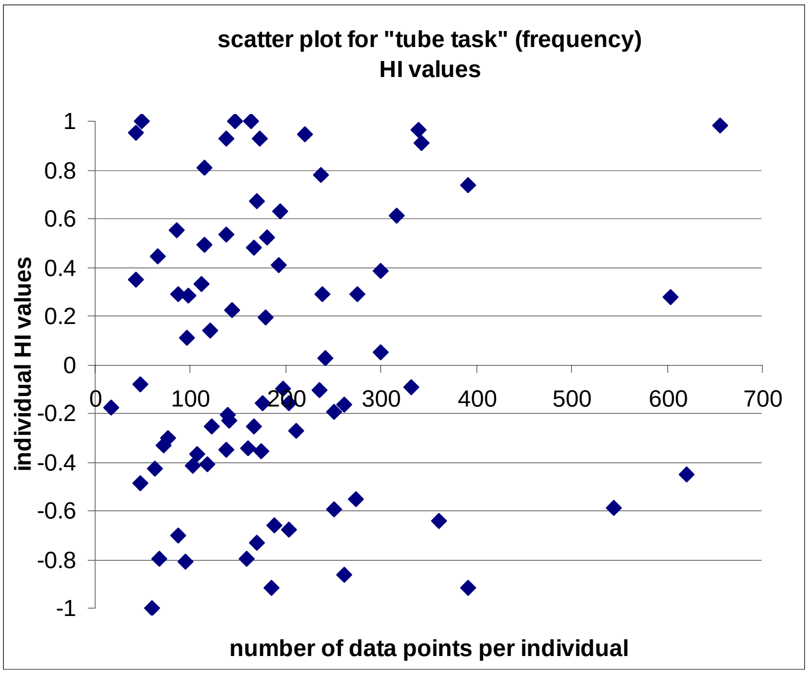

Figure 9: Scatter plot showing the distribution of HI values with increasing number of data points for frequency (Lola + zoos sample).
No correlation (Spearman, rho=0.042, p=0.716, N=77).

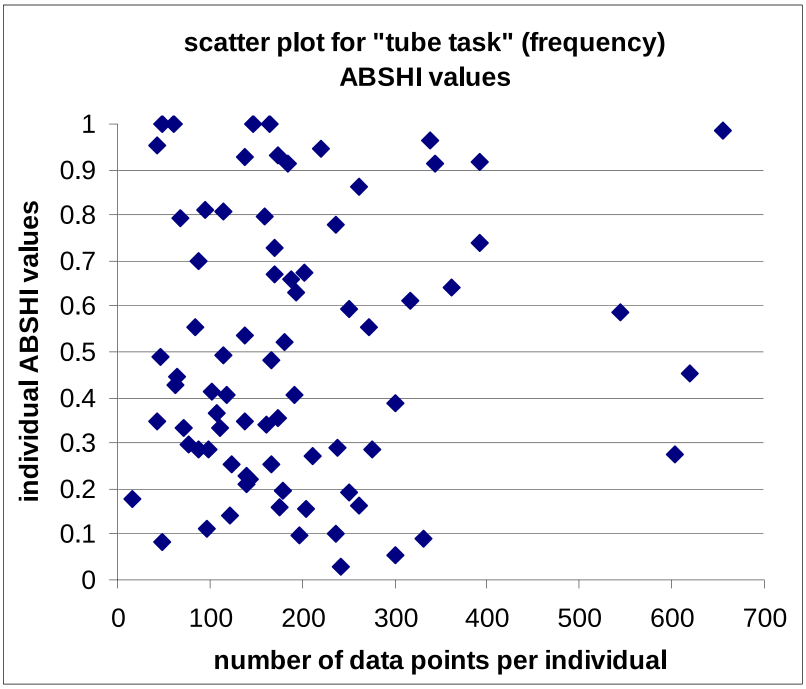

Figure 10: Scatter plot showing the distribution of ABSHI values with increasing number of data points for frequency (Lola + zoos sample).
No correlation (Spearman, rho=0.023, p=0.843, N=77).

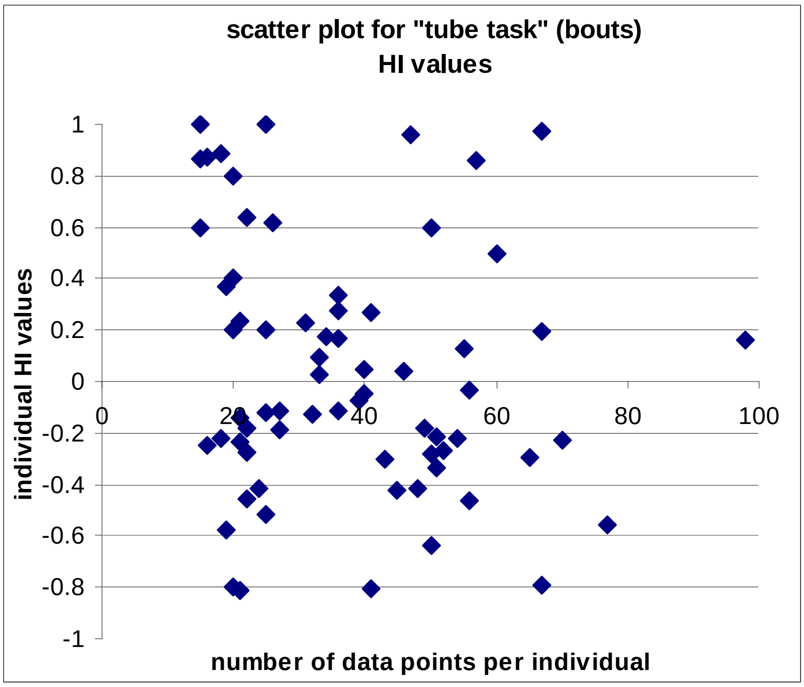

Figure 11: Scatter plot showing the distribution of HI values with increasing number of data points for bouts (Lola + zoos sample).
No correlation (Spearman, rho=-0.174, p=0.153, N=69).

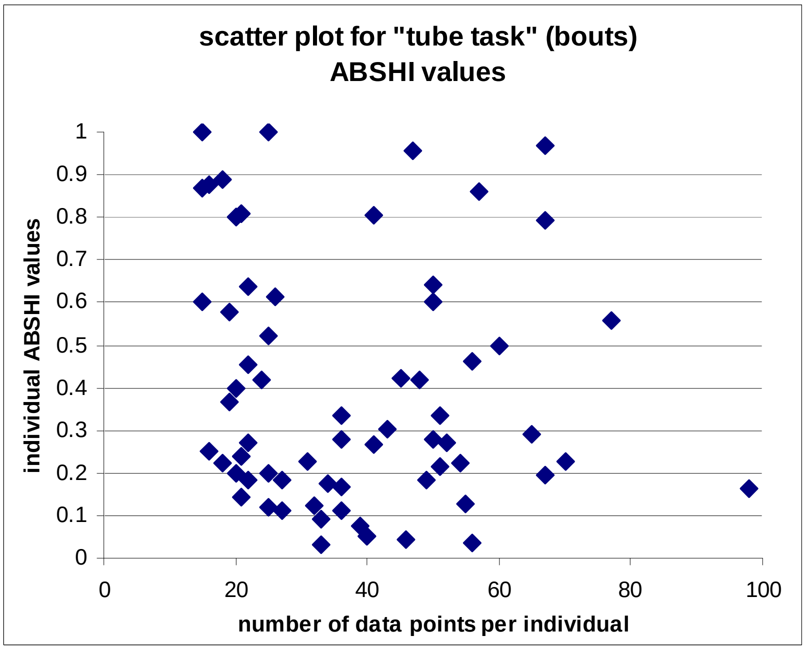

Figure 12: Scatter plot showing the distribution of ABSHI values with increasing number of data points for bouts (Lola + zoos sample).
No correlation (Spearman, rho=-0.194, p=0.11, N=69).

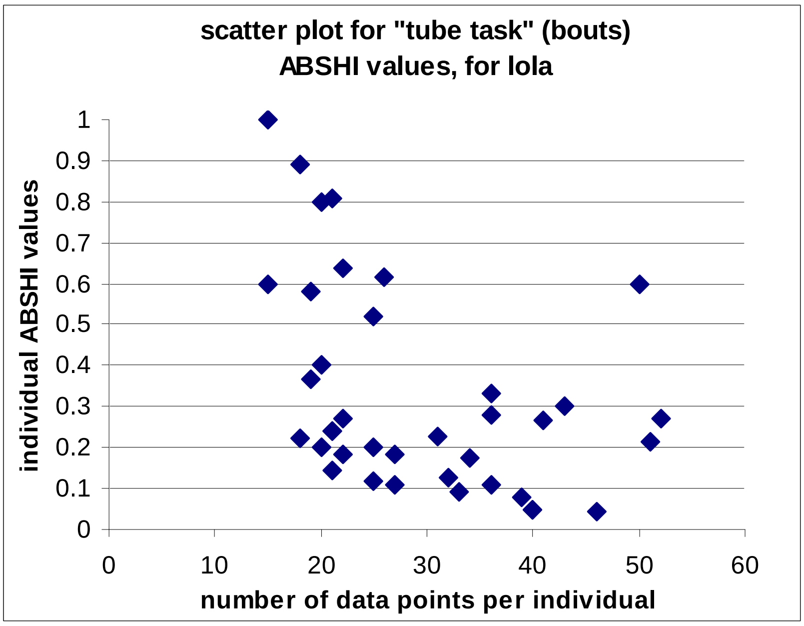

Figure 13: Scatter plot showing the distribution of ABSHI values with increasing number of data points for bouts (Lola).
Significant correlation (Spearman, rho=-0.529, p=0.0004, N=40).

- I compared the number of data points per subject between right-handed, left-handed and unlateralized individuals; and between lateralized versus unlateralized subjects. I found no difference, except in one case: at lola with bouts, there were more data points in unlateralized compared to lateralized subjects.

Therefore, the results suggest that the sample size did not significantly influence laterality (direction and strength), though there was a caveat with a significant effect on the strength at lola with bouts.

2.6. Other analyses:

Finger use:

I investigated which finger was used to dip inside the tube. I calculated the percentage of use of each finger (or fingers combination) (of the cases when the finger was visible). The index finger was the most frequently used (84.66% in zoos and 76.636% at lola), while the thumb and the middle finger were occasionally used (thumb: 6.9% in the zoos, 7.92% at lola; middle finger: 6.14% in the zoos, 10.259% at lola) and other fingers or combination of several fingers were seldom used (2.3% in the zoos, 5.185% at lola).

Effect of kinship:

To investigate the heritability of hand preference (predictions 7 and 17), I compared the direction of preference (R, L, Nlat and also R and L, excluding Nlat) in pairs of related individuals (for analysis with frequency) (Table 12 and 13 in chapter study 1). The results do not show a similarity of preference within related pairs, regarding mother-infant pairs, father-infant pairs and siblings pairs. However, there were many pairs with different preferences (even when excluding unlateralized individuals). In fact, the number of pairs with different preferences was higher than that of matched preferences (B test p=0.004) for father-infant pairs and as a trend for mother-infant pairs (B test p=0.057). This finding suggests a trend for opposite preferences between parents and offspring. However, this could also be related to an age effect since young subjects tended to be more left-handed and adults more right-handed (see above).

Comparison with chimpanzees:

For comparison, I have reanalyzed previously published data of chimpanzees (N=110) (Hopkins, 1995) (analysis based on frequency). I found that the number of lateralized individuals was greater than the number of unlateralized subjects (B test, z=5.53, p<0.001). The mean HI value was significantly different from zero (t(109)=2.552, p=0.012). Thus, the HI values were skewed towards the right side, indicating a bias towards right hand use. There was a group-level right bias in the distribution of the individuals, with significantly more right-handed than left-handed chimpanzees (B test, z=2.619, p=0.012). I compared these chimpanzee data (N=110) with my data for the combined bonobo sample (N=77). No significant between-species difference appeared regarding HI values (MW test, U=3803.5, p=0.236, N1=77, N2=110) and ABSHI values (MW test, U=4234.5, p=0.999, N1=77, N2=110).

I examined the effect of age in the chimpanzee sample, using the same age categories as those used with the bonobos (Badrian and Badrian, 1984). When considering each age group separately, a significant bias towards right hand use (right skewed HI values) occurred in the adult group (*t*(78)=2.335, p=0.022) and in the adults + adolescents category (*t*(92)=2.224, p=0.029) and not in the other groups of individuals. When comparing the data between the three age groups (infants + juveniles N=17, adolescents N=14, adults N=79), no difference appeared regarding HI values (KW test, H=0.895, df=2, p=0.639) and ABSHI values (KW test, H=2.972, df=2, p=0.226). When I compared each age group to each other group and to combined categories (as done for the bonobos). I found no significant effect of age on the HI values (MW test, $p \geq 0.367$) and ABSHI values (MW test, $p \geq 0.087$).

Chapter 3: Results of study 3: Tool-use

The study on tool-use was an important point of this PhD thesis (see section I.4.3.4). I here investigated hypotheses related to "tool-use" (predictions 1 and 6). In this chapter, I present the results regarding spontaneous actions and for the observations of the enrichment procedure "termite fishing".

3A. Spontaneous tool-use actions

The spontaneous tool-use actions studied yielded insufficient data for analysis (N=4). The data are presented in Table 22.

Table 22: Raw data for spontaneous tool-use actions and throwing (study 3a). Right hand: number of right hand responses, Left hand: number of left hand responses; total: total number of trials. B test: p value of the Binomial test performed on the number of right versus left hand trials. Cat: category in which the individual was classified based on Binomial test: L: left-handed, R: right-handed, Nlat: not lateralized.

		Right hand	**Left hand**	**total**	**HI**	**ABSHI**	**B test**	**cat**
scratch itself with an object	Jasongo	5	22	27	-0.63	0.63	0.002	L
clean the wall/ground with a rag	Cheka	2	5	7	-0.429	0.429	0.453	Nlat
take container to the mouth and drink from it	Cheka	4	3	7	0.143	0.143	1	Nlat
crack open nuts with a stone	Dilolo	0	9	9	-1	1	0.004	L
crack open nuts with a stone	Likasi	0	7	7	-1	1	0.016	L
throw an object toward target	Api	7	0	7	1	1	0.016	R
throw an object toward target	Dilolo	3	11	14	-0.571	0.571	0.057	Nlat (L trend)
throw an object toward target	Tatango	0	8	8	-1	1	0.008	L

3B. “Termite fishing” task

I now present the results of the “termite fishing” task, which was the first study on hand use for tool-use in bonobos. I first present the data from the videos (for which I recorded both bouts and frequency). Investigation of the effects of influential factors was not possible for these data because of the small sample size (N=7). I then present these data combined with the data collected during direct observations (for which only bouts were recorded).

Table 6 in methods section gives the number of data analyzed.
The descriptive statistics are presented in (Table 23).
The results of analyses on the effect of the number of data points, sex, age, settings, rearing history are presented in tables (Table 16app, Table 17app), and are discussed at the end of this chapter.

3.1. Data from the videos:

The raw data for each individual are presented in Table 23.

Table 23: Raw data for “termite fishing”, data from the videos, for each individual, for bouts and frequency (study 3b).
Right: number of right hand responses, Left: number of left hand responses; total: total number of trials. B test: p value of the Binomial test performed on the number of right versus left hand trials. Cat: category in which the individual was classified based on Binomial test: L: left-handed, R: right-handed, Nlat: not lateralized.

	bouts							frequency						
	Right	Left	total	HI	ABSHI	B test	cat	Right	Left	total	HI	ABSHI	B test	cat
Banya	4	30	34	-0,765	0,765	6E-06	L	10	362	372	-0,946	0,946	3E-93	L
Diatou	39	39	78	0	0	1,090	Nlat	171	230	401	-0,147	0,147	0,004	L
Kichele	44	26	70	0,257	0,257	0,041	R	235	132	367	0,281	0,281	8E-08	R
Cheka	65	7	72	0,806	0,806	7E-13	R	756	28	784	0,929	0,929	5E-185	R
Jasongo	5	1	6	0,667	0,667	0,219	Nlat	22	3	25	0,76	0,76	0,0002	R
Kakowet	13	12	25	0,04	0,04	1	Nlat	43	33	76	0,132	0,132	0,302	Nlat
Keke	28	19	47	0,192	0,191	0,243	Nlat	209	45	254	0,646	0,646	2E-26	R
Total	198	134	332					1446	833	2279				
Mean			47.429	0.171	0.389					325.571	0.236	0.549		
SD			27.227	0.513	0.347					250.822	0.643	0.357		
Min			6	-0.765	0					6	-0.946	0.132		
Max			78	0.806	0.806					784	0.929	0.946		

Frequency (number of responses per subject):

Amongst the 7 bonobos, 6 (85.714%) were significantly lateralized (B p ≤ 0.004) and only 1 (14.286%) showed no preference (B p ≥ 0.3) (Table 23). The numbers of lateralized and unlateralized bonobos were similar (B p=0.125). For the group, the mean ABSHI was 0.549 (SD=0.357), which indicates a strong laterality. Moreover, among lateralized subjects, the mean percentage of use of the preferred hand was 80.902% (SD=16.74, N=6), which indicates strong preferences. Two individuals (Banya, Cheka) exhibited a close-to-exclusive preference.

Regarding the direction of laterality, the mean HI value for the group was 0.236 (SD=0.643), which was quite right skewed, but not significantly different from 0 (T t(6)=0.972, p=0.369). Thus, there was no bias toward the use of one particular hand.
4 bonobos were classified as right-handed and 2 were left-handed, which were similar numbers (B p=0.688).

Bouts (number of bouts per subject):

Amongst the 7 bonobos, 3 (42.857%) were significantly lateralized (B $p \leq 0.042$) and 4 (57.143%) had no preference (B $p \geq 0.218$) (Table 23). The number of lateralized and unlateralized bonobos were similar (B p=1). The mean ABSHI for the group was 0.389 (SD=0.347), which indicates not a strong laterality. When considering lateralized subjects, the mean percentage of use of the preferred hand was 80.457% (SD=15.276, N=3), which indicates strong preferences.
Regarding the direction of laterality, the mean HI value for the group was 0.171 (SD=0.511), which was not significantly different from 0 (T t(6)=0.882, p=0.412). Therefore, there was no bias toward the use of one particular hand. Group-level bias could not be tested (2R and 1L).

Comparison between frequency and bouts:

I assessed the possible difference between the two recording techniques. The ABSHI values were higher with frequency than with bouts (W z=-2.366, p=0.018), indicating that the laterality was stronger with frequency than with bouts. The HI values were similar with the two measures (W z=-0.507, p=0.612), suggesting that the direction of laterality was not influenced by the measure. The HI values with frequency and bouts were correlated (Spearman rho=0,964, p=0,0005, N=7) and so were the ABSHI values (Spearman rho=0,893, p=0,007, N=7).

3.2. Data from direct observations combined with data from the videos:

I now combine the data from videos with the data collected during direct observations, for the action "dipping the stick into the hole and holding it to the mouth" with one hand. The raw data for each individual are presented in Table 24.

Table 24: Raw data for the "termite fishing" task, for each individual for the data from videos and direct observation combined (bouts) (study 3b).
Right: number of right hand responses, Left: number of left hand responses; total: total number of trials. B test: p value of the Binomial test performed on the number of right versus left hand trials. Category: category in which the individual was classified based on Binomial test: L: left-handed, R: right-handed, Nlat: not lateralized.

	Right	**Left**	**total**	**HI**	**ABSHI**	**B test**	**category**
Banbo	2	18	20	-0,8	0,8	0,0004	L
Banya	4	38	42	-0,81	0,81	6E-08	L
Cheka	81	7	88	0,841	0,841	4E-17	R
Chipita	64	55	119	0,076	0,076	0,464	Nlat
Daniela	37	8	45	0,644	0,644	2E-05	R
David	5	5	10	0	0	1,246	Nlat
Diatou	44	50	94	-0,064	0,064	0,606	Nlat
Diwani	68	63	131	0,038	0,038	0,727	Nlat
Jasongo	5	1	6	0,667	0,667	0,219	Nlat
Kakowet	13	12	25	0,04	0,04	1	Nlat
Keke	29	26	55	0,055	0,055	0,788	Nlat
Khaya	30	0	30	1	1	2E-09	R
Kichele	53	30	83	0,277	0,277	0,015	R
Kirembo	54	0	54	1	1	1E-16	R
Kombote	13	1	14	0,857	0,857	0,002	R
Lina	1	57	58	-0,966	0,966	4E-16	L
Louisoko	0	70	70	-1	1	2E-21	L
Lucuma	3	4	7	-0,143	0,143	1	Nlat
Mixi	51	3	54	0,889	0,889	3E-12	R
Total	557	448	1005				
Mean			52.895	0.137	0.535		
SD			37.154	0.67	0.408		
Min			6	-1	0		
Max			131	1	1		

Bouts (number of bouts per subject):

Amongst the 19 bonobos, 11 (57.895%) were significantly lateralized (B $p \leq 0.016$) and 8 (42.105%) showed no preference (B $p \geq 0.218$) (Table 24). The numbers of lateralized and unlateralized bonobos were similar (B p=0.648). For the group, the mean ABSHI was 0.535 (SD=0.399), indicating a strong laterality. Moreover, for lateralized subjects, the mean percentage of use of the preferred hand was 91.289% (SD=10.615, N=11), which shows very strong, almost exclusive, preferences. 3 subjects exhibited exclusive preference (and 1 showed almost exclusive preference).

Regarding the direction of laterality, the mean HI value was 0.137 (SD=0.665), which was not significantly different from 0 (T t(18)=0.891, p=0.385). 7 bonobos were classified as right-handed and 4 were left-handed, indicating no group-level bias (B p=0.549).

The percentage of right-handers in the group was 36.842%. When excluding unlateralized individuals, the proportion of right-handers amongst lateralized subjects, was 63.636%.

3.3. Comparison between the "termite fishing" task and the other actions:

I compared the data for the tool-use "termite fishing" task and the data for the 13 main spontaneous non-social actions and with the "tube task" (study 2) to test whether this tool-use action was more strongly lateralized than the other actions studied (predictions 1). This analysis is based on bouts as only bouts were recorded for the spontaneous actions. The results of the MW tests are presented in Table 25.

Table 25: Comparisons between the “termite fishing” task and the other actions (study 3b).
Results of the MW test, p values for HI, ABSHI and total comparisons between the “termite fishing” task and other actions. Significant p values are in bold.

“termite fishing” task (bouts) (N=19) versus:	**MW on total**	**MW on HI values**	**MW on ABSHI values**
“reaching for big items, general” N=26	U=83 **p=0,0002**	U=225 p=0,613	U=214 p=0,448
“reaching for small items (seeds), general” N=33	U=292 p=0,683	U=308 p=0,917	U=274 p=0,452
“reaching in the fixed object (dipping) (unimanual)” N=8	U=29.5 **p=0,014**	U=73.5 p=0,894	U=53.5 p=0,232
“feeding, general” N=65	U=567 p=0,589	U=552 p=0,484	U=432 **p=0,047**
“quadrupedal movement holding food/object in one hand” N=32	U=131 **p=0,001**	U=260 p=0,391	U=252.5 p=0,315
“tripedal movement holding food/object in one hand + while feeding” N=27	U=78 **p=6,46E-05**	U=232 p=0,584	U=241 p=0,729
“pushing an object” N=10	U=53 *p=0,054*	U=77 p=0,408	U=81 p=0,52
“dragging an object” N=11	U=36.5 **p=0,003**	U=102 p=0,914	U=95.5 p=0,698
“swinging + hanging” N=15	U=111 p=0,274	U=71.5 **p=0,014**	U=97.5 p=0,118
“pulling grass out” N=11	U=32.5 **p=0,002**	U=103.5 p=0,966	U=75 p=0,201
“inserting a finger (self directed)” N=6	U=20 **p=0,018**	U=50.5 p=0,679	U=55.5 p=0,924
“raking seeds on the floor” N=7	U=61.5 p=0,772	U=41.5 p=0,148	U=38.5 p=0,104
“reaching in the water pond” N=6	U=15.5 **p=0,008**	U=52.5 p=0,774	U=54 p=0,848
“tube task” N=77	U=539 p=0.077	U=629.5 p=0.348	U=639.5 p=0.397

- Regarding the HI values, the tool-use task was similar to the other actions; except “swinging + hanging” which was an outlier action (Table 25).

- Regarding the ABSHI values, the data for tool-use were similar to that of most other actions. However, the ABSHI values were significantly higher for “termite fishing” compared to feeding (Table 25).

- The difference in the number of data points was significant in many cases or close to significant (except for “reaching for small items”, “feeding”, “swinging + hanging”, “raking seeds on the floor”), with more data points for tool-use compared to the other actions, which hindered the comparisons.

- At the individual-level, half of the subjects showed the same preference for the “termite fishing task” and the “tube task”, and half of the subjects showed opposite preferences between the two tasks (Table 25) (these analyses excluded unlateralized subjects).

3.4. Effect of possible influential factors:

In the next paragraphs, I investigate the effects of several possible influential factors including: living conditions (settings), sex, age, rearing history (testing predictions 7, 15 and 16) and the number of data points, for the data from videos and direct observations combined.

Effect of the settings:

- When analyzing separately Stuttgart zoo (N=12) and Twycross zoo (N=7), there was no group-level bias at any location (in the number of individuals (B test p>0.05) and in the HI values (T test p>0.05)) (Table 16app).
- I compared the data between the two zoos. I found no difference in the HI and ABSHI values (MW p>0.05) (Table 17app), suggesting no effect of the settings on laterality.

Effect of sex:

- I first examined each sex group separately (Table 16app). I found no group-level bias in males (N=8) nor in females (N=11) (in the number of individuals (B test p>0.05) and in the HI values (T test p>0.05)). However, females tended to be more strongly lateralized than males (for females: mean ABSHI=0.657 and 18.182% of unlateralized subjects, for males: mean ABSHI: 0.368 and 75% of unlateralized subjects). Also, females tended to use the right hand more than males (mean HI=0.177 for females, 0.082 for males; and 6 females were right-handed for 1 right-handed male).
- I compared the data between males and females and found no difference in the HI and ABSHI values (MW p>0.05) (Table 17app), which suggests no significant effect of sex on laterality.

Effect of age:

Because of the small number of young subjects (N=5 for infants + juveniles, N=3 for adolescents), I grouped all these non-adult subjects into one category.

- When I analyzed separately the two age categories (non-adults and adults), there was no group-level bias in any group (in the number of individuals (B test p>0.05) and in the HI values (T test p>0.05)) (Table 16app).
- I compared the adults with the non-adult bonobos and found no difference in the HI and ABSHI values (MW p>0.05) (Table 17app), which suggests no effect of age on laterality.

Effect of rearing:

- When I analyzing separately each rearing category of individuals, there was no group-level bias in any group (in the number of individuals (B test p>0.05) and in the HI values (T test p>0.05)) (Table 16app).
- I compared the data between “human-hand reared” and “parent-reared” bonobos and found no significant difference in the HI and ABSHI values (MW p>0.05) (Table 17app), which suggests no effect of rearing history on laterality.

Effect of the number of data points:

I tested the possible effect of the number of data points in two ways.

- I first assessed the correlation between the number of data points per subject and the HI and ABSHI values. I found no significant correlation (Spearman test, rho=-0.73, p=0.766 for HI, rho=-0.048, p=0.844 for ABSHI) (Table 17app).
- I then compared the number of data points in lateralized and unlateralized individuals. I found no significant difference between the two categories (MW N1=8, N2=11, U=42, p=0.869 for total) (Table 17app).

Thus, the data suggest that the number of data points did not significantly influence the results (direction and strength of laterality).

- The scatter plots confirm this absence of relation between the laterality and the number of data points per subjects (Figure 14 and 15).

On Figure 15, we can see that the individuals are split into two distinct groups, being either very strongly lateralized or unlateralized, there is no intermediate category.

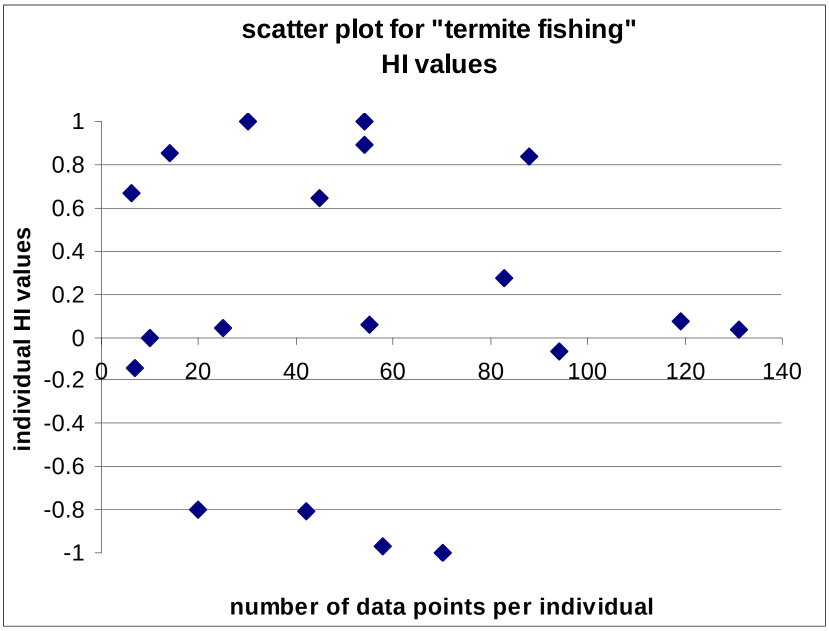

Figure 14: Scatter plot showing the distribution of HI values with increasing number of data points for the "termite fishing" task.

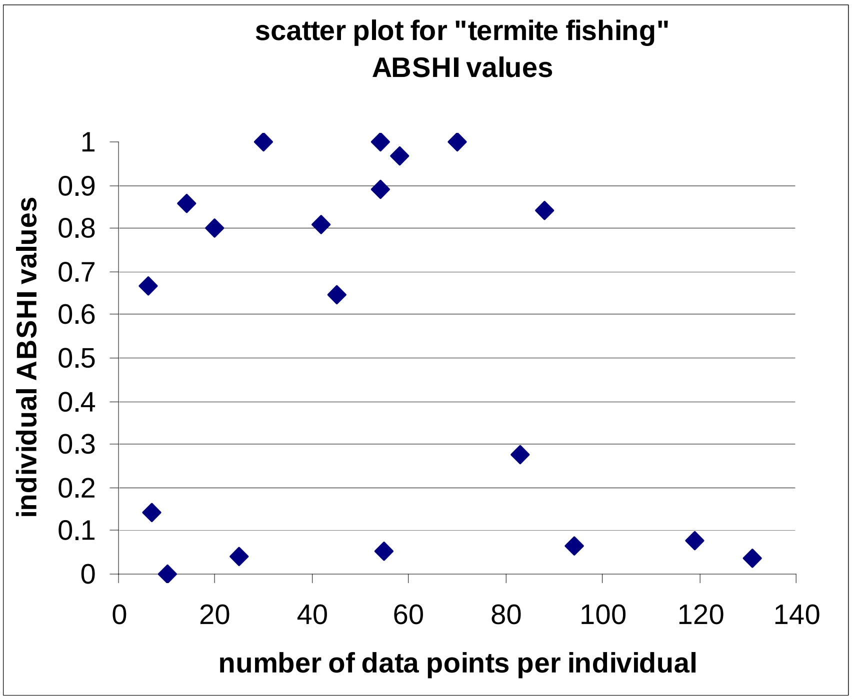

Figure 15: Scatter plot showing the distribution of ABSHI values with increasing number of data points for the "termite fishing" task.

3.5. Other analyses:

Effect of kinship:

To investigate the heritability of hand preference (predictions 7 and 17), I compared the direction of preference (R, L, Nlat and also R and L, excluding Nlat) in pairs of related individuals (Table 12 and 13 in chapter study 1). There were about identical numbers of pairs with matched laterality and pairs with different laterality, suggesting no particular relationship between the laterality of related individuals.

Chapter 4: Results of study 4: Social actions

4A. Spontaneous social actions and gestures

With study 4a, I examined hand use for social actions and gestures, hereby investigating the "social related hypothesis" (predictions 8) and language related hypotheses (predictions 3). In this chapter, I present the results of this study. I aimed to analyze the social actions at the dyad-level, but the data were insufficient to allow such a detailed level of analysis. I analyzed Lola ya bonobo and the zoos combined (very few social data were collected at Lola ya bonobo. see section II.2). The effects of the posture and other hand activity were not specifically investigated in this study, and could not be tested due to the small sample size available. However, these variables were controlled for by excluding specific cases, i.e. excluding the infrequent cases when the other hand was unavailable by holding an object or food item (see Table 9 for details) to standardize the action studied. The data available were insufficient to allow analysis of the detailed variables (identity of the recipient, context of the interaction, meaning of the gesture, emotional valence, degree of violence, facial expressions, distance).

The descriptive statistics are presented in (Table 26).
The results of analyses on the effect of the number of data points are presented in tables (Table 21app) and are discussed at the end of this chapter.

Table 26: Results for each spontaneous behavioural pattern (social actions) (study 4a).
N analyzed: number of subjects analyzed (subjects with min $n=6$); Left-handed, Nlat and right-handed: number of subjects that were classified as left-handed, unlateralized and right-handed based on the Binomial test; (n.b. for "suckling": left-handed means suckling left breast and right-handed means suckling right breast); sum lat: number of subjects that were classified as lateralized; B test: p value of the Binomial test performed on the number of right-handed versus left-handed subjects (for actions with at least 6 lateralized subjects); % Right handed: proportion of right-handed subjects in the group. % Nlat: proportion of unlateralized subjects in the group. B test lat vs unlat: p value of the Binomial test performed on the number of lateralized versus unlateralized subjects; mean HI: mean value for the group (for actions with $N \geq 6$); T test: p value of the T test performed on the individual HI values (for actions with $N \geq 6$); mean ABSHI: mean ABSHI value for the group (for actions with $N \geq 6$).

	N analyzed	**Left handed**	**Nlat**	**Right handed**	**sum lat**	**B test**	**% Right handed**	**% Nlat**	**B test lat vs unlat**	**mean HI**	**T test**	**mean ABSHI**
suckling at mother's breast	13	4	6	3	7	1	23.077	46.154	1	-0.057	0.664	0.343
sitting with crossed arms around the infant	8	2	1	5	7	0.453	62.5	12.5	0.07	0.256	0.358	0.666
tripedal movement holding the infant under belly with one arm	6	1	1	4	5		66.667	16.667	0.219	0.286	0.42	0.748
sitting holding the infant with one arm	5	1	1	3	4							
retrieving the infant with one arm	5	1	1	3	4							
standing and placing the infant under belly	2	0	0	2	2							
holding the partner during ventro-ventral mount	10	3	6	1	4		10	60	0.754	-0.089	0.535	0.356
crossed arms around the partner during ventro-ventral mount	3	0	1	2	2							
putting arm around the mounting partner during ventro-dorsal mount	2	0	1	1	1							
holding the mountee partner during ventro-dorsal mount (including mount walk)	3	1	2	0	1							
pulling the partner in close contact	4	0	4	0	0							
waist thrusting while holding infant under belly (tripedal posture)	1	1	0	0	1							

table 26 continued	**N analyzed**	**Left handed**	**Nlat**	**Right handed**	**sum lat**	**B test**	**% Right handed**	**% Nlat**	**B test lat vs unlat**	**mean HI**	**T test**	**mean ABSHI**
touching the genitals of the partner	7	0	6	1	1		14.286	85.714	0.125	-0.075	0.712	0.452
following with hand on the genitals of the partner	2	0	2	0	0							
sitting with arm around the partner	3	0	3	0	0							
moving with arm around the partner	10	1	9	0	1		0	90	0.021	0.078	0.422	0.257
slapping the partner during grooming	2	0	2	0	0							
touching the partner's body (genitals excluded)	10	0	10	0	0		0	100	0.002	-0.14	0.109	0.217
patting the partner's body (with the palm or back of the hand)	3	0	3	0	0							
slapping the floor with one hand	4	0	4	0	0							
stamping the floor with one foot	2	0	0	2	2							
banging the glass with one hand	1	0	1	0	0							
arm held towards the other (invitation)	6	0	5	1	1		16.667	83.333	0.219	0.336	0.102	0.399
inviting related behaviours (global)	7	0	6	1	1		14.286	85.714	0.125	0.315	0.076	0.365
kicking the other	1	0	1	0	0							
punching the other	2	0	2	0	0							
hitting the other	4	0	4	0	0							
hunching over the other (not gentle)	1	0	1	0	0							
lateral embrace	10	0	9	1	1		10	90	0.021	0.175	0.152	0.256
face embrace	1	0	0	1	1							
holding the hand or foot of the other	6	0	5	1	1		16.667	83.333	0.219	0.214	0.22	0.303
pushing away the approacher + holding the partner of	2	0	2	0	0							
catching the other	3	0	2	1	1							
playing	8	0	7	1	1		12.5	87.5	0.07	0.082	0.583	0.294
dragging the other	7	1	6	0	1		0	85.714	0.125	0.016	0.918	0.289
play related behaviours (global)	15	0	15	0	0		0	100	6E-05	0.038	0.59	0.196

table 26 continued	**N analyzed**	**Left handed**	**Nlat**	**Right handed**	**sum lat**	**B test**	**% Right handed**	**% Nlat**	**B test lat vs unlat**	**mean HI**	**T test**	**mean ABSHI**
plucking the other's hair	1	0	0	1	1							
begging (towards another bonobo or humans)	1	0	0	1	1							
hand clapping	4	0	4	0	0							
bipedal branch shaking display	2	1	0	1	2							

Data analyzed:

Table 6 in the methods section gives the number of data analyzed. I analyzed 41 behavioural patterns.

4a.1. Analysis for each behavioural pattern:

Table 26 gives the data for each behaviour and each behavioural pattern for the group.
In the next paragraphs, I first examine each behavioural pattern separately. Then, I compare the behavioural patterns to examine the effect of different factors that may affect laterality.

- Proportion of unlateralized subjects:
Many (25) of the behavioural patterns induced significant individual preferences, but there was a number of actions (15) for which there was no lateralized subjects.
- I calculated the proportion of unlateralized subjects in the group for each manual action (for actions with N ≥ 6) (non-manual behaviours excluded). For the 12 manual actions analyzed, the average percentage of unlateralized subjects was 80.665 (min=16.667, max=100, SD=22.527). Therefore, on average, there was a high proportion of unlateralized subjects in the group, and very few lateralized subjects (below 20%).
- I compared the numbers of lateralized and unlateralized subjects, whenever possible (actions with N ≥ 6). For the 14 actions tested, there were significantly more unlateralized than lateralized subjects in 4 cases (and 1 trend) (Table 26). In no case was the number of lateralized subjects greater than the number of unlateralized subjects (though there was a trend for “sitting with crossed arms around the infant”) (Table 26).
Thus, these data indicate a weak laterality in spontaneous social actions.

- Group-level biases:

- I examined group-level biases in the proportion of right-handed and left-handed subjects. I compared the numbers of right-handed and left-handed subjects, whenever possible (actions with at least 6 lateralized subjects). Only two actions could be tested and they showed no group-level bias: “sitting with crossed arms around the infant” and “suckling at mother’s breast”) (B $p>0.05$) (Table 26).

- I also tested biases in the HI values (for actions with $N \geq 6$), which reflects biases toward the use of one hand. Among the 14 actions tested, the HI values were never significantly skewed toward one side. However, there was a trend toward using the right hand for “inviting related behaviours” ($t(6)=2.144$, $p=0.076$).

- I examined the percentage of right-handers in the group (for actions with $N \geq 6$) (non-manual behaviours excluded). For the 12 manual behavioural patterns analyzed, the average percentage of right-handers in the group was 13.423 (min=0, max=66.67, SD=18.097). The data did not allow analysis on the proportion of right handers amongst lateralized subjects.

4a.2. Effect of task-related factors:

I now investigate whether the laterality varied between the different actions studied.

Direction of laterality:

- I consider laterality on a continuum and use the HI values to examine the general trend in the direction of laterality. Considering all the behavioural patterns (for actions with $N \geq 6$) (non-manual behaviours excluded), the HI values ranged from -0.14 to 0.336. The median was 0.08 (SD=0.163), which suggests a right bias in hand use. Moreover, most of the behavioural patterns displayed positive HI values. Actually, none of these actions showed frankly negative HI values.

Therefore, whatever the action, the bonobos hand use was rather toward the right hand (not significant preference with the exception of the trend described above).

- Ranking: To visualize the pattern of laterality across actions, I ranked the actions according to their HI values (Table 18app). The top 5 actions could be considered relatively right skewed, with HI ≥ 0.15. These include: “lateral embrace”, “holding the hand or foot of the other”, “tripedal movement holding the infant under belly with one arm”, inviting related behaviours (global) and “arm held toward the other (invitation)”. No action could be considered relatively left skewed, with HI ≤ -0.15.

- Below, I focus the analysis on the main manual behaviours and compare them to each other (actions with N ≥ 6). Figure 16 shows the mean HI values for these 11 behaviours.

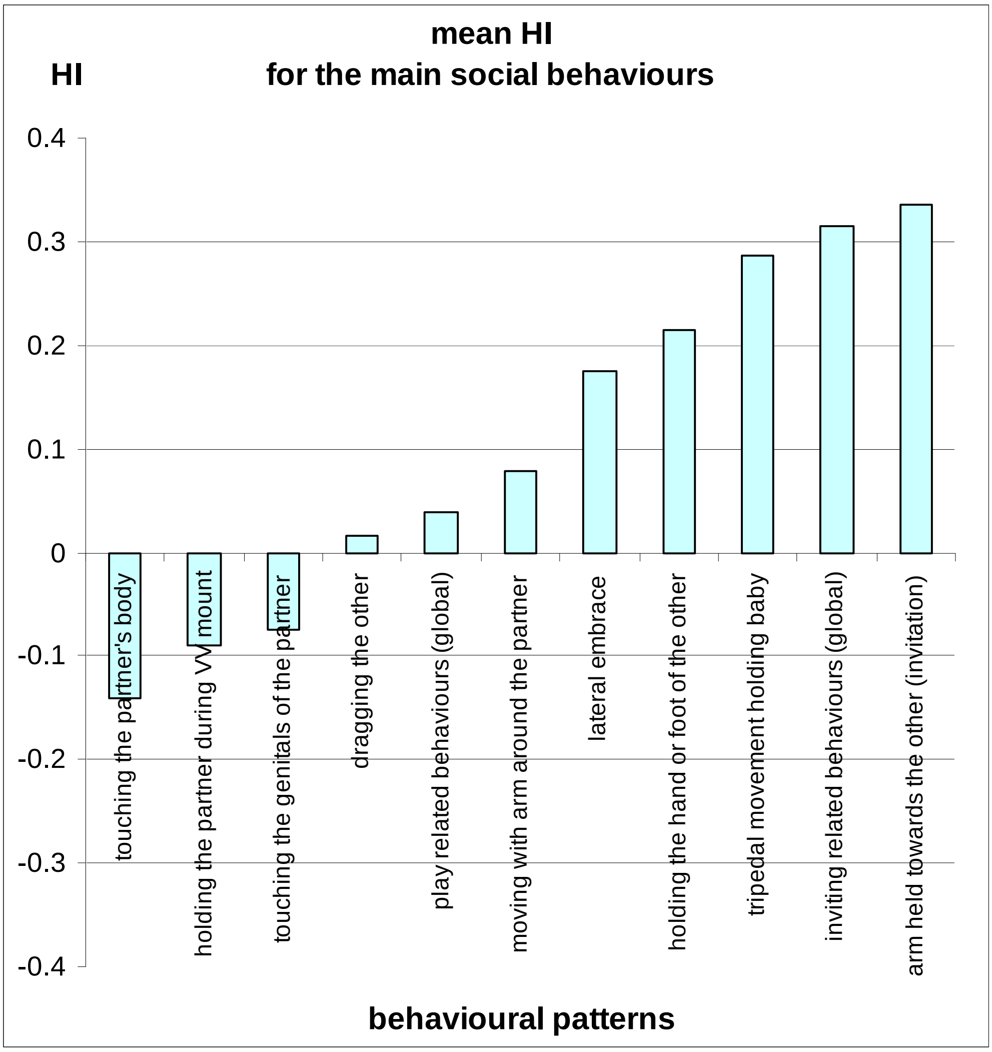

Figure 16: Mean HI values for the 11 main social behaviours.

Global analysis showed that the HI values did not significantly vary according to the behaviour (KW df=10, p=0.181). However, I performed further analyses with paired comparisons to test my hypotheses regarding specific behaviours of interest (Winer, 1971). Table 20app presents the results of the MW tests.

- Testing predictions 3: I investigated whether the right hand was particularly preferred for gesturing. In my study, the following behaviours could be considered as gestures: “arm held toward the other (invitation)”, “inviting related behaviours (global)”, “hand clapping”, “arm held toward the other (begging)”, “slapping the floor with one hand”, “banging the glass with one hand” and “stamping the floor with one foot”.

Only the first two provided enough data to be considered here ($N \geq 6$). For “arm held toward the other (invitation)”, “inviting related behaviours (global)”, most subjects were unlateralized. However, these actions showed right skewed HI values and were the most right skewed of all actions studied (Table 18app, Figure 16). When I compared these actions to the other actions with paired comparisons, there was no significant difference in the HI values (MW $p>0.05$); except in one case (“arm held toward the other (invitation)” versus “touching the partner’s body” (Table 20app)).

- Testing predictions 8’: I investigated whether one particular hand was involved in mother-infant behaviours. I examined the following actions: “tripedal movement holding the infant under belly with one arm”, “sitting holding the infant with one arm”, “retrieving the infant with one arm”, “standing and placing the infant under belly”. Only the first one provided enough data to be considered here ($N \geq 6$). The HI values for “tripedal movement holding the infant under belly with one arm” were amongst the most right skewed of all actions studied (Table 18app, Figure 16), though there was no significant difference with the other actions (MW $p>0.05$).

At the individual-level, the subjects showed consistency of hand preference between the different maternal actions (Table 27). I then compared maternal actions with other actions, at the individual-level. 2 subjects showed a clear opposite preference (and 1 subject showed the same preference) between maternal actions and the general trend observed for non-social actions. Regarding, carrying object and carrying infant, the 2 analyzable subjects showed the same preference in both actions (Table 27). Finally, I examined the relationship between the mother's arm used to cradle and the breast preference of the infant to suckle. In the two analyzable cases, this was the same side (Table 27).

Table 27: Individual-level analysis on maternal behaviours compared to other actions and to infant breast preference (study 4a).

	"tripedal movement holding the infant under belly with one arm"	"retrieving the infant with one arm"	"sitting holding the infant with one arm"	"tripedal movement holding food/object in one hand"	general trend for non-social actions	breast suckling preference of the infant
Banja	L	L	L	/	R	L
Cheka	R	R	R	/	/	Nlat
Daniela	R	Nlat	R	R	/	Nlat
Diatou	R	R	R	Nlat	L	Nlat
Liboso	R	R	Nlat	R	R	R

Strength of laterality:

- I consider laterality on a continuum and use the ABSHI values to examine the general pattern of laterality. Considering all the behavioural patterns (for actions with N ≥ 6) (non-manual behaviours excluded), the ABSHI values ranged from 0.076 to 0.918. The median was 0.421 (SD=0.075), indicating a not strong laterality. Therefore, whatever the action, the laterality was rather weak.

- Ranking: To visualize the pattern of laterality across actions, I ranked the actions according to their ABSHI values (Table 19app). Only the first action could be considered relatively strongly lateralized, displaying ABSHI ≥ 0.485 (close to 0.5). This was "tripedal movement holding the infant under belly with one arm". The bottom 7 actions could be considered relatively weakly lateralized, with ABSHI ≤ 0.3. These included: play related behaviours, "touching the partner's body", "lateral embrace", "moving with arm around the partner", "dragging the other", "playing" and "holding the hand or foot of the other".

- Below, I focus the analysis on the main manual behaviours and compare them to each other (actions with N ≥ 6). Figure 17 shows the mean HI values for these 11 behaviours.

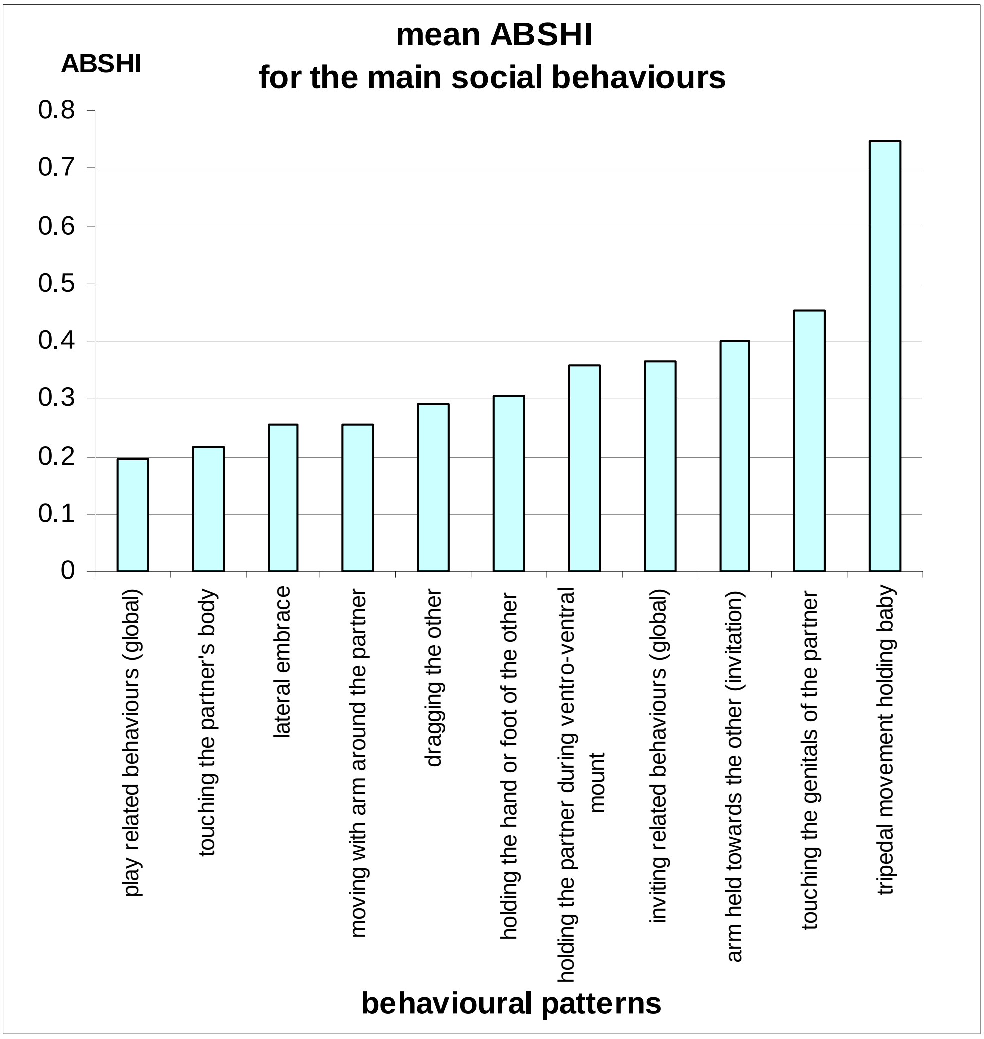

Figure 17: Mean HI values for the 11 main social behaviours.

Global analysis showed that the ABSHI values varied significantly according to the behaviour (KW df=10, p=0.019). Post-Hoc analyses with paired comparisons showed that several behaviours stood out, with values that significantly differed from that of other behaviours. These were “tripedal movement holding the infant under belly with one arm” (see below) and “touching the genitals of the partner” with very high ABSHI values.

Table 20app presents the results of the MW tests.

- Testing predictions 3: I examined whether the laterality was stronger in gestures compared to the other actions (see above). When comparing “arm held toward the other (invitation)” and “inviting related behaviours (global)” to the other actions with paired comparisons, there was no significant difference in the ABSHI values (MW p>0.05).

- Testing predictions 8’: I investigated whether there was a particularly strong laterality for mother-infant behaviours (see above). This was clearly the case with “tripedal movement holding the infant under belly with one arm”, which exhibited a very strong laterality, its ABSHI values being significantly higher than that of most other actions (Table 19app, 20app, Figure 17).

4a.3. Effect of the posture:

The effect of posture on laterality (predictions 2, 4, 5 and 6) was not specifically investigated in this study. However, I would like to report the data for a very interesting bipedal behaviour: the bipedal branch shaking display (Table 28). Mwindu exhibited almost exclusive right hand use for this bipedal action.

Table 28: Raw data for the bipedal branch shaking display (study 4a).
Right hand: number of right hand responses, Left hand: number of left hand responses; total: total number of trials. B test: p value of the Binomial test performed on the number of right versus left hand trials. Cat: category in which the individual was classified based on Binomial test: L: left-handed, R: right-handed, Nlat: not lateralized. %pref: percentage of use of the preferred hand.

	Right hand	Left hand	total	HI	ABSHI	B test	cat	% pref
Mwindu	140	23	163	0.718	0.718	p<0.001	R	85.89

4a.4. Effect of possible influential factors:

The sample of data for the social actions ($N \leq 15$) did not allow investigation of the effects of variables related to the individual (settings, sex, age, rearing history) (predictions 7, 15 and 16).

Effect of the number of data points:

I investigated the possible effect of the number of data points on laterality in two ways.

- I first assessed the correlation between the number of data points and the HI and ABSHI values for each action (for actions with $N \geq 6$). The number of data points per subject was not correlated to the HI or ABSHI values, with 2 exceptions (Table 21app). Namely, for “holding the hand or foot of the other”, there was a negative correlation with the HI values (Spearman, rho=-0.841, p=0.036) and for “touching the genitals of the partner”, there was a negative correlation with the ABSHI values (Spearman, rho=-0.789, p=0.035).
- I then compared the number of data points per subject in lateralized and unlateralized individuals. The data available only allowed testing of one action: “suckling at mother’s breast” and no difference was found (MW U=11.5, p=0.174).

These data suggest that the number of data points did not significantly influence the results (direction and strength of laterality) (with two exceptions).

4a.5. Other analyses:

The laterality was strongly related to the individual. For a given action some individuals exhibited right hand preference, while other individuals showed left hand preference and others were unlateralized.

Table 31, 32, 33 present the laterality data of each individual for each behavioural pattern.

Consistency of hand preference between actions:

I investigated intra-individual consistency across manual actions, i.e. whether the individuals changed hand preference between the different actions. Only the individuals that had data for at least 3 actions were included in this analysis. The individuals lateralized for at least 2 actions were tested for consistency across lateralized actions. The other individuals were classified as “always unlateralized”, if they had no lateralized action, and “almost always unlateralized”, if they had only one lateralized action. The results are presented in Table 29.

Table 29: Within-subject consistency of hand preference across social actions (study 4a).

		individuals with fewer than two lateralized behaviours		individuals with at least two lateralized behaviours	
	number of bonobos tested	always unlateralized	almost always unlateralized	same preference across actions	different preference between actions
Behavioural patterns	20	7	5	4	4

Therefore, the data show that: a) more than half of the bonobos showed no preference in most of the actions studied, b) several bonobos changed hand preference between the different actions, c) several bonobos exhibited the same preference between different actions. There was consistency of preference in half of the bonobos analyzed, while the others showed changes of preference across behavioural patterns.

Effect of Kinship:

I considered the question of heritability of hand preference (predictions 7 and 17). This was the first time that this issue was addressed in bonobos. I examined laterality in pairs of related individuals. I compared the preference: a) R, L, Nlat, b) R, L only, excluding Nlat, between related subjects. The results are presented in Table 12 and 13 in chapter study 1. Only the behaviour “play category” could be analyzed. I observed similarities of laterality between related individuals, but this is difficult to interpret as all subjects were unlateralized.

Consistency of hand preference over time:

I investigated the issue of consistency of hand preference over time (predictions 7). This was the first time that this question was addressed in bonobos. I compared my data with data collected in the same subjects several years before my study (May to November 2000 by Harrison and Nystrom (2008) N=14 and June to August 1992 by Hopkins et al. (1993) N=1). These previously published data were reanalyzed with my statistical method to allow reliable comparison. I compared the classification (L, R, Nlat) of each individual for the behaviours that were comparable. The results are presented in Table 30.

Table 30: Consistency of hand preference over time for spontaneous social actions (study 4a).
This table presents the results of Harrison and Nystrom (2008) and of Hopkins et al. (1993) compared to my results for the same individuals.

	Harrison and Nystrom 2008	This study		
	gestures	begging (spontaneous)	inviting related behaviours (global)	arm held towards the other (invitation)
Banja	Nlat		Nlat	Nlat
Chipita	Nlat			
Daniela	Nlat			
Diatou	Nlat		Nlat	Nlat
Diwani	Nlat	Nlat		
Jasongo	Nlat			
Keke	Nlat	Nlat	Nlat	Nlat
Kichele	Nlat			
Kirembo	R			
Kombote	Nlat			
Lina	Nlat			
Louisoko	Nlat			
Zorba	L			
	Hopkins et al. 1993	This study		
Jill	Nlat		Nlat	Nlat

- The data collected by Harrison and Nystrom (2008) for spontaneous gesturing were defined as “gesture: use hand for communicative purposes toward another (e.g. reconciliatory), keeper or public (e.g. begging)”. There was no separation between the different kinds of gestures. I compared these data with my data for the gestures:

“begging (spontaneous)”, “inviting related behaviours (global)” and “arm held towards the other (invitation)”. The 4 analyzed subjects were similarly classified in both studies, i.e. unlateralized.

- Hopkins (Hopkins et al. 1993) collected data for spontaneous gesturing, defined as “gestures: animal uses its hands for communicative purposes, such as clapping to another animal, or by itself and begging toward the caretakers or observers”. There was no separation between the different kinds of gestures. I compared these data with my data for the gestures “begging (spontaneous)”, “inviting related behaviours (global)” and “arm held towards the other (invitation)”. he subject was similarly classified in both studies, i.e. unlateralized.

Thus, the results show consistency between studies that are separated by several years, but concerns a lack of laterality.

Table 31: Data per subject for spontaneous social actions. Apenheul zoo. (study 4a)

	Jasiri	**Jill**	**Kumbuka**	**Liboso**	**Lingala**	**Lomela 1**	**Mobikisi**	**Mwindu**	**Nayembi**	**Zuani**
suckling at mother's breast	R		L		L				R	
sitting with crossed arms around the infant		R		R		R				
tripedal movement holding the infant under belly with one arm			Nlat	R						
sitting holding the infant with one arm				Nlat						
retrieving the infant with one arm				R						
standing and placing the infant under belly				R						
waist thrusting while holding infant under belly (tripedal posture)										
holding the partner during ventro-ventral mount	Nlat	L	R			Nlat				L
crossed arms around the partner during ventro-ventral mount		R				R				Nlat
putting arm around the mounting partner during ventro-dorsal mount										
holding the mountee partner during ventro-dorsal mount (including mount walk)		Nlat	L							Nlat
pulling the partner in close contact						Nlat				Nlat
touching the genitals of the partner		Nlat			Nlat					
following with hand on the genitals of the partner					Nlat					
sitting with arm around the partner	Nlat		Nlat							
moving with arm around the partner	Nlat		Nlat		Nlat					
slapping the partner during grooming										
touching the partner's body (genitals excluded)	Nlat	Nlat		Nlat						
patting the partner's body (with the palm or back of the hand)				Nlat						
slapping the floor with one hand										
stamping the floor with one foot					R					
banging the glass with one hand			Nlat							
arm held towards the other (invitation)		Nlat								

table 31 continued	**Jasiri**	**Jill**	**Kumbuka**	**Liboso**	**Lingala**	**Lomela 1**	**Mobikisi**	**Mwindu**	**Nayembi**	**Zuani**
inviting related behaviours (global)		Nlat								
kicking the other										
punching the other										
hitting the other										
hunching over the other (not gentle)										
lateral embrace	Nlat		Nlat		R					
face embrace										
holding the hand or foot of the other										
pushing away the approacher + holding the partner of										
catching the other										
playing							Nlat			
dragging the other										Nlat
play related behaviours (global)	Nlat			Nlat		Nlat	Nlat			Nlat
plucking the other's hair							R			
begging										
hand clapping										
bipedal branch shaking display								R		

Table 32: Data per subject for spontaneous social actions. Twycross zoo. (study 4a)

	Banja	Bokela	Cheka	Diatou	Gemena	Jasongo	Kakowet II	Keke	Kichele	Luo
suckling at mother's breast		L			Nlat					Nlat
sitting with crossed arms around the infant	R		L	R						
tripedal movement holding the infant under belly with one arm	L		R	R						
sitting holding the infant with one arm	L		R	R						
retrieving the infant with one arm	L		R	R						
standing and placing the infant under belly			R							
waist thrusting while holding infant under belly (tripedal posture)	L									
holding the partner during ventro-ventral mount			Nlat			Nlat	Nlat		L	
crossed arms around the partner during ventro-ventral mount										
putting arm around the mounting partner during ventro-dorsal mount			Nlat						R	
holding the mountee partner during ventro-dorsal mount (including mount walk)										
pulling the partner in close contact	Nlat								Nlat	
touching the genitals of the partner	R	Nlat						Nlat	Nlat	Nlat
following with hand on the genitals of the partner	Nlat									
sitting with arm around the partner										
moving with arm around the partner	Nlat	L	Nlat					Nlat		Nlat
slapping the partner during grooming										
touching the partner's body (genitals excluded)	Nlat		Nlat			Nlat	Nlat	Nlat	Nlat	Nlat
patting the partner's body (with the palm or back of the hand)	Nlat					Nlat				
slapping the floor with one hand							Nlat	Nlat		
stamping the floor with one foot										
banging the glass with one hand										
arm held towards the other (invitation)	Nlat	R	Nlat	Nlat				Nlat		
inviting related behaviours (global)	Nlat	R	Nlat	Nlat			Nlat	Nlat		

table 32 continued	Banja	Bokela	Cheka	Diatou	Gemena	Jasongo	Kakowet II	Keke	Kichele	Luo
kicking the other						Nlat				
punching the other						Nlat		Nlat		
hitting the other	Nlat					Nlat		Nlat		Nlat
hunching over the other (not gentle)								Nlat		
lateral embrace	Nlat	Nlat	Nlat					Nlat		Nlat
face embrace				R						
holding the hand or foot of the other	Nlat		Nlat			R		Nlat	Nlat	
pushing away the approacher + holding the partner of						Nlat	Nlat			
catching the other	R		Nlat					Nlat		
playing	R		Nlat	Nlat		Nlat	Nlat	Nlat	Nlat	
dragging the other	L		Nlat	Nlat				Nlat		Nlat
play related behaviours (global)	Nlat		Nlat	Nlat		Nlat	Nlat	Nlat	Nlat	Nlat
plucking the other's hair										
begging		Nlat						Nlat		
hand clapping							R			
bipedal branch shaking display										

Table 33: Data per subject for spontaneous social actions. Stuttgart zoo (italic names) and Lola ya bonobo. (study 4a)

	Bisengo	Bolobo	Dilolo	Lodja	Malaika	Maniema	Moyi	*Daniela*	*Dankie*	*David*	*Diwani*	*Kasai*	*Kirembo*	*Lina*	*Lucuma*
suckling at mother's breast	R				L		Nlat		Nlat			Nlat			Nlat
sitting with crossed arms around the infant								Nlat						L	
tripedal movement holding the infant under belly with one arm								R							
sitting holding the infant with one arm								R							
retrieving the infant with one arm								Nlat							

table 33 continued	Bisengo	Bolobo	Dilolo	Lodja	Malaika	Maniema	Moyi	*Daniela*	*Dankie*	*David*	*Diwani*	*Kasai*	*Kirembo*	*Lina*	*Lucuma*
standing and placing the infant under belly															
waist thrusting while holding infant under belly (tripedal posture)															
holding the partner during ventro-ventral mount														Nlat	
crossed arms around the partner during ventro-ventral mount															
putting arm around the mounting partner during ventro-dorsal mount															
holding the mountee partner during ventro-dorsal mount (including mount walk)															
pulling the partner in close contact															
touching the genitals of the partner															
following with hand on the genitals of the partner															
sitting with arm around the partner															Nlat
moving with arm around the partner				Nlat											Nlat
slapping the partner during grooming											Nlat			Nlat	
touching the partner's body (genitals excluded)															
patting the partner's body (with the palm or back of the hand)															

table 33 continued	Bisengo	Bolobo	Dilolo	Lodja	Malaika	Maniema	Moyi	*Daniela*	*Dankie*	*David*	*Diwani*	*Kasai*	*Kirembo*	*Lina*	*Lucuma*
slapping the floor with one hand											Nlat			Nlat	
stamping the floor with one foot			R												
banging the glass with one hand															
arm held towards the other (invitation)															
inviting related behaviours (global)															
kicking the other															
punching the other															
hitting the other															
hunching over the other (not gentle)															
lateral embrace										Nlat					Nlat
face embrace															
holding the hand or foot of the other													Nlat		
pushing away the approacher + holding the partner of															
catching the other															
playing															
dragging the other													Nlat		
play related behaviours (global)											Nlat		Nlat		
plucking the other's hair															
begging		Nlat									Nlat				
hand clapping						L									
bipedal branch shaking display															

4B. Induced begging gesture

The experiment on begging gesture was a very interesting piece of this PhD thesis. With study 4b, I examined language related hypotheses (predictions 3). The results are presented in this chapter.

4b.1. Begging experiment:

Table 6 in methods section gives the number of data analyzed.
The descriptive statistics are presented in Table 34.
The results of analyses on the effect of sex and age (Table 22app and 23app in appendix) are presented in tables, and are discussed at the end of this chapter.

The raw data for each individual are presented in Table 34.

Table 34: Raw data for each individual for the induced begging gesture (study 4b). Right: number of right hand responses, Left: number of left hand responses; total: total number of trials. B test: p value of the Binomial test performed on the number of right versus left hand trials. Category: category in which the individual was classified based on Binomial test: L: left-handed, R: right-handed, Nlat: not lateralized.

	right	**left**	**total**	**HI**	**ABSHI**	**B test**	**category**
Bandundu	0	14	14	-1	1	0.0001	L
Beni	17	3	20	0.7	0.7	0.003	R
Bili	1	5	6	-0.667	0.667	0.219	Nlat
Boende	2	10	12	-0.667	0.667	0.039	L
Bolobo	6	7	13	-0.077	0.077	1	Nlat
Dilolo	2	11	13	-0.692	0.692	0.023	L
Ilebo	2	10	12	-0.667	0.667	0.039	L
Isiro	16	3	19	0.684	0.684	0.004	R
Kikongo	29	0	29	1	1	4E-09	R
Kikwit	0	11	11	-1	1	0.001	L
Kubulu	11	0	11	1	1	0.001	R
Likasi	16	14	30	0.067	0.067	0.856	Nlat
Lisala	16	0	16	1	1	3E-05	R
Matadi	2	14	16	-0.75	0.75	0.004	L
Maya	11	1	12	0.833	0.833	0.006	R
Mbandaka	8	0	8	1	1	0.008	R
Mimia	2	17	19	-0.789	0.789	0.001	L
Mixa	1	14	15	-0.867	0.867	0.001	L
Nioki	13	1	14	0.857	0.857	0.002	R
Opala	7	1	8	0.75	0.75	0.07	Nlat (R trend)
Pole	6	0	6	1	1	0.031	R
Semendwa	18	1	19	0.895	0.895	8E-05	R
Tembo	10	0	10	1	1	0.002	R
Tshilomba	1	14	15	-0.867	0.867	0.001	L
Total	197	151	348				
Mean			14.5	0.114	0.785		
SD			6.058	0.833	0.255		
Min			6	-1	0.067		
Max			30	1	1		

Bouts (number of bouts per subject):

Amongst the 24 bonobos, 20 (83.333%) were significantly lateralized (B $p \leq 0.039$) and only 4 (16.67%) showed no preference (B $p \geq 0.07$) (Table 34). There were significantly more lateralized than unlateralized individuals (B p=0.002). For the group, the mean ABSHI was 0.785 (SD=0.255), which indicates a very strong laterality. Moreover, for the lateralized subjects, the mean percentage of use of the preferred hand was 93.17%

(SD=7.968, N=20), showing very strong, almost exclusive, preferences. Indeed, 8 bonobos exhibited exclusive preferences and several showed almost exclusive preference.

Regarding the direction of laterality, the mean HI value for the group was 0.114 (SD=0.833), which was not significantly different from 0, the value expected by chance (T t(23)=0.673, p=0.508). The HI values were not skewed toward one side, so there was no group-level bias in hand use. 11 bonobos were classified as right-handed (and 1 exhibited a right trend) and 9 were left-handed. The numbers of right-handed and left-handed subjects were not different (B p=0,824), indicating no group-level bias.

The percentage of right-handers in the group was 45.833%. When excluding unlateralized individuals, the proportion of right-handers amongst lateralized subjects was 55%.

4b.2. Comparison between the begging experiment and the other actions:

I compared the data for the begging experiment with the data for the 13 main spontaneous non-social actions and with the “tube task” (study 2) and the “termite fishing task” (study 3b), to test whether begging induced a specific laterality compared to other actions (predictions 3). The results of the MW tests are presented in Table 35.

Table 35: Comparisons between the begging experiment and the other actions (study 4b).
Results of the MW test, p values for HI, ABSHI and total comparisons between the begging experiment and the spontaneous actions. Significant p values are in bold.

“begging experiment” (N=24) versus:	**MW on total**	**MW on HI values**	**MW on ABSHI values**
“reaching for big items, general” N=26	U=235 p=0.134	U=273 p=0.448	U=101.5 **p<0.01**
“reaching for small items, general” N=33	U=169.5 **p<0.01**	U=362.5 p=0.588	U=133.5 **p<0.01**
“reaching in the fixed object (dipping) (unimanual)” N=8	U=93.5 p=0.913	U=91 p=0.827	U=14 **p<0.01**
“feeding, general” N=65	U=201 **p<0.01**	U=722.5 p=0.595	U=165.5 **p<0.01**
“quadrupedal movement holding food/object in one hand” N=32	U=337.5 p=0.44	U=354 p=0.619	U=123 **p<0.01**
“tripedal movement holding food/object in one hand + while feeding” N=27	U=248.5 p=0.152	U=273 p=0.335	U=176 **p=0.005**
“pushing an object” N=10	U=114.5 p=0.835	U=109 p=0.675	U=95 p=0.338
“dragging an object” N=11	U=127.5 p=0.873	U=127 p=0.858	U=66 **p=0.018**
“swinging + hanging” N=15	U=177.5 p=0.942	U=140 p=0.247	U=44.5 **p<0.01**
“pulling grass out” N=11	U=103.5 p=0.310	U=131.5 p=0.986	U=120.5 p=0.676
“inserting a finger (self directed)” N=6	U=69.5 p=0.896	U=61.5 p=0.584	U=39 *p=0.082*
“raking seeds on the floor” N=7	U=22 **p=0.003**	U=69 p=0.476	U=78 p=0.773
“reaching in the water pond” N=6	U=38.5 *p=0.081*	U=64.5 p=0.695	U=46 p=0.171
“tube task” N=77	U=230 **p<0.01**	U=866.5 p=0.646	U=347.5 **p<0.01**
“termite fishing” task N=19	U=80.5 **p=0**	U=215.5 p=0.759	U=148 **p=0.048**

- Regarding the HI values, the begging experiment was similar to the other actions (Table 35).

- There was a notable difference regarding the strength of laterality: the ABSHI values for the begging experiment differed significantly from that of all (except 5) other actions, including the “tube task” and the “termite fishing” task (Table 35). This result indicates a stronger laterality for the begging experiment compared to other actions.

- The number of data points per subject was similar for begging and spontaneous actions (except for “tripedal movement holding the infant under belly with one arm” and as a trend for “touching the genitals of the other”, with fewer data points for begging) (Table 35).

- At the individual-level, the subjects generally showed the same preference for the begging experiment and the “tube task” (12 cases of similar preference versus 3 cases of different preferences; B test p=0.035) (these analyses excluded unlateralized subjects).

4b.3. Effect of possible influential factors:

In the next paragraphs, I investigate the effects of several possible influential factors including: living conditions (settings), sex, age (testing predictions 7, 15 and 16) and the number of data points.

Effect of sex:

- I examined each sex group separately and found no group-level bias in males (N=15) nor in females (N=9) (in the number of individuals (B p>0.05) and in the HI values (T p>0.05)) (Table 22app).
- I compared the data between males and females and found no difference in the HI and ABSHI values (MW p>0.05) (Table 23app), suggesting no significant effect of sex on laterality.

Effect of age:

- I first examined each age group separately. I found no significant group-level bias (in the number of individuals (B p>0.05) and in the HI values (T p>0.05)) (Table 22app).
- I then compared the data between the different age groups. Because of the small number of adolescent subjects (N=4), I combined them with others and analyzed by categories. I first compared the youngest individuals (infants + juveniles) with the older bonobos (adolescents + adults) and found no difference in the HI and ABSHI values

(MW p>0.05) (Table 23app). I then compared the adults and the other bonobos (infants + juveniles + adolescents) and found no difference in the HI and ABSHI values (MW p>0.05) (Table 23app). Therefore, the results suggest no significant effect of age on laterality.

Effect of the number of data points:

I tested the possible effect of the number of data points in two ways.

- I first assessed the correlation between the number of data points per subject and the HI and ABSHI values and found no significant correlation (Spearman test, rho=-0.138, p=0.521 for HI, rho=-0.176, p=0.411 for ABSHI).
- Other analyses were not possible due to the small number of unlateralized subjects (N=4).

Thus, the data suggest that the number of data points did not significantly influence the results (direction and strength of laterality).

- The scatter plots confirm this absence of relation between the laterality and the number of data points per subjects (Figure 18 and 19). The figures also illustrate and show the very interesting distribution of the individuals, i.e. almost only very strongly lateralized subjects (with very few unlateralized subjects).

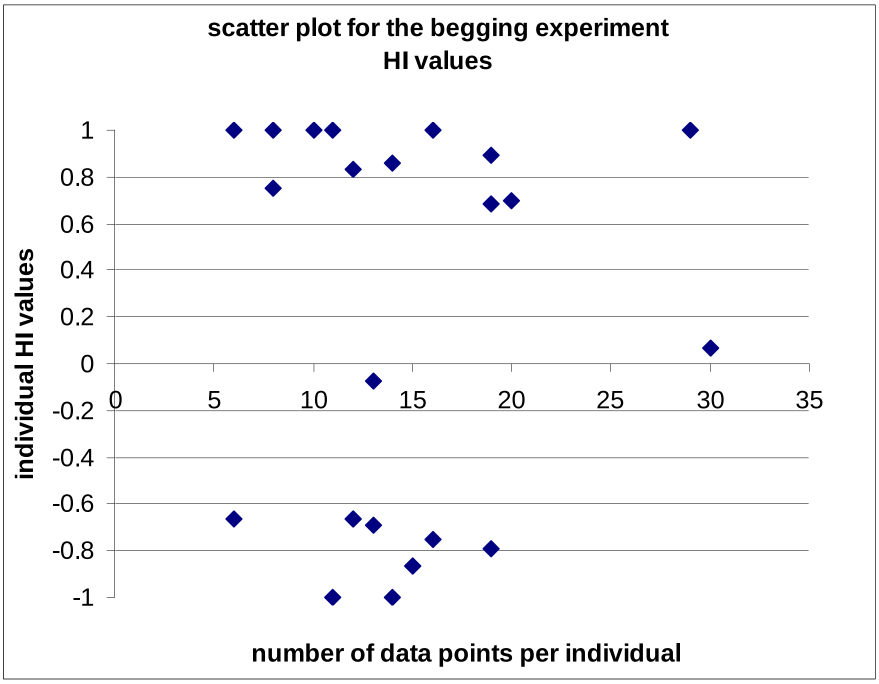

Figure 18: Scatter plot showing the distribution of HI values with increasing number of data points for the begging experiment.

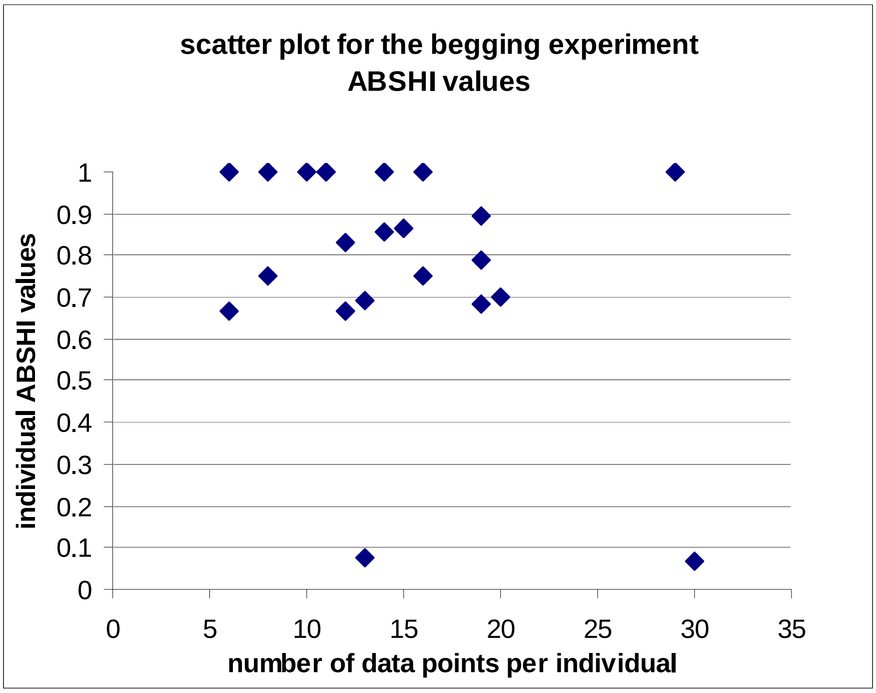

Figure 19: Scatter plot showing the distribution of ABSHI values with increasing number of data points for the begging experiment.

4b.4. Other analyses:

Effect of kinship:

Only one mother-infant pair could be analyzed: Pole exhibited a right hand preference and its mother (Opala) showed no preference (but a right trend).

Comparison between induced begging and spontaneous begging:

I investigated possible differences in laterality between "induced and inter-specific" gestures (study 4b) and "spontaneous and intra-specific" gestures (study 4a) (predictions 7). Namely, I compared the begging experiment and the spontaneous begging.

For the spontaneous begging, only 30 bouts were analyzed, from 4 individuals. All 4 subjects were unlateralized (100%) (Table 36). Therefore, the data were insufficient to allow statistical comparison of laterality between the two kinds of begging gestures. When considering the individual-level, only one subject provided data for both kinds of begging (Bolobo) and it was unlateralized for both.

Table 36: Raw data for spontaneous begging gestures (study 4a).
Right hand: number of right hand responses, Left hand: number of left hand responses; total: total number of trials. B test: p value of the Binomial test performed on the number of right versus left hand trials. Cat: category in which the individual was classified based on Binomial test: L: left-handed, R: right-handed, Nlat: not lateralized.

		Right hand	**Left hand**	**total**	**HI**	**ABSHI**	**B test**	**cat**
lola	Bolobo	3	4	7	-0.143	0.143	1	Nlat
stuttgart	Diwani	4	3	7	0.143	0.143	1	Nlat
twycross	Keke	3	4	7	-0.143	0.143	1	Nlat
twycross	Bokela	3	6	9	-0.333	0.333	0.508	Nlat

Table 37: Summary table of the main results of each of the studies.

Study	summary of the main findings
Study 1: spontaneous non-social actions	- The laterality observed for spontaneous non-social actions was weak, with generally a high percentage of unlateralized individuals and low ABSHI values. - No group-level bias appeared for any of the actions studied (with one exception). The HI values were significantly skewed in several cases (generally toward the right hand).
Study 2: "tube task" experiment	- The laterality was very marked for the "tube task". There were strong individual preferences, with up to 100% use of the preferred hand. Moreover, the majority of individuals were lateralized (with frequency). The proportion of lateralized subjects was very high (88%), the highest of all the actions studied in this PhD research. The ABSHI values were also high and stood in the top 30 most lateralized actions studied. - The bonobos showed no group-level bias for the "tube task", with about equal number of left-handed and right-handed subjects.
Study 3a: spontaneous tool-use actions	few data
Study 3b: "termite fishing task	- The bonobos exhibited a very marked laterality for the "termite fishing task". Many individuals were lateralized. With frequency, the percentage of lateralized subjects (86%) was amongst the highest of all the actions studied in this PhD research. Moreover, the percentage of use of the preferred hand was very high, indicating that the individuals that were lateralized showed very strong, almost exclusive preferences. - No group-level bias occurred for the "termite fishing" task.
Study 4a: spontaneous social actions and gestures	- The laterality observed for social actions was weak, with a high proportion of unlateralized individuals and low ABSHI values. - The samples analyzed were small and the data available did not allow investigation of group-level biases or performing detailed analysis.
Study 4b: induced begging gesture experiment	- I observed an extremely strong laterality in the begging experiment. 20 of the 24 bonobos were lateralized (i.e. 83%), which was the highest value observed among all the actions studied in this PhD research (after the "tube task" with frequency). The mean ABSHI value was the strongest value observed (after "raking seeds on the floor"). Moreover, the bonobos that were lateralized exhibited very strong, almost exclusive preferences, with an average of 93% use of the preferred hand. Finally, the begging experiment was significantly more lateralized than almost all the other actions studied in this PhD thesis. - No group-level bias occurred for the begging experiment.

Section IV :

Discussion

In this section, I present the discussion of the results. Prior to the discussion, I summarize the study and main findings, and present the limitations and strengths of the study. Then, in the second chapter, I discuss my data in relation to the hypotheses suggesting that the hand preferences of non-human primates may be artefacts of experimental designs, environmental biases or human-rearing (predictions 7). I also examine the effects of the internal factors sex and age (predictions 15 and 16). In the third chapter, I investigate the effects of factors that have been proposed as possible selective pressures for the emergence of handedness and that may influence hand preference (predictions 1-6’’ and 8-8’). This is followed by a general conclusion and some recommendations for future research.

Chapter 1: Summary of the thesis

1.1. Summary and main findings:

The present database on hand preference in non-human primates provides inconsistent and inconclusive findings and is plagued by important methodological issues and gaps. I studied hand preference in bonobos. Bonobos are very close to humans in the phylogeny and display particular features in terms of language, bipedalism and tool-use; factors that have been proposed as selective pressures for the emergence of human handedness. Thus, this is an invaluable model species for investigating the evolution of brain lateralization and handedness; and best candidate for exhibiting precursors of human handedness and sharing common traits with humans. There are few previous data on bonobos and their interpretation is hindered by small sample sizes and other methodological issues.

I considered a very large sample of bonobos (N=94) (40% of the worldwide captive population) that included four different populations. I examined a wide range of actions, including spontaneous actions and experimentally induced actions. My studies were designed in relation to the hypotheses tested and the gaps in the current database; and with the aim of providing data that can be reliably compared to that of other studies.

I briefly recall the studies that have been done in this PhD research:

1 - Study of hand use for spontaneous actions (non-social):

The bonobos were observed during their spontaneous daily activities. I analyzed 32 behaviours (53 behavioural patterns), and I tested the effects of several variables (e.g. posture of the subject, activity of the other hand, grip type).

2 - Study of hand use for manipulation and bimanual coordination:

The bonobos were tested with the “tube task”, which is a complex task that requires a precise, manipulative bimanual coordinated action.

3 - Study of hand use for tool-use:

I recorded data on hand use for spontaneous tool-use actions and for an enrichment task that requires using a stick as a probe ("termite fishing" task).

4 - Study of hand use for social actions and gestures:

I recorded hand use for social actions and gestures. a) I considered behaviours that occurred spontaneously during the social interactions (intra-specific) and during interactions with humans (inter-specific). b) I also assessed hand preference for induced inter-specific gestures in an experiment that involved begging towards a human observer.

In each study, I tested the influence of several factors that have been proposed or shown to influence laterality in primates, including: external factors (e.g. living conditions, rearing history, experimental design) and internal factors (e.g. sex, age).

Thus, to summarize this research, I investigated whether bonobos exhibit manual laterality and to what extent (small or high proportion of lateralized subjects, weak or exclusive preferences, individual-level or group-level laterality) and I examined which factors - related to the task or to the individual – can elicit or influence laterality in bonobos.

I found evidence of laterality in almost all of the actions studied. This shows that bonobos do exhibit manual laterality. The preferences were present on an individual basis. That is, the numbers of right-handed and left-handed individuals were similar. No group-level bias occurred for any of the actions studied (with one exception: feeding with the other hand for postural support). I also examined the HI values, which are indicative of biases in hand use. Almost all the actions studied presented positive HI values, but significant biases towards right hand use (right biased HI values) only occurred in a few cases. With regard to possible influential factors, I found no significant effect of the settings, rearing history, sex and age on laterality. In only one case, there was an effect of age: in study 2, adults were more right-handed than younger subjects. I particularly examined the effects of factors that have been proposed as selective pressures for the emergence of human handedness, and that may influence laterality in non-human primates. The results indicate that laterality was affected by: postural demands (posture, activity of the other hand); precision of the action; grip type; manipulation, bimanual coordination; tool-use; throwing and gestures.

Before interpreting and discussing the findings, I first consider the limitations and strengths of this research work.

1.2. Limitations and strengths of this research work:

1.2.1. Limitations:

The main issues and limitations of this research were related to sample sizes of subjects and data points per subject.

- Sample size of subjects (for certain actions)
In many cases (e.g. for the spontaneous actions that occurred with low frequency), few subjects had sufficient data to reach the inclusion criteria, so I could not perform analyses (when N<6) or I had to perform analyses on small samples. As discussed in section I.3.3 and II.1.2, considering small samples of subjects may yield false negative findings, because group-level biases in the number of right-handed and left-handed subjects are more difficult to reveal with small samples (Hopkins 2006). To reveal relatively small laterality biases, like those found in chimpanzees (65%), a very large sample would be necessary (i.e. N=40). Therefore, in cases when the sample was smaller than 40 subjects, the absence of group-level bias observed might have been related to the small size of the sample examined (Hopkins 2006; Hopkins and Cantalupo 2005; Marchant and McGrew 1991; McGrew and Marchant 1997a). According to that, only study 2 and 7% of the actions in study 1 had very large sample sizes ($N \geq 40$). The fact that no group-level bias occurred even with these large samples, suggests that the absence of group-level bias was not related to small sample size issues. Moreover, and importantly, if the bonobos exhibited a human-like laterality (i.e. 90% of right-handers), this bias would have been revealed, even with small samples.

- Number of data points per subject

The same sample size issue occurred regarding the number of data points per subject. Considering small samples of data per subject may yield false negative findings, because significant laterality biases are more difficult to reveal with small samples (Hopkins 2006). In my studies, the data available only enabled me to restrict the analyses to the subjects that had a minimum of 6 data points (15 for study 2). Therefore, some of my individual-level analyses were performed on small samples (i.e. n<40). In these cases when the sample of data per subject was small, the absence of laterality might have been related to the small sample, instead of reflecting a real absence of laterality.

There was also a great variability between the subjects regarding the number of data points that varied between 6 and 359 with bouts, and between 6 and 784 with frequency. Differences in sample sizes have been suggested to influence laterality (strength and direction) (McGrew and Marchant 1997a; Palmer 2002).

It was not possible to avoid the sample size issues, but I investigated whether the sample size could influence the results. I assessed the possible effect of the number of data points on laterality in different ways.

- First, in study 2, I tested the effect of the number of data points and of the variability between subjects. I modified the individual data by cutting the data over 50 out. For the frequency, the mean number of data point per subject was 272. I restricted these data to 50 data points per subjects only. I compared the results of the two variables, “frequency” versus “50 data points frequency”. I found a difference regarding the HI values (higher with frequency), which suggests that the direction of laterality was affected by the sample size. However, there was no difference regarding the ABSHI values, suggesting no effect of the sample size on the strength of laterality.
- Secondly, I tested the correlation between the number of data points and the HI and ABSHI values in studies 1 to 4. In study 1, there was no effect of the sample size for almost all the actions studied. Only for “feeding” there was a significant effect: the strength of laterality (ABSHI values) decreased with increasing number of data points. Similarly, in study 2, there was no effect of the sample size in all cases; with one exception: for bouts at Lola ya bonobo, I found the same negative correlation as that observed for “feeding”. This correlation also appeared in study 4a for “touching the genitals of the partner”. No significant correlation was found in studies 3 and 4b.

- Thirdly, I compared the number of data points in lateralized and unlateralized subjects. In study 1, the number of data points was higher in lateralized compared to unlateralized individuals for many actions. This suggests that laterality was often weaker in the individuals that had few data points. In study 2, there was no effect of the sample size; except for bouts at Lola ya bonobo, for which there were more data points in unlateralized compared to lateralized subjects. In studies 3, 4a and 4b, there was no significant effect.

In sum, my data suggest that both the direction of laterality (HI values) and the strength of laterality (ABSHI values) could be affected by sample size in some cases. These findings are difficult to interpret because the effect was inconsistent between cases, indicating either an increase or a decrease of laterality with increasing number of data points. This however suggests that the sample size is a variable that may influence laterality and that should be taken into account when interpreting the data.

- Sample size differences in the comparisons

Within the same vein, some of the analyses were hindered by differences in sample size. There were indeed differences in the mean number of data points per subject between the actions or categories compared. As differences in sample size may lead to differences in the results (especially regarding the strength of laterality), in these cases, it was difficult to conclude, whether the difference of laterality observed between the two groups reflected a real effect or could have been related to the sample size difference.

Therefore, this research was faced with problems of small sample sizes and of differences of sample size between the subjects and categories compared. These problems are the common fate of such behavioural studies and there are no satisfactory means to avoid them. However, I investigated in which cases the effect of the sample size was significant and interpreted these findings with caution.

This work also presented several exceptional strengths, which makes it stand out from the previous studies on laterality in non-human primates. These strengths have been described in section I.4 and II, and are briefly listed in the next paragraph.

1.2.2. Strengths:

- Sample size of subjects

I studied a very large sample of bonobos that included 94 individuals. This is the largest bonobo sample considered to date. It was much larger than those tested in previous studies. The previous largest bonobo sample was N=22, which is four times smaller than my sample.

- This large sample allowed for investigation of the effects of several possible influential variables that are related to the individual, i.e. the living conditions, rearing history, sex and age.
- The large sample also allowed for addressing the question of heritability of hand preference in bonobos, which had never been done before.
- The sample included four different populations of bonobos that were housed at different places and tested with the same methodology, which has rarely been done before in non-human primates.
- The sample included 40% of the worldwide population of captive bonobos. This is thus a very representative sample that would allow making inferences at the species-level (regarding captive subjects) (McGrew and Marchant 1997a).

All these points are unique to this study and allowed for investigations that have never been done before, or not at this level of details.

- Actions studied

- I studied a wide range of actions, which allowed for examining a representative sample of the ethogram of the species.
- Considering multiple tasks, enabled me to examine each action separately, to compare the actions to each other and to combine the actions into relevant categories. This approach allowed for investigation of the effects of several task-related factors and determining which of these factors - that have been proposed as selective pressure for the emergence of handedness - can really elicit laterality.
- I recorded the data in a thorough detailed manner to allow examination of other factors (i.e. posture, action of the other hand, grip type), to assess the influence of the postural

demands and precision of the action, which have also been proposed as selective pressures for laterality.

- Finally, I used methods - measures of hand preference and statistical analyses - that allowed for reliable comparisons with previous studies.

In the next chapter, I present a discussion on the effects of different factors, that have been proposed or shown to influence laterality, and that were tested in my study. First, I consider the external factors (i.e. experimental design, captivity, human-rearing). Second, I examine the internal factors (i.e. sex, age). This is followed by a general discussion on the origins of the observed preferences. The next chapter discusses the effects of task-related factors (i.e. manipulation, bimanual coordination, tool-use, throwing, postural demands) that have been proposed as possible selective pressures for the emergence of handedness and that may elicit laterality in bonobos.

Chapter 2: Investigation of the effects of possible influential factors

2.1. External factors:

Warren and other researchers have suggested that the hand preferences of non-human primates could be an artificial phenomenon, created by experimental, environmental or other unnatural influences (McGrew and Marchant 1997a; McGrew and Marchant 2001; Warren 1980). I have tested these hypotheses (predictions 7) in my study and I below discuss the findings.

- Effect of experiments

Warren (1980) proposed that laterality was created by the experiments. If this was the case then laterality should appear only in experimental tasks.

- However, the bonobos exhibited significant preferences in spontaneous actions that occurred naturally in the daily activities. Thus, my data, consistent with previous findings on spontaneous activities (e.g. Chapelain et al. 2006; Fletcher and Weghorst 2005; Fragaszy and Adams-Curtis 1993; Heestand 1986; Rothe 1973; Teichroeb 1999; Vauclair and Fagot 1987), are evidence against Warren's hypothesis (Warren 1980).
- I compared spontaneous and experimental actions to determine whether laterality was stronger in experimental conditions. I observed a high proportion of unlateralized subjects (above 60%) for many of the spontaneous actions. However, this was dependent on the behaviour considered, since the laterality was very marked for certain spontaneous actions (Table 9). For the experimental tasks, there was a smaller proportion of unlateralized subjects (always below 60%, except for the "tube task" at lola with bouts). Thus, these findings indicate that laterality was stronger in experimental compared to spontaneous actions.

- I further compared the laterality observed in each experiment (or enrichment procedure) with that observed in each main spontaneous action. Regarding the “tube task” and the “termite fishing” task, their ABSHI values were in the range of those of the spontaneous actions. However, most of these comparisons were hindered by differences of sample size. There were more data points for the experiments compared to the spontaneous actions, which may have infuenced the strength of laterality (see section IV.1.2.1). In the case where there was no hindering difference in sample size, i.e. for “feeding”, the ABSHI values were stronger for the “tube task” and the “termite fishing” task compared to the spontaneous action. Regarding the begging experiment, there was a very marked difference in strength, with higher ABSHI values for begging than for most spontaneous actions. Therefore, some of my data suggest a stronger laterality for the experimental actions compared to the spontaneous actions.

This finding matches previous studies that report weaker laterality in spontaneous compared to induced actions (e.g. Chapelain et al. 2006; Fagot and Vauclair 1991; Fragaszy and Adams-Curtis 1993; Heestand 1986; McGrew and Marchant 1997a; Rothe 1973; Trouillard and Blois-Heulin 2005) and could go along with Warren’s hypothesis (Warren 1980). However, it is not possible to conclude that the experimental character of the action was responsible for the stronger laterality observed, because there were other factors involved. For instance, for the “tube task” and the “termite fishing” task, the task complexity was greater than that of the spontaneous actions, which may elicit a stronger laterality (Fagot and Vauclair 1991). Regarding begging, this task also had special characteristics (gestural communication) that might explain the laterality difference with the other actions. Thus, the specific characteristics of these actions might have been responsible for the stronger laterality observed, independently of the fact that they were experimental actions. This idea is further supported by the fact that the most strongly lateralized spontaneous actions were not less lateralized than the induced actions.

Therefore, my data show that laterality was not restricted to experimentally induced actions, which refutes Warren’s hypothesis. The laterality seemed to be stronger in induced compared to spontaneous actions, but the tasks compared were different, which hinders data comparisons. It would be interesting to compare data for the same task performed in spontaneous condition versus induced condition.

- Effect of the settings

The validity of studies on captive animals has been questioned and the preferences observed in captive animals have been suspected to be artefacts of the captive settings (McGrew and Marchant 1997a; McGrew and Marchant 2001). To discuss this point, I tested the effects of several captivity related factors (described in section I.4.3.6) that have been proposed to influence the laterality of captive animals. Namely, I investigated whether laterality differed between different settings that varied regarding these factors. When comparing the data between the four settings (Twycross zoo, Stuttgart zoo, Apenheul zoo and Lola Ya Bonobo sanctuary) or between the zoos and the sanctuary, I found no difference in the HI and ABSHI values, for any of the actions studied. In only one case did a significant difference appear: for the "tube task" with bouts there were higher ABSHI values in the zoos compared to the sanctuary, but this analysis was hindered by a difference in sample size (see section IV.1.2.1). Therefore, my data indicate that laterality did not vary between the different settings (with one exception).

This finding goes along with previous data in bonobos: Shafer (1997) who compared two zoos (San Diego zoo N=8 and San Diego wild animal park N=6) and Harrison and Nystrom (2008) who compared three zoos (Berlin N=5, Stuttgart N=11, Twycross N=6). My result also matches some data in other species (e.g. chimpanzees: (Hopkins et al. 2004; Hopkins and Cantalupo 2005)).

Thus, my findings suggest that the factors that varied between the different settings did not significantly affect laterality. This means that the captivity-related factors at stake, including: the degree of daily interactions with humans (keepers and public), the amount of space available and the asymmetry of the environment, did not influence laterality. Importantly, the settings that were compared also varied greatly regarding the naturalistic level, ranging from very unnatural (small concrete cages) to natural-like (large forest enclosure) settings. The fact that laterality did not differ between these settings suggests that this factor may not affect laterality either.

Therefore, my data support the idea that the hand preferences observed in captive animals are not artefacts of the captive settings. To further support this idea, it would be important to compare captive subjects and wild subjects that live in their natural environment; which is not yet possible due to the lack of data from wild bonobos.

- Effect of rearing history

Within the same vein, some researchers have suspected rearing by humans to induce hand preferences in captive animals (McGrew and Marchant 1997a). To examine this question, I tested the effect of rearing history on laterality. Namely, I investigated whether laterality was different in the subjects that were raised by humans. I compared three categories of individuals: "parent-reared", "human hand-reared" and "Lola-reared"; and also "parent-reared" and "human hand-reared + lola-reared", a category that combined all bonobos that have been in contact with humans during infancy. I found no significant effect of rearing history on the HI and ABSHI values in any of the studies.

These are the first bonobo data on the effect of rearing history. They are consistent with several studies that indicated no effect of rearing on laterality in great apes (e.g. Fletcher and Weghorst 2005; Fletcher 2006; Hopkins 1995; Hopkins and Rabinowitz 1997; Hopkins and Leavens 1998; Hopkins and Wesley 2002; Hopkins et al. 2003; Hopkins et al. 2004; Hopkins et al. 2005a; Hopkins et al. 2005b; Hopkins et al. 2005c).

Therefore, my data, along with previous data, suggest that being raised by humans may not significantly influence laterality. The issue remains controversial as there are also data suggesting some effect of human rearing (e.g. Hopkins et al. 1993b; Hopkins and Cantero 2003). It would be important to further address this issue by comparing captive subjects and wild subjects that were born and raised in the wild, with no contact with humans at all (which is not possible without field bonobo data).

- Consistency of hand preference over time

One point that led Warren (Warren 1980) to claim that hand preferences were not organismic but artificially created, was his observation of inconsistency over time. He observed changes of preference within subjects between test sessions, suggesting that hand preference would not be a stable trait. If hand preferences were not stable in time, this could suggest that they may not be related to brain lateralization, but might stem from random factors that vary between test sessions or over time (e.g. experimental conditions, motivation, presence of congeners, position of the object relative to the hands). I did not test consistency across test sessions in my study. I investigated the consistency of hand preference over time, by comparing my data (collected between September 2005 and December 2007) with data collected in the same subjects several years before my study (May to November 2000 by Harrison and Nystrom (2008); June to August 1992 by Hopkins et al. (1993c)). In many cases, I found no consistency between my data and the previously published data. However, these inconsistencies concerned only the classification as lateralized or unlateralized. In only one case, there was a preference in the opposite direction between my study and the previous study. These findings are difficult to interpret because they may be related to between-studies methodological differences (regarding data collection procedures and definition of the behaviours) or to differences in sample sizes (see section I.4.2), instead of reflecting real inconsistencies of laterality. Importantly, in several cases, I observed the same laterality in my study and in the previous study, which indicates a consistency of hand preferences over years in some cases and goes against Warren's hypothesis.

This was the first time that this question was addressed in bonobos. When considering previous data in other species, several studies have shown consistency of hand preference over time (up to several years) (e.g. for the "tube task": (Hopkins et al. 2001c; Hopkins et al. 2005a; Meunier and Vauclair 2007; Vauclair et al. 2005; Westergaard and Suomi 1996)). Therefore, some of my data and data in other species suggest that laterality may be a stable trait.

2.2. Internal factors:

As seen in section I.4.3.6, sex and age have been shown to influence laterality in human and non-human primates, and they have been suggested to account for the variability observed between individuals (Vauclair and Fagot 1987). I have tested the effects of sex and age in each of my studies (predictions 15 and 16) and I below discuss the findings.

- Effect of sex

I compared the data between males and females to test whether sex influenced laterality. I found no difference of laterality between sexes in most cases. Specifically, no effect of sex appeared in the studies on spontaneous actions (social and non-social) and in the begging experiment. For the "tube task", there was no effect of sex; except in two cases : in the zoos sample, males tended to show a stronger laterality than females (with frequency and bouts); in the combined sample (lola + zoos), males exhibited a greater right hand use than females (with bouts). However, in two of these three cases, there was also a difference of sample size between males and females, which hindered these comparisons (see section IV.1.2.1). For the “termite fishing” task, there was no significant influence of sex on the HI and ABSHI values, but there was a trend for more lateralized subjects in females, and for more right-handed subjects in females than males. Therefore, my results suggest little and unclear effects of sex on laterality.

When considering previous bonobo data, Hopkins and collaborators found that males were more right-handed than females for gesturing and carrying, and that females were more right-handed than males for the leading limb in locomotion (combined data from (Hopkins et al. 1993c; Hopkins and DeWaal 1995)). Harrison and Nystrom (2008) reported that females favoured the right hand more than males. Therefore, whilst my data and previous data suggest some influence of sex on hand preference in bonobos for certain behaviours, this effect remains unclear and is likely to be small. These findings in bonobos are consistent with the literature in non-human primates (see section I.4.3.6). Thus, taken together the data suggest that sex may influence laterality in non-human primates, but the effect varies between tasks, studies and species; so there would be no such clear effect as that observed in humans. Humans consistently show greater left-handedness in males (Fagard 2004; Faurie 2004). Sex effects on handedness are thought to be related to differences in brain organization that may be related to testosterone (Geschwind and Galaburda 1985). The relationship between hormons and laterality has been little investigated in non-human primates, but there are data suggesting that hormons may actually influence laterality (Westergaard and Lussier 1999; Westergaard et al. 2000; 2003). Further investigation are necessary to improve our understanding of sex effects on laterality.

- Effect of age

I compared the data between the different age groups to test whether age influenced laterality. I investigated hypotheses proposing that immature subjects should exhibit a different laterality compared to older individuals, in accordance with maturational processes.

- With regard to the strength of laterality, the ABSHI values did not vary between age groups in all of my studies. This important finding suggests that age did not influence the strength of laterality. Laterality was not weaker in young compared to mature subjects. This result does not support the hypothesis proposing that laterality is undevelopped in young subjects and needs maturational processes to develop.

Harrison and Nystrom (2008) also found no effect of age on the strength of laterality in bonobos, but Shafer (1997) reported a stronger laterality in old versus young bonobos.

These findings in bonobos are consistent with most of the data in other non-human primate species. However, several studies have reported an increase of the strength of laterality with age (see section I.4.3.6), suggesting a possible maturation of laterality. Therefore, all together, the data are inconclusive, but indicate that age may influence the strength of laterality in some cases. Here again, the effects of age in non-human primates would not be as marked as that observed in humans. In humans, the strength of hand preference clearly increases with age in immature subjects, probably in relation with combined effects of maturational processes and practise with the dominant hand (i.e. the preference may increase with the increased use of the preferred hand) (see below) (Fagard 2004; Dellatolas and De Agostini 2004).

- With regard to the direction of laterality, I found no effect of age in most cases. But I also observed a significant effect of age on HI values in several cases. In study 1, group-level right biases appeared in young subjects but not in adult subjects, for feeding and for reaching for small items. In study 2 in zoos, the youngest individuals (infants + juveniles) exhibited a greater left hand use than the adults; and they showed a bias towards left hand use (with frequency and bouts). In the lola sample, there was a bias towards left hand use in the adolescents (with bouts). In the combined sample (lola + zoos), the adults showed a greater right hand use than the youngest individuals (infants + juveniles) and than the non-adults category (infants + juveniles + adolescents) (with frequency); and they showed a bias towards right hand use. Therefore, the results indicate a decrease of left hand use and an increase of right hand use with age, in the “tube task” study.

When considering previous bonobo data, Hopkins also showed a greater right hand use in adults compared to young subjects in several behaviours (feeding, reaching, bimanual feeding) ((Hopkins et al. 1993c) and combined data from (Hopkins et al. 1993c; Hopkins and DeWaal 1995)). Therefore, some of my data and previous findings suggest an increase of right hand use with age in bonobos, for certain behaviours. Such an age effect has been reported in several other non-human primate species (e.g. lemurs: (Ward *et al.*, 1990), macaques: (Westergaard and Lussier, 1999), capuchin monkeys: (Westergaard and Suomi, 1993, 1994)). These findings may support the maturational hypothesis (Geschwind and Galaburda 1985) proposing that the left-hemisphere (right hand) develops more slowly than the right-hemisphere (left hand), which causes a greater use of the right hand with age. However, any interpretation must be cautious because I found the effect only in study 2. No such effect was reported in the other actions studied; and two actions in study 1 suggested an age effect in the opposite direction.

Therefore, whilst the analyses on the strength suggest that age did not affect laterality, a significant effect of age on the direction of laterality was found in several cases (notable effect in study 2), which suggests that age influenced laterality in some cases. Thus, my data, along with previous data suggest that age may influence hand preference in bonobos for certain behaviours. This finding is consistent with the literature in other species (see section I.4.3.6), which suggests that age effects on laterality may exist in non-human primates, but are variable and remain unclear. Longitudinal studies that follow the same individuals over several years (especially over the maturation period) and on different behaviours, are necessary for understanding age effects on laterality. Such studies would enable us to determine whether hand preference needs maturation to establish and whether it exhibits shifts during maturation, as observed in humans (Fagard 2004; Dellatolas and De Agostini 2004).

2.3. Conclusion on the effects of possible influential factors:

To summarize, I investigated hypotheses proposing that the hand preferences of non-human primates are artefacts that stem from experimental or environmental influences (Deuel and Dunlop 1980; McGrew and Marchant 1997a; McGrew and Marchant 2001; Warren 1980) (predictions 7). I found that the laterality was not affected by several possible influential external factors. Namely, my results suggest that the observed preferences could not stem from: a) the experimental design (see data for spontaneous actions); b) factors related to the settings in which the animals lived (see analysis on the settings); c) the contacts with humans (see analysis on rearing history). These findings go against the hypotheses, and support the view that the hand preferences were not artificially created, but would be related to biological factors (Fletcher and Weghorst 2005; Hopkins 2006; Hopkins and Cantalupo 2005). Thus, the observed preferences can be considered as biological traits (Fletcher and Weghorst 2005; Hopkins and Cantalupo 2005; Hopkins 2006).

I also investigated hypotheses proposing that sex and age influence laterality. My findings show a limited effect of sex on laterality (strength and direction). Regarding age, I found no effect on the strength of laterality, and I found no effect of age on the direction of laterality in most cases. The data for the "tube task" suggest that age may influence the direction, but this effect was not found in the other actions studied. Therefore, my data indicate that, although they might have influenced in some cases, sex and age did not have a strong and uniform effect on laterality. This result shows that these factors could not explain the individual variability.

Therefore, my data suggest that: a) the observed laterality could not be an artefact of experimental, environmental or human influence, b) the individual variability observed, which led to an absence of group-level bias, could not be explained by the individual factors sex and age (although age effects need further investigation using longitudinal approaches).

2.4. Possible origins of the observed laterality:

What are the origins of the observed laterality? Above, I showed that laterality was unlikely to be issued from unatural influences, but can be viewed as a natural phenomenon. The proximate causes of laterality are largely unknown, in non-human primates as well as in humans. Many researchers assume that hand preferences stem from brain lateralization. This hypothesis proposes that when only one hemisphere is competent to solve the task (i.e. specialized), this leads to a preference for using the associated hand. That is, the hand associated with the specialized hemisphere is more efficient than the other hand and is used preferentially. Thus, a preference for using one hand is thought to reflect the specialization of the contralateral hemisphere for the task considered (at least for complex tasks) (Fagot and Vauclair 1991; McNeilage 1987). Alternatively, others think that hand preference is created by a positive feedback, i.e. it is the use of the preferred hand that enhances its skills; there is no pre-existing difference in hand skills related to hemispheric specialization (Byrne and Byrne 1991). Finally, other views (Uomini 2009) propose that the origin of hand preference may be a combination of the two : genes that determine brain lateralization, reinforced by practise and positive feedback.

In my study, I asked what mechanisms may be involved in the determination of the preferences observed in bonobos. I tested hypotheses proposing that hand preferences are genetically determined, innate and related to brain lateralization, as well as hypotheses proposing that hand preferences stem from practise or learning. Specifically, I examined heritability, non-manual functions and early biases as well as the effects of age, practise and learning.

- Heritability of hand preference

I compared hand preference in pairs of related individuals to assess the heritability of laterality (prediction 17). My findings show no particular link between the preferences of mother and infant, father and infant or between siblings. Although, notable relationships appeared in some cases (e.g. Diatou and Kichele, and Mwindu and Jasiri showed almost always matched preferences). For the "tube task", there was an interesting trend for opposite preferences between parents and offspring. However, this may be related to an age effect as young subjects were more left-handed and adults more right-handed. This needs to be examined by assessing the preferences of the infants when they are adults, to check whether they retain their left-hand preference (Fletcher and Weghorst 2005).

My results do not support the hypothesis proposing that hand preference are transmitted from parent to offspring. Thus, my data do not provide evidence for a genetic determination of hand preferences.

These are the first data on heritability of hand preference in bonobos, and they add to the few available data in other species which are largely inconclusive (see section I.4.3.6).

The mechanisms of transmission of laterality may include genetic as well as non-genetic factors (Hopkins 1999; Hopkins et al. 2000a; Hopkins et al. 2001b; Teichroeb 1999) (see section I.4.3.6). I examined the influence of a non-genetic factor that has been proposed to influence laterality: cradling. Hopkins (Hopkins et al. 1993a; Hopkins

2004) suggested that the cradling preference of the mother may determine the hand preference of the infant in chimpanzees. I assessed hand preference for several maternal behaviours, including carrying infant when moving tripedal and cradling infant when seated. The arm preferentially used by the mother to cradle was opposite to the hand preferred by its infant in two cases, while it was the same as that of the infant in two other cases. Thus, the results do not support the cradling hypothesis.

I emphasize the need for further investigation on heritability of hand preference in non-human primates. Particularly, examining large samples of subjects and considering multiple tasks would be essential to complement the scarce and inconclusive data available and help in understanding the mechanisms that underlie laterality.

- Relationship between manual laterality and other lateralized functions

Studying other lateralized functions is also an interesting way of investigating the genetical basis of laterality. Indeed, finding a link between different lateralized functions within an individual would indicate a genetic determination of laterality. I collected data for several non-manual functions, including: turning, crossing legs and lying on one side in foetus position. Unfortunately, there were too few lateralized individuals for these actions and it was not possible to compare the lateral biases between lateralized functions.

- Early biases

If laterality was present very early in life, this would support the idea that it is based on genes. In my study, I examined lateral biases in a wide range of age : from 3 months to 40 years old. The youngest subject for which I had data on manual actions (Bokela) was aged 2 years old, and she exhibited a significant laterality. Moreover, I found evidence of significant laterality for non-manual functions (suckling) in a subject aged 3 months old (Nayembi). Thus, laterality was present early in life, which goes along with the genetic hypothesis. However, there may also be other early influences, such as the position of the foetus in utero, the pre-natal hormonal environment and pregnancy or birth stressors (Fagard 2004; Hopkins et al. 2000a; Hopkins et al. 2001b; Hopkins 1999) that could not be tested in this study.

- Practise and learning

Alternatively to brain lateralization, hand preferences may stem from pratice or learning. There may be no pre-determined tendency to prefer using one particular hand, in relation to genes and brain lateralization; but instead, the subject would learn to prefer using one hand over time, along with practise.

Warren (1980) proposed that the hand preferences stem from practice on a task, i.e. the preferences would be learnt throughout the repetitive trials on a given task. This was formulated with regard to experimental biases, but it can also apply in natural conditions. Indeed, for very complex tasks (e.g. tasks requiring precise fine movements, sequential movements, manipulation, coordination with the two hands or tool-use), the subject may need practise to learn to perform the task efficiently and to develop a preference for one hand (Byrne and Byrne 1991; Schmitt et al. 2008). These hypotheses predict that there should be no preference on the first trials on a new task. The preferences should appear and increase with practise on the task. To test this hypothesis, it is necessary to examine manual preferences on a novel task. In my study, only the "tube task" was novel to the subjects. The bonobos exhibited preferences that reached extreme values (up to 100% use of the preferred hand). This result shows that the preferences were obvious from the first trials on a new task. This indicates that naïve animals showed preferences with no need of intensive training or practice on the task. Thus, my data suggest that the strength of preference did not increase with practice and go against Warren's hypothesis.

Within the same line, some have proposed that the habitual use of the dominant hand produces more consistent hand use (Fagard 2004; Dellatoas and De Agostini 2004). This predicts that hand preference should increase with the general use of one particular hand. Based on this hypothesis, the fact that the bonobos displayed preferences from the first trials on this novel task does not mean that they have not learnt the preference on other tasks, and generalized it to this novel task. To test whether the preference increases with general practise with one hand, I asked whether old subjects exhibited stronger preferences than young subjects that are less experienced. Specifically, I tested the effect of age on hand preference in each of my studies (see section IV.2.2). The results show that the strength of laterality did not increase with age, in any of the actions studied. This suggests that hand preferences did not increase with practise.

The data on consistency over time can also provide interesting clues to determine whether the subjects become more lateralized over time. I compared my data with data collected in the same subjects several years ago (Harrison and Nystrom 2008; Hopkins et al. 1993). In a few cases (e.g. Jill), the subjects were unlateralized in the previous study but lateralized in my study, which goes along with the practise hypothesis. However, in several cases, I did not find this effect, or I even found an opposite effect (subject lateralized in previous study but unlateralized in my study), which does not support the hypothesis. Again, I would like to emphasize that comparisons between studies that did not use exactly the same methods are difficult and imply cautious interpretation.

Finally, hand preferences may stem from learning by imitating other individuals. They may be socially learnt by observing social partners, especially the mother (Fletcher and Weghorst 2005, Uomini 2009). This hypothesis predicts that there should be consistent preferences between the model and the observer. My analysis on kinship showed an absence of correlation between mother and infant, suggesting that, if the infant learns to prefer one hand, it does not learn the hand preference from his mother.

Therefore, my data do not support hypotheses proposing that practise or learning create the hand preferences. Previous data in the literature are also inconclusive regarding this matter, with contradictory findings (e.g. Warren 1980; Sanford et al. 1984, Westergaard and Suomi 1996). Thus, I strongly emphasize the need for studies that investigate the effect of learning and practise on laterality, notably by examining hand use in novel tasks that are complex, take a long time to master and are learnt in a social context.

Moreover, comparing experienced and non-experienced subjects regarding laterality, and regarding efficiency, would also be very important. Indeed, comparing efficiency can help for demonstrating that laterality really increases efficiency and provides advantages. This is a crucial issue that seems to be supported by some recent findings (see section I.1), but it could not be tested in this study as I had no data on efficiency.

- Conclusion

The hand preferences of non-human animals have been suspected to stem from the effects of random external or internal factors. My data indicate that the laterality observed here in bonobos was not significantly affected by such factors. Instead, my findings add to the growing evidence showing that the hand preferences would be natural biological traits. I investigated the mechanisms that may be involved in the determination of the observed preferences, testing hypotheses based on genes and brain lateralization, as well as hypotheses based on practise and learning. My results indicate that the laterality did not stem from the intensive practise on a given task, learning during childhood or observing the mother, which suggests that the laterality observed is unlikely to be a learnt phenomenon. Therefore, the findings indicate that the laterality observed may be related to brain lateralization. They suggest that the brain of bonobos may be lateralized for manual functions. However, my data do not provide support for hypotheses proposing that hand preferences are genetically determined, although there was evidence of early biases. Thus, like in other species, further investigations are necessary to understand the mechanisms underlying laterality. Notably, the possible genetic basis remains to be demonstrated, as well as the possible involvment of other factors like learning, and the extant to which the two mechanisms may act together to create laterality.

Nevertheless, based on my findings and along with most other researchers, I believe that the hand preferences observed can be considered as natural features that stem from Natural Selection (Darwin 1859), and can be valuable clues for discussing evolutionary hypotheses. This is done in the next chapter, where I discuss the effects of task-related factors that have been proposed as selective pressures for the emergence of human handedness, and that may elicit laterality in non-human primates.

Chapter 3: Investigation of the effects of task-related factors

In this chapter, I relate the findings to evolutionary hypotheses on the emergence of human handedness. As seen in section I, brain lateralization would be a means to improve brain efficiency (Rogers 2002; Rogers and Andrew 2002; Rogers et al. 2004; Vallortigara and Rogers 2005), and lateralization would have emerged to improve brain skills to solve increasing cognitive problems (Rogers and Andrew 2002). What are these problems? What caused brain lateralization to appear? Which complex action was a selective pressure for the emergence of handedness? There are many hypotheses that propose different factors to be involved in the emergence of human handedness. Most of these factors are features that are typical of humans, like tool-use, bipedalism or language (see section I.2). Studies in non-human species can tell whether handedness is actually unique to humans or whether it is shared with other primates, and they can help in understanding which factors may have been involved in the selection of handedness.

I studied bonobos, which are a model of particular interest to the topic (see section I.4.1). I asked whether bonobos exhibit manual laterality in a variety of different tasks. I found evidence of significant laterality. I found that the proportion of unlateralized subjects, the strength of laterality and the ABSHI and HI values depended on the task. This result shows that the laterality varied according to the task and indicates that laterality was influenced by the attributes of the task. I investigated which task-related factors, i.e. which attributes of the task, influenced hand preference. I examined the effects of several factors, giving special attention to the factors that can make a task complex and requiring laterality; and that may be selective pressures for handedness. I made the assumption that factors that induce a marked laterality in non-human primates may be factors that have been involved in the emergence of human handedness.

Specifically, I examined and compared laterality between different kinds of actions to assess the effects of the: precision of the action (imprecise versus precise grasping), complex balance control (low versus high postural demands), manipulation (non-manipulative versus manipulative actions), the need to involve the two hands (in different or coordinated complementary roles) (unimanual versus bimanual actions) and the need to use the subordinate hand as postural support (other hand used for support versus other categories of other hand activity).

3.1. Manipulation and bimanual actions:

First, I investigated the effects of manipulation and bimanual actions on laterality. These actions are very complex and have been proposed as selective pressures for the emergence of handedness. I examined several bimanual actions and manipulations, which had rarely been done in bonobos. I considered bimanuality and manipulation together as these two factors are often confounded. I tested the prediction that manipulation and bimanual actions should elicit a marked laterality and a group-level bias, and that the right hand should be preferred for manipulation and for the most active component in bimanual coordination (predictions 4 and 6). The results are discussed below.

- Bimanual tasks without coordination

A commonly studied bimanual task is “bimanual feeding”, which was defined in my study as “feeding while seated with the other hand holding a food item”. No group-level bias was found for this action. The HI values also indicated no preference for using the right hand for feeding while the left hand held food items. This is surprising because I observed a bias toward right hand use (skewed HI values) for feeding when the other hand was inactive or engaged in postural support, and this bias did not appear when the other hand was holding a food item. This finding could suggest a competition between using the right hand for feeding and using the right hand for holding food. Regarding the ABSHI values (strength of laterality), there was no difference between “feeding when the other hand was inactive” and “feeding when the other hand was holding a food item”. This result does not support hypotheses predicting a stronger laterality in bimanual compared to unimanual actions.

Hopkins also reported only individual preferences in bonobos for bimanual feeding. However, he found a trend towards a preferred right hand use (Hopkins et al. 1993c; Hopkins and DeWaal 1995) and found that “of all the bimanual feeding patterns, bonobos most favoured using their right hand for feeding while holding food items with their left hand” (but the bonobos also tended to preferentially feed with the right hand when the other hand was inactive). In these studies, bimanual feeding was also more strongly lateralized than unimanual feeding, which was not found in my study. I have no explanation for this difference between my findings (based on 65 subjects) and that of Hopkins (based on 21 subjects), but none of us found a significant group-level bias in the distribution of the individuals. Therefore, these bonobo data do not support hypotheses predicting that bimanual actions should elicit a group-level right bias.

When considering the data in other species for bimanual feeding, my results are consistent with that of orang-utans that exhibited individual preferences in Peters and Rogers (2008) and no preference in O'Malley and McGrew (2006), but they differ from that of chimpanzees that showed a group-level right bias (Hopkins 1994).

In conclusion, my results on bimanual feeding do not support the hypotheses. However, this bimanual task with no coordination may not be sufficiently complex to elicit a marked laterality. In further work, I have studied bimanual tasks with coordination, which may elicit a stronger laterality.

- Bimanual tasks with coordination and manipulation

In study 1, I examined several behaviours that involved bimanual coordination and manipulation, i.e. manipulation of an object that was held by the other hand. I examined “breaking a piece from the food item”, “peeling the fruit”, “pulling leaves out”, “reaching in the object (dipping) (bimanual)”. Unfortunately, few subjects provided enough data for analysis, the samples were too small to allow analysis ($N \leq 5$) and no notable pattern appeared.

In study 2, I used a task referred to as the “tube task” for studying bimanual coordinated actions. This task combines bimanuality, coordination between the two hands, precise action and manipulation, which makes it the most complex task studied in this PhD research (after tool-use). Thus, it was expected to induce a particularly marked laterality, i.e. strong individual preferences and a group-level bias. In fact, given the previous findings in other species for manipulative bimanual coordinated actions and for the “tube task” in particular (see section I.4.3.3), the “tube task” was the action that was expected to reveal handedness in bonobos.

- I found only individual preferences : the bonobos displayed no group-level bias for the “tube task”. This result is reliable because it was based on a very large sample (more than 65 subjects). Thus my data do not support hypotheses predicting that bimanual coordination should elicit group-level laterality. Moreover, regarding the direction of laterality, there were no more right-handers than left-handers, and the HI values were not skewed toward the right. Thus, the findings do not support the prediction of a right hand preference for the manipulative act in bimanual coordination (prediction 4). One can note that there was a bias towards right hand use in adults (skewed HI values) in the combined sample (lola + zoos) with frequency. This is an interesting effect and one could wonder whether a significant group-level right-bias could have occurred with a larger group of adults. Indeed, there was no bias in the distribution of the individuals (17R versus 9L), but if I had twice this sample, keeping the same ratio, a significant bias would have occurred (34R versus 18L). I encourage further work on manipulative bimanual coordination in adult bonobos.

The next paragraph compares my data with that of other studies that used the same “tube task” (reviewed in section I.4.3.3) (Table 3). When considering the HI values, several previous studies have found significant biases in HI (Hopkins et al. 2001; Hopkins et al. 2004; Hopkins et al. 2005a; Scweitzer et al. 2007; Vauclair et al. 2005), while others have found no bias (Westergaard et al. 1997a; Schmitt et al. 2008), as observed here. With regard to the distribution of the individuals, my finding matches several results that show only individual-level preferences (in gorillas, white-faced capuchins, tufted capuchins, rhesus macaques and De Brazza’s monkeys) (Table 3). However, there are other studies that found significant group-level biases (in orang-utans, infant rhesus macaques, baboons and chimpanzees). The difference with chimpanzees is particularly surprising because the two species are so closely related in the phylogeny (Takahata and Satta, 1997). A large number of chimpanzees have been tested with the “tube task” (N=467) and group-level right biases have been reported in several populations (Hopkins, 1995, 1999; Hopkins *et al.*, 2001, 2004, 2005). The difference between bonobos and chimpanzees is difficult to explain and interpret. It could reflect a real difference in laterality between the two species of *Pan*, or it could be related to differences in the methods used (e.g. number of test sessions, data collection procedure) (Table 3). The chimpanzee studies methods have been criticized, notably on the grounds of lack of data independence (McGrew and Marchant 1997a; Palmer 2002; Palmer 2003). Nevertheless, the biases have been replicated in several studies, in several populations, and both with frequency and bouts (Hopkins 1995; Hopkins 1999; Hopkins et al. 2001c; Hopkins et al. 2004; Hopkins et al. 2005a). I reanalyzed the data of a sample of chimpanzees with the statistics used in my study to enhance the reliability of the comparisons and I confirmed the group-level right bias in the number of individuals and in the HI values. When I compared the HI and ABSHI values between the chimpanzees and the bonobos, I found no difference. However, the age effect (greater right hand use in adults) occurred only in bonobos. I emphasize the need for further investigation to understand the effects of age and species in *Pan*.

- I now consider the strength of laterality for the “tube task”. I found that the laterality was very marked. In fact, the majority of the bonobos were lateralized, with frequency, and this proportion was the highest of all the actions studied in this thesis. Morever, several bonobos exhibited very strong preferences. The ABSHI values were also particularly high. I compared the laterality for the “tube task” with that observed in other actions that are not manipulative or bimanual, to test hypotheses predicting a stronger laterality for manipulation or bimanual coordination compared to simpler actions. The data suggest no stronger laterality for the “tube task” compared to the spontaneous actions (except feeding), but these comparisons were hindered by sample size differences, which hampers interpretation. When comparing the “tube task” and “feeding, general” that had similar and reasonable sample sizes, the laterality was higher for the “tube task”, suggesting a stronger laterality for the manipulative bimanual coordinated task. When further comparing the “tube task” that involved bimanual coordination, with “bimanual feeding” that involved bimanual action with no coordination, the laterality tended to be stronger for the “tube task”. This would go along with hypotheses on manipulation and bimanual coordination and with the hypothesis of task complexity (Fagot and Vauclair 1991).

My results in bonobos are consistent with the findings of “tube task” studies in other species that reported a marked laterality, with strong individual preferences and most individuals being lateralized (with frequency) (review in section I.4.3.3). My findings also tend to match other studies that found a stronger laterality for the "tube task" compared to other tasks (reaching: (Meunier and Vauclair 2007; Schweitzer et al. 2007; Vauclair et al. 2005)). Thus, my data, along with previous data support the hypothesis that bimanual coordination can elicit a strong laterality.

- To summarize, I found individual-level preferences with no goup-level bias. This result does not support hypotheses proposing group-level biases and right hand preference for manipulation and bimanual actions. It also does not support the "postural origins hypothesis" (McNeilage *et al.* 1987) predicting a right hand preference for manipulation and bimanual coordination in higher primates (monkeys and apes). This finding is consistent with several "tube task" studies and with most previous data on bimanual and/or manipulative tasks in apes (e.g. Colell et al. 1995a; Corp and Byrne 2004; Olson et al. 1990; Rogers and Kaplan 1996); with the exception of the group-level right trend reported in gorillas for fine manipulation of a food item held by the other hand (Byrne and Byrne 1991) and the group-level right biases found in chimpanzees for the "tube task" (discussed above).

Regarding the strength, I found a marked laterality (with frequency), with a high proportion of lateralized subjects, high ABSHI values and cases of very strong preferences. This finding matchs those of all other "tube task" studies and also go along with the data for natural bimanual food processing in chimpanzees and gorillas (Byrne and Byrne 1991; Byrne and Corp 2003; Corp and Byrne 2004). Thus, my data and previous data indicate that the "tube task" - like other tasks that are complex and involve bimanuality, coordination between the two hands, precise action and manipulation - elicit a very strong individual-level laterality in non-human primates. This indicates that manipulation and bimanual coordination can induce laterality and suggests that these factors might have been involved in the emergence of handedness. Specifically, the results for the "tube task" and for natural tasks suggest that laterality could have evolved for the complex bimanual coordinated manipulations that are involved in food foraging processes.

- Conclusion regarding bonobos

Because of their proximity to humans regarding several important aspects (see section I.4.1), bonobos may be expected to exhibit a laterality that is the closest to that of humans (compared to other non-human primate species). As seen in section (I.4.2), previous data in bonobos are relatively scarce and they are based on small samples and concern only simple tasks. Notably, there were almost no data on complex tasks, and particularly, there were virtually no data concerning bimanual manipulative coordination, while these actions are the best candidates for revealing handedness. My "tube task" study was the first work on hand use for a manipulative coordinated action in bonobos.

I here compare my data with the scarce previous bonobo data on bimanual coordination and manipulation. Ingmanson (1998; 2005) studied the peeling of sugar cane in wild bonobos. She reported that "individuals tended to be very consistent in the use of either the right or left hand". She found similar numbers of right-handed and left-handed subjects in the whole population. However, "within a unit group, individuals tended to be consistent with each other", with 65% of left-handers for manipulation in the E1 group and 78% of right-handers in the E2 group. However, this work was only published as abstracts and the sample size, methods and results were not available. For "carry and object manipulation", Harrison and Nystrom (2008) found no group-level bias and a rather weak laterality, with 14 unlateralized bonobos for 7 lateralized individuals. However, this result is difficult to interpret because the analysis was perfomed on a category that grouped different actions together, and also because this category grouping manipulative actions also included "carry" ("carry and object manipulation"). For "large objects manipulation" and small objects manipulation", again categories merging different actions together, Shafer (1997) found no significant group-level bias, although there was a slight right trend in both categories (7R vs 2L for large objects and 9R vs 2L for small objects). His results indicate a relatively strong laterality, with 5 unlateralized bonobos for 9 lateralized individuals for large objects and 3 unlateralized bonobos for 11 lateralized individuals for small objects manipulation. Therefore, my data do not differ from the previous data and, together, the findings show no right hand preference, but suggest a strong laterality for manipulation and bimanual coordination in bonobos.

3.2. Precision:

I investigated the effects of the precision of the action and of the grip type on laterality. Performing precise actions requires very developed skills that may require lateralization, so precision has been proposed as a factor involved in the emergence of handedness. I tested the prediction that precise actions should elicit a marked laterality and a group-level right bias in non-human primates (prediction 6''). I also tested whether precise actions elicited a stronger laterality than imprecise actions, as would be expected if precision was an important factor regarding laterality. I examined and compared laterality in actions that involved different degrees of precision and different grip types. The results are discussed below.

- Precise digit use

I first consider the actions that involved precise digit use, with actions that required the subject to insert a finger into a hole. The "tube task" and "inserting a finger (self directed)" showed a strong laterality (they were in the top 30 most lateralized actions), which supports the hypothesis. However, the laterality was particularly weak (lower than that of several other actions and all subjects unlateralized) for "reaching in the fixed object (dip) (unimanual)". This surprising finding might be related to the fact that there were high postural constraints in this task, with a need to use one hand for hanging to the rope while performing the task, which could have acted against laterality (Marchant and McGrew 2007). When considering the distribution of the individuals, no group-level bias occurred in any of the precise digit use dipping actions, and the right hand was not particularly preferred, which does not support the hypotheses.

- Precise versus imprecise actions

To specifically test the effect of the precision of the action on laterality, I compared laterality for reaching for big items and reaching for small items, which was the same behaviour with only the precision varying. The hypothesis predicts a more pronounced laterality with small items (precise action) compared to big items (imprecise action). I found no difference in the ABSHI values. However, the proportion of unlateralized subjects was higher with big than small items, suggesting a stronger laterality for small items. With regard to the direction of laterality, my data suggest a slightly greater right hand use for small items. Thus, the results indicate that the precision of the hand movement could slightly influence laterality. They suggest a slight increase of the strength of laterality and of right hand use with the precision, which would go along with the hypothesis.

- Grip type

Within the same line, I examined different types of grip to test the effect of grip type on laterality. I found very marked effects of the grip type (at the group-level and at the individual-level), indicating a relationship between grip type and hand preference. Specifically, the data suggest that the dorsal grip elicited left hand use, while the lateral grip (1p2mlat) induced right hand use. Therefore, my results suggest a relationship between grip type and hand preference. This finding is consistent with data in chimpanzees; and particularly, Hopkins also found a greater right hand use associated with the use of a thumb-index grip in chimpanzees (Hopkins et al. 2002). The mechanisms underlying these grip types effects are unclear and further investigation is necessary.

In conclusion, my data do not show a group-level right bias for precise actions, so do not indicate a left hemisphere specialization for fine motor skills. In chimpanzees, there are data on hand preference for grasping small items (e.g. Hopkins et al. 2002) that suggest a left hemisphere specialization for fine motor skills. This is also suggested by the data on relative **hand performance** (Hopkins and Russell 2004; Hopkins et al. 2002). Thus, I encourage future studies that examine hand preference for different kinds of precise actions, and compare with imprecise actions.

I also underline the need for studying hand performance, i.e. the relative efficiency of the two hands on precise and complex tasks. Finding that one hand performs better than the other is thought to indicate that the associated hemisphere is specialized for the task considered. Hand performance is commonly used to assess brain lateralization in humans (Fagard 2004), but there are few data in non-human primates, for which preference is generally used as an indicator of brain lateralization. Recording data on relative hand performance, along with hand preference (in the same subjects) can provide crucial clues to the issue of brain lateralization and its relationship to laterality.

3.3. Tool-use:

I wanted to study laterality in bonobos for tool-use because these data are particularly important to the knowledge. Tool-use actions involve extremely high cognitive and motor skills that may require and elicit lateralization. In fact, tool-use has been specifically proposed as the selective pressure for the emergence of human handedness (Frost 1980; Kimura 1979). These hypotheses predict a very marked laterality and a group-level right bias for tool-use in non-human primates (prediction 1). Moreover, laterality should be stronger for tool-use compared to simpler actions.

- “Termite fishing” task

I examined hand use for “dipping a stick into a hole” to extract food, which involved: manipulation, coordination with the objects, a sequential action and a precise action. This was the most complex action studied in this thesis. It implies extremely high cognitive demands so may require and induce laterality.

- The bonobos showed no group-level bias for this task. This result does not match the prediction of a group-level bias for tool-use. It goes along with the findings in wild chimpanzees for “termite fishing” (Marchant and McGrew 1996; McGrew and Marchant 1992; McGrew and Marchant 1999; Nishida and Hiraiwa 1982) (although an almost significant group-level left bias was reported by Lonsdorf and Hopkins (2005)). In captive chimpanzees, a group-level left bias was found in Fletcher and Weghorst (2005) and no bias occurred in Hopkins and Rabinowitz (1997) for similar artificial “termite fishing” tasks. Therefore, my data, along with that of chimpanzees, show no evidence of group-level right bias for using a probe to dip into holes. This goes along with the data for other kinds of tool-use (reviewed in section I.3.1). Therefore, together the tool-use data do not support the hypothesis predicting right hand preference for tool-use (Frost 1980; Kimura 1979).
- With regard to the strength of laterality, I found a very marked laterality for the “termite fishing” task. The lateralized individuals exhibited very strong, often exclusive preferences. Moreover, the proportion of lateralized subjects was high (with frequency), amongst the highest of all the behaviours studied in this thesis. This result supports the

hypothesis predicting a very marked laterality for tool-use. It is consistent with the data in other species for “termite fishing” tasks. Indeed, wild chimpanzees show almost always exclusive use of one hand and most individuals are lateralized (Lonsdorf and Hopkins 2005; Marchant and McGrew 1996; McGrew and Marchant 1992; McGrew and Marchant 1999; Nishida and Hiraiwa 1982). In captivity, most chimpanzees were lateralized in the study of Hopkins and Rabinowitz (1997) and half of them in the study of Fletcher and Weghorst (2005). Therefore, my findings, along with previous chimpanzee data, indicate a very strong laterality for “termite fishing”. This is in line with data on other tool-use tasks (reviewed in section I.4.3.4). Thus, together the data support the hypothesis proposing that tool-use would be a factor that induces laterality.

I compared the laterality for “termite fishing” and for the other actions that are not tool-use, to test the prediction of a stronger laterality for tool-use. Some have indeed suggested that tool-use would markedly differ from the other actions regarding the strength of laterality (Marchant and McGrew 2007; McGrew et al. 2007b; McGrew and Marchant 1997b; McGrew et al. 1999). The strength of laterality (ABSHI values) was greater for the “termite fishing” task compared to “feeding, general” (the other comparisons were not significant and were hindered by sample size differences) but it was similar to that of the “tube task”. This suggests that the laterality may be greater for tool-use compared to non-tool-use activities, but not stronger than manipulation and bimanual coordinated actions. Previous studies (chimpanzees: (Boesch 1991; Sugiyama et al. 1993), orang-utans: (O'Malley and McGrew 2006)) have also found stronger laterality for tool-use compared to simpler actions. Therefore, together the data support the tool-use hypothesis and the hypothesis of task complexity (Fagot and Vauclair 1991) regarding the strength of laterality.

- Other tool-use actions

I assessed hand-use for other tool-use actions, including: using a stone to crack open nuts on an anvil, using a container to take water in the pond, using a container to drink, using a stick to scratch itself, using a rag to clean the wall or ground, using a stick as a rake to get out-of-reach items. Unfortunately, very few individuals performed these actions and the data collected did not allow analysis.

- Conclusion regarding bonobos

Bonobo is a very important species to study because they are very close to humans but may exhibit limited tool-use compared to chimpanzees (see section I.4.1). If tool-use was an important factor in the emergence of handedness, bonobos should exhibit a weaker laterality than chimpanzees (prediction 12). My study was the first work investigating hand use for tool-use in bonobos.

I here consider the scarce previous bonobo data. For “using sticks and grass blades to poke into holes in a log occasionally stocked with honey”, Shafer (1997) found that the bonobo “did this almost exclusively with her left hand”. For “tool-use” defined as “use an object to alter more efficiently the form, position or condition of another object, another individual or the users themselves”, Harrison and Nystrom (2008) found 7 lateralized bonobos (3 left-handed, 4 right-handed) and 5 unlateralized subjects. These data are difficult to interpret as the tool-use actions were not analyzed separately but as a category merging different actions together. However, it should be noted that the preferences found were extremely strong as the lateralized individuals showed almost exclusive preference. Therefore, my data go along with the previous findings in bonobos, and together the results indicate a very marked individual-level laterality, which is present in half of the subjects. This supports the prediction of a marked laterality for tool-use, but not the prediction for a right-hand preference. The laterality may be more marked in chimpanzees who exhibit a majority of lateralized subjects, but the chimpanzees did not show group-level biases either. Thus, there is relatively little difference of laterality between bonobos and chimpanzees, which does not support the hypothesis. I emphasize the need for further investigation on tool-use in bonobos, using different kinds of tool-use actions and larger samples of subjects.

3.4. Throwing:

I recorded hand use for throwing in bonobos because throwing is also an action that implies very sophisticated cognitive skills that may require and evoke laterality. I aimed to test the hypotheses predicting that throwing should induce a marked laterality and right-hand use (Calvin 1983a; Calvin 1983b) (prediction 1).

I observed spontaneous throwing of objects in bonobos. This behaviour was very rare, occurring in the context of displaying/playing/attracting attention of humans. Only three individuals provided enough data for analysis, and the number of data points per subject was small (between 7 and 14). However, the results were interesting as almost all the individuals were lateralized (1R, 1L, 1 Left trend) despite the small sample; and the lateralized individuals exhibited exclusive preferences. This might suggest that throwing would be strongly lateralized in bonobos.

In other species, there are very few data on laterality for throwing and they are mostly from chimpanzees. Strong hand preferences have been reported (Colell et al. 1995b; Hopkins et al. 1993a) and the studies found either individual-level preferences (Colell et al. 1995b; Marchant 1983), a group-level right trend (Hopkins et al. 1993a) or a group-level right bias (Hopkins et al. 2005c). Thus, the data tend to support the hypothesis proposing that throwing can induce laterality.

In bonobos, the only data were from the study of Shafer (1997) and the two subjects displayed no hand preference. Therefore, I highlight the need for future studies to examine hand preference for throwing in bonobos.

3.5. Postural demands:

Several hypotheses propose that postural demands may influence laterality (see section I. 2) (predictions 2, 4, 5, 6, 13 and 14). I first investigated hypotheses proposing that high postural demands (e.g. bipedal posture, tripedal posture) elicit laterality, based on the idea that maintaining balance can be a complex task that requires laterality. I have studied the effects of postural demands on laterality in bonobos. I first tested whether the tasks that involved high postural demands displayed a particularly marked laterality. Namely, I examined and compared postures that had different demands. First, I discuss the findings for the bipedal posture. Then, I consider actions for which one hand was used to support the body weight, with different degrees of postural support: tripedal posture when still, when leaning over water and when moving and seated posture with other hand in postural support. This is followed by a general conclusion on the effects of postural demands on laterality.

- Bipedal posture

Bipedal posture is a highly demanding posture (only two points of support, upright position of the body and high unstability) that may elicit a particular laterality. The “bipedalism hypothesis” proposes that the high requirements of the unstable bipedal posture elicit laterality. It predicts that, when assuming a bipedal posture, non-human primates should exhibit a laterality that is more similar to that of humans, i.e. most individuals being lateralized, strong individual preferences and a group-level right bias.

Given the particularities of bonobos regarding bipedalism (predisposition for bipedalism and most frequent use of bipedalism) (see section I.4.1), they may be expected to exhibit an outstanding form of laterality in bipedal posture compared to other species (prediction 11).

In my studies, few behaviours were performed in bipedal posture, so I had not enough data to analyse the effect of bipedal posture on laterality. Only one action can be discussed : the bipedal branch shaking display of Mwindu. This display was performed while walking or running bipedal on a short distance and was the studied action closest to human bipedalism. Interestingly, Mwindu showed an almost exclusive right-hand use for this action, which goes along with the hypothesis. However, Mwindu was generally right-handed in my studies.

Some previous data in bonobos showed that the bipedal posture enhanced right hand use (compared to tripedal posture) in Hopkins et al. (1993c) (N=8), supporting the bipedalism hypothesis, but another study (De Vleeschouwer et al. 1995) (N=5) found opposite effects (enhanced left hand use). Therefore, my data and previous data do not allow drawing any conclusion regarding laterality in bipedal posture in bonobos. I emphasize the need for future studies that examine laterality when the bonobos adopt a bipedal posture, both in spontaneous and experimental conditions.

- Tripedal posture

I examined laterality when the bonobos were in tripedal posture, a posture that can be considered as demanding since one hand is used for supporting body weight.

- I found a right bias in HI values for reaching for small items, which appeared only in tripedal posture. This finding suggests a preference for using the right hand for performing the action when the left hand was used for support in tripedal posture (still animal). I also considered the behaviours performed when the animal was moving in the environment, with one hand used for support in locomotion. These actions involved higher demands in terms of posture and spatiotemporal coordination and should elicit a strong laterality, but they showed no particular pattern of laterality (except “pushing an object” that had a high mean HI).
- When considering the strength of laterality, I observed a straightforward effect. Namely, there was a very marked laterality in tripedal posture, when still, when leaning over water (particularly for “reaching in the water pond”) and when moving (especially for “pushing an object”). In fact, the actions performed in tripedal posture were amongst the most lateralized actions of this PhD research.

- Seated posture with other hand used for postural support

I considered the seated posture with one hand used for postural support. For “feeding with other hand as postural support”, I found a group-level right bias (in the number of individuals and in the HI values) that did not appear when the other hand was inactive or holding a food item. This result may suggest a preferential use of the right hand for performing the action when the left hand was used for support. However, there was no bias in the tripedal posture where the postural demands are higher than when feeding seated.

Regarding the strength of laterality, I found no particular effect of having one hand used for postural support.

- Comparison between postures

I compared laterality between postures for the behaviour "feeding" (the only behaviour that allowed such analyses). I found no effect of posture on the direction of laterality. Regarding the strength of laterality, there was a significant effect of posture: the laterality was stronger in tripedal compared to seated posture with other hand in postural support. This goes along with the higher postural demands in tripedal posture and supports the idea that laterality may increase with postural demands.

I compared the displacements that presented different degrees of postural demands, with the following gradient: from "quadrupedal displacement holding food/object in one hand" (four points of support), "tripedal displacement holding food/object in one hand" (three points of support), "dragging an object" (three points of support, infrequent posture, implies manoeuvring a large object, twisted posture partly oriented behind) to "pushing an object" (usually done when running fast, implies manoeuvring an object, three points of support). I found a stronger laterality for "pushing an object" compared to quadrupedal displacement, which supports the hypothesis.

- Conclusion on the effects of postural demands

Therefore, my data suggest that the postural demands influenced laterality.

- Regarding the direction, in some cases, the bonobos tended to preferentially act with the right hand when using the left hand for postural support. It is interesting to note that the right hand preference tended to appear only when the left hand was used in postural support (not otherwise). This finding could suggest a division of labor, with the left hand being used for support when the right hand was used for more demanding actions. However, this effect was found only in few cases and cannot be generalized. When considering the "postural origins hypothesis" (McNeilage 1993), my finding goes along with the idea that the right hand preference for postural support, that is allocated to prosimians, may be absent in great apes (possibly replaced by a right hand preference for manipulations and bimanual coordination that remains to be demonstrated) (predictions 4).

- Regarding the strength, my results indicate that the strength of laterality increased with postural demands. This finding is consistent with data in other species (Chapelain et al. 2006) (especially data for bipedal posture: (Hopkins 1993; Larson et al. 1989; Olson et al. 1990; Sanford et al. 1984)). Therefore, my results for these terrestrial actions, along with previous results, support the hypothesis that high postural demands can be a factor that elicits laterality.

Other hypotheses propose that having to use the hands for postural support and locomotion prevents the development of laterality, i.e. that laterality would be hindered by postural constraints (see predictions 5). I tested the prediction that the behaviours performed in the trees should display no laterality, leaving both hands equally able to perform the crucial task of preventing the animal from falling (Marchant and McGrew 2007). I examined laterality in "hanging" and "swinging" that are arboreal behaviours (hanging with one arm when still and balancing/swinging when still, respectively). I found a very weak laterality for these actions. This finding supports the idea that laterality would be disadvantageous in arboreal behaviours, and is consistent with previous findings showing that arboreal behaviours tend to be unlateralized (e.g. Marchant and McGrew 2007).

I also examined the prediction that a strong laterality may occur when the animal is seated on the ground with both hands free, and that the laterality should be more likely to appear when both hands are equally available for use compared to when one hand is used to support body weight (Byrne and Byrne 1991; McGrew and Marchant 1997a). Along with this hypothesis, I found a strong laterality for bimanual actions, which are actions that are necessarily performed when both hands are available. Moreover, when investigating the effect of the other hand activity, for "feeding", I found a stronger laterality when the other hand was inactive compared to "active" (whatever the action), which also supports the hypothesis.

Therefore, my findings are difficult to interpret regarding whether postural demands elicit or hinder laterality. On one hand, I found that high postural support may elicit laterality for behaviours performed on the ground; but on the other hand, I found a weak laterality for actions performed in the trees, a strong laterality for the bimanual "tube task" and a stronger laterality for feeding when both hands were free compared to occupied, which supports the idea that laterality may be hindered by postural constraints. Further investigation are necessary to disentangle the issue of the effects of postural demands on laterality. Notably, work on the effects of high postural demands, particularly in controlled experimental conditions would be very useful. I also emphasize the need for more data on arboreal locomotion and on other behaviours that are performed in the trees.

- Conclusion regarding bonobos

It is interesting to test the effects of postural demands on laterality in bonobos, because they are heavy arboreal primates (meaning high postural constraints in the trees) that also spend a considerable amount of time on the ground manipulating objects (meaning laterality allowed and useful) (Susman 1984).

When considering previous bonobo data, an effect of posture on the direction of laterality has been reported in spontaneous actions (for bipedal posture) (Hopkins et al. 1993c) and in experiments (for various postures) (De Vleeschouwer et al. 1995; Hopkins et al. 1993c) (described in section I.4.2). However, these two studies yielded contradictory and inconclusive results and used small samples (N=5 and N=8 respectively). Thus, my findings add to the previous results to suggest an influence of postural demands on hand preference in bonobos. More investigations, with observation of spontaneous actions, testing in experimental designs and studying larger samples of subjects are necessary to clarify the effects of postural demands on laterality in bonobos.

3.6. Gestural communication:

I did a separate study on gestures because this is an interesting aspect of laterality to study, particularly in bonobos that may exhibit the greatest linguistic skills of primates (see section I.4.1). Communicative manual actions are a particular type of actions that may elicit a specific laterality. Indeed, communicative actions are thought to be controlled by a separate system that is related to language (Hewes 1973). Several hypotheses propose a link between the evolution of handedness and language (see section I.2). I investigated the hypothesis proposing that the left hemisphere is specialized for gestural communication. Specifically, I tested the prediction for a strong laterality and a group-level right bias for gesturing in non-human primates (Corballis 2002; Vauclair 2004) and for a special laterality associated with gestural communication (see predictions 3).

- Spontaneous gestures

In the study on spontaneous actions (study 4a), I examined several behaviours that could be considered as gestures, including: “arm held toward the other (invitation)”, “inviting related behaviours (global)”, “hand clapping”, “arm held toward the other (begging)”, “slapping the floor with one hand”, “banging the glass with one hand” and “stamping the floor with one foot” (only the first two provided enough data for analysis).

- I found a trend towards right hand use for inviting related behaviours (right skewed HI values), which appeared in no other social action. These HI values were the most right skewed of all the social actions studied, but the difference with the other actions was not significant. Moreover, the sample was small and few individuals were significantly lateralized for inviting. Thus, the results provide little support to the hypotheses. Also, there were not enough data for analyzing spontaneous gestures directed towards humans. Therefore, further investigation is necessary to examine laterality for spontaneous gestures and I strongly encourage future studies on this important aspect of laterality in bonobos.

- Induced gestures

I did a specific study to investigate hand use for induced begging gestures. Specifically, I observed inter-specific gestures in an experiment that implied begging towards the observer.

- I found an extremely strong laterality: most subjects were lateralized and exhibited almost exclusive preferences. The laterality was the highest of all the actions studied in this PhD research. In fact, it was significantly different from most other actions; even the "tube task" and the "termite fishing" task that were particularly strongly lateralized. Therefore, my data show an outstandingly pronounced laterality for begging. This effect should be very strong because it appeared despite the small sample size of data per subject (see section II.3). The finding of a strong laterality is consistent with some data in chimpanzees that suggest that more individuals show exclusive hand use for gesturing in comparison to other actions (Hopkins and Wesley 2002). Thus, my finding supports the idea proposing a particular link between laterality and gestural communication.

- However, when considering the direction of laterality, no group-level bias occurred, in the number of individuals or in the HI values. This result does not support the prediction for a right hand preference for gesturing, which would be related to a left-hemisphere specialization (Corballis 2002). My data differ from the results in chimpanzees who were reported to exhibit a group-level right bias for begging for food from the experimenter (Hopkins and Leavens 1998; Hopkins and Wesley 2002; Hopkins et al. 2005b). As for the "tube task", this is a between-species difference for which I have no explanation, and that could either reflect a real difference between the two species or be related to differences in the methods used in the studies (see section I.4.3.5 and II.2.4b).

Finally, I compared laterality in the begging experiment with that observed for other actions and found no difference in the HI values. This finding differs from some data in chimpanzees that suggest that they may be more right-handed for gesturing in comparison to other actions (Hopkins et al. 2005b). In further analysis, I tested whether gesturing elicited a special laterality by comparing hand preference for begging and for other actions within individual. I found no evidence that begging induced a different preference. This finding differs from chimpanzees studies that reported no association between the laterality observed in gestures and that observed in other actions (Hopkins and Leavens 1998; Hopkins and Wesley 2002) (simple reaching, "tube task", bimanual feeding (Hopkins and Cantero 2003)).

- Conclusion regarding bonobos

Bonobo are thought to exhibit the highest linguistic skills amongst non-human primates (Savage-Rumbaugh et al. 1985; 1986). If the evolution of language and handedness were related, bonobos might exhibit the most marked laterality compared to other non-human primate species (prediction 10).

There are some previous data on gestural communication in bonobos (Harrison and Nystrom 2008; Hopkins et al. 1993c; Hopkins and DeWaal 1995; Shafer 1997). These studies reported that most individuals were unlateralized, and none of them found a group-level bias in the number of right-handers and left-handers (although (Hopkins et al. 1993c; Hopkins and DeWaal 1995) reported a group-level right-bias in hand use (right skewed HI values)). My data showing a very strong laterality for gesturing are thus markedly different from previous bonobo data. However, this difference may be due to the fact that previous studies analyzed gestures as categories that merged different actions together (e.g. gestures: “animal uses its hand for communicative purposes, such as clapping to another animal or by itself and begging toward the caretakers or observers” (Hopkins et al. 1993c; Hopkins and DeWaal 1995)), which may hide significant effect of individual actions.

In conclusion, the bonobo data show no group-level bias for gesturing, and my data indicate an extremely strong laterality. I emphasize the need for further investigations that use larger samples of subjects and study several kinds of gestures.

The above paragraphs examined the effects of several different factors individually. It can be noted that these factors are often confounded and interactive, which makes it difficult to isolate them to disentangle the influence of each factor. In the next paragraph, I briefly summarize the findings in relation to the evolutionary hypotheses. Then I present a general conclusion.

3.7. Conclusion on the effects of task-related factors:

I investigated the effects of several task-related factors that have been proposed as selective pressures for the emergence of human handedness, and that may elicit or influence laterality in non-human primates. I found that the strength and direction of laterality varied between actions, both at the group-level and at the individual-level. This result is in keeping with previous data in bonobos and other species (e.g. Chapelain et al. 2006; Harrison and Byrne 2000; Heestand 1986; Hook-Costigan and Rogers 1995; Hopkins et al. 1993c; Hopkins and Pearson 2000; Marchant and McGrew 1996; Sanford et al. 1984; Spinozzi and Cacchiarelli 2000; Spinozzi and Truppa 1999; Teichroeb 1999; Ward and Cantalupo 1997; Westergaard et al. 1998b). The variability between tasks shows that the hand preference was influenced by factors that were related to the task. Specifically, the laterality was affected by: manipulation, bimanual coordination, precision of the action, grip type, tool-use, throwing, postural demands and communication. Below, I summarize my conclusions regarding each of the hypotheses tested.

- My data stand in contrast with the hypotheses about artefactual preferences in captive non-human primates (McGrew and Marchant 1997a; McGrew and Marchant 2001; Warren 1980) (predictions 7). These hypotheses were first formulated by Warren (1980) thirty years ago. In the introduction (sections I.2 and I.4.3.6), I explained why some findings can lead authors to be suspicious about evidence of laterality in captive animals.

Since Warren (1980), research has provided evidence of laterality in spontaneous actions, laterality in wild animals, consistency of hand preference over time and group-level laterality, which refutes several of his hypotheses. However, the effects of the captive settings and human-rearing may remain a matter of controversy until we can demonstrate that captive and wild animals display identical laterality. Finding evidence of group-level laterality in wild animals and showing heritability of laterality will also be crucial to refute these hypotheses. Thus, whilst most data do not support Warrens' hypotheses, these are still topical questions that demand investigation in wild animals.

- My findings go along with the idea that laterality is related to the requirements of the task (Fagot and Vauclair 1991) (predictions 6). With regard to the strength, along with the hypothesis, complex tasks tended to elicit a stronger laterality than simple tasks. Notably, the strength of laterality was particularly marked for the “tube task” and the “termite fishing” task, which were the most complex tasks studied here. However, none of the actions studied induced a group-level bias, and this applied for both simple tasks and very complex tasks. Thus, the “hypothesis of task complexity” (Fagot and Vauclair 1991) is partly supported by my results.

Of all the hypotheses that have been formulated, the “hypothesis of task complexity” (Fagot and Vauclair 1991) is the one that receives most support from the data in non-human primates. Indeed, as seen in the introduction (section I.3), the literature consistently shows that laterality is generally weak for simple tasks and stronger for complex tasks that involve high cognitive skills. The apes show strong hand preferences for complex tasks, and these tasks elicit group-level trends or biases in some cases. Thus, the data support the hypothesis for an increase of the strength of laterality with complexity. Nevertheless, whether the hand preferences observed in complex tasks are actually related to brain lateralization remains a matter of debate. This issue requires further investigation on the mechanisms that underlie laterality (see section IV.2.4).

- Regarding the “tool-use hypothesis” (Frost 1980; Kimura 1979) (predictions 1), my results do not support the prediction of a right hand preference for tool-use. However, the strong laterality observed supports the idea that tool-use can be a factor that elicits laterality.

The “tool-use hypothesis” (Frost 1980; Kimura 1979) is ancient, but it has recently received support from studies in apes that showed that the preferences were extremely strong and the majority of individuals were lateralized for tool-use, and tool-use tasks elicited the strongest laterality compared to other tasks (data reviewed in section I.4.3.4). Therefore, previous data and my data suggest that tool-use can induce a very strong laterality. However, no group-level right bias occurred in any of the studies. Thus, the hypothesis is partly confirmed by the data, and whether tool-use was a crucial selective pressure that created right-handedness in humans remains to be demonstrated.

- When considering the “throwing hypothesis” (Calvin 1983a; Calvin 1983b) (predictions 1), my data only allowed me to tackle this hypothesis, but they suggest a strong laterality for throwing, which would go along with the prediction that throwing can induce laterality.

There are limited previous data on laterality for throwing. They show strong hand preferences (Colell et al. 1995b; Hopkins et al. 1993a) and the studies reported either individual-level preferences (Colell et al. 1995b; Marchant 1983), a group-level right trend (Hopkins et al. 1993a) or a group-level right bias (Hopkins et al. 2005c) in chimpanzees for throwing, which tends to support the hypothesis. Further investigation is necessary before any conclusion can be drawn regarding the “throwing hypothesis” (Calvin 1983a; Calvin 1983b).

- The “hypothesis of bipedalism” (predictions 2) could not be tested with the data available here. It is a pity because bonobos display particular features regarding bipedalism that make them the best candidate to exhibit right-handedness in bipedal posture (see section I.4.1).

There are previous studies that assessed hand use for bipedal reaching (reaching for food placed at height) in non-human primates (review in Westergaard et al. (1998a)). Several authors found that the great apes showed enhanced right hand use to reach from a bipedal posture compared to a tripedal posture (chimpanzees: (Hopkins 1993); gorillas and orang-utans: (Olson et al. 1990)); and group-level right biases were found in chimpanzees (Hopkins 1993) and gorillas (Olson et al. 1990) for bipedal reaching. Thus, there are data suggesting that induced bipedal stance may enhance laterality and right-hand use, and may elicit group-level right biases. This suggests a special link between bipedal posture and laterality, and provides some support to the prediction that non-human primates may exhibit a laterality that is more similar to that of humans when assuming a bipedal posture. Thus, previous research has provided clues suggesting that the requirements of the bipedal posture can elicit laterality and right-hand use. However, the “bipedalism hypothesis” is also based on the release of the hands from postural duties, which is discussed below.

- I assessed the effects of postural demands on laterality, and examined hypotheses proposing that postural demands are a constraint on the development of laterality (predictions 5). My data are difficult to interpret regarding whether postural demands elicit or hinder laterality, but rather support the second idea.

Several hypotheses propose that postural demands are key in the evolution of handedness. I here consider hypotheses proposing that laterality may be disadvantageous in animals that rely on their hands for locomotion and postural support, which is the case of all primates except humans. Indeed, the hands of all primates (except humans) have to be involved in postural support and locomotion, which may compete with using the hands for other activities (such as manipulation or bimanual coordination) and may prevent the development of handedness. Most hypotheses on the evolution of human handedness assume that the hands were released from postural duties when handedness evolved. It makes sense to think that the release of the hands from postural duties may be the key condition for the emergence of human handedness (McGrew and Marchant 1997a; McNeilage 1993). Freeing the hands enabled humans to evolve hands that are outstanding regarding manipulative skills, hereby allowing very precise fine manipulations and tool-use. But most importantly, releasing the hands from postural duties allowed to leave one hand less efficient, while the other hand is specialized and better for performing most tasks. Such a specialization would be disadvantageous when the hands have to be used for postural support and locomotion, as both hands must be equally able to perform this task (Marchant and McGrew 2007). My data provide some support to this idea, and there are previous findings that strongly supports this hypothesis. For instance, behaviours that are performed in the trees tend to show a weak laterality (e.g. Marchant and McGrew 2007), suggesting that laterality is disadvantageous in the arboreal condition. Therefore, I believe that hypotheses on postural constraints in non-human primates are very sensible for explaining why humans differ from non-human primates regarding laterality. Further investigation is necessary to support this idea. Notably, we need more studies that examine laterality for arboreal behaviours and investigate the effects of posture and other hand activity in spontaneous natural actions.

- The prediction of a right hand preference for manipulation and bimanual coordination (predictions 4 and 6') was not supported by my data. However, the laterality observed for these actions was very marked, which supports the idea that these factors can elicit laterality.

In the literature, most studies also fail to find a right hand preference for manipulation. But there are also several positive findings : the group-level right bias found in chimpanzees for the "tube task" (see section I.4.3.3) and the group-level right trend found in gorillas for food processing (Byrne and Byrne 1991). Moreover, like my data, previous data indicate a strong laterality for manipulation and bimanual coordination, which suggests that these may be important factors for eliciting laterality. Thus, this hypothesis remains a matter of investigation.

- Finally, my data support the hypotheses proposing a special link between laterality and communication (predictions 3), as I found an extremely marked laterality for gesturing. However, no group-level right bias occurred, which does not support the prediction for a right hand preference reflecting a left hemisphere specialization for gestural communication.

In chimpanzees, the data consistently show a group-level right bias for induced begging gestures (Hopkins and Leavens 1998; Hopkins and Wesley 2002; Hopkins et al. 2005b), which supports the hypothesis. Therefore, this hypothesis receives some support from the studies in chimpanzees (although there are issues with some of them. see section I.4.3.5 and II.2.4b). More investigation is necessary, notably in other non-human primate species.

- Finally, I aimed to investigate the "social related hypothesis" (Vallortigara and Rogers 2005) (predictions 8) because it is a crucial recent hypothesis, proposing that individual-level laterality can be advantageous, and that group-level laterality may occur when a social alignment is advantageous. This is an important hypothesis because, for a long time, only group-level laterality was considered to reflect brain lateralization. Individual-level laterality was suspected to come from other factors, such as sex, age, experience or experimental biases. However, group-level biases are thought to reflect brain lateralization, based on the assumption that the same hemisphere is specialized for the function considered in all individuals; but there is no a priori reason why all individuals should exhibit the same organisation of lateralized functions. The hypothesis proposes that “if a brain has to be lateralized to function more efficiently, the direction may not matter, only the fact that lateralization is present is important” (Rogers 1989). Thus, individual-level laterality should be advantageous. I wish I could have tested this crucial point, but I had no data that allowed comparing the efficiency of lateralized and unlateralized subjects.

In the literature, there are empirical data suggesting that lateralized subjects would actually be more efficient than unlateralized subjects (in humans, non-human primates and other animals (Faurie 2004; Fragaszy and Mitchell 1990; McGrew and Marchant 1992; McGrew and Marchant 1999; Rogers 2000; Rogers et al. 2004; Sovrano et al. 2005)) and that the direction would not matter. I strongly emphasize the need for future work on this issue. Notably, comparing the efficiency between right-handers and left-handers, and between the minority type and the majority type, would provide crucial clues to the discussion.

I also aimed to test the second prediction of the “social related hypothesis” (Vallortigara and Rogers 2005), which proposes that social factors create alignment of the direction of asymmetries between the individuals. Then, group-level laterality should appear in social related behaviours and laterality should be more marked in social compared to non-social actions. I examined laterality in social behaviours, i.e. hand use for social manual actions, but the data were insufficient and group-level laterality could not be assessed. I encourage future work studying this particular aspect of laterality, because I believe that the social related hypothesis can yield important new light to the evolution of group-level laterality.

In conclusion, I asked which complex action can be the selective pressure for the emergence of handedness. I investigated which factors can make a task complex and requiring laterality. Namely, I tested which attributes of the task influenced hand preference, based on the assumption that the factors that induce a marked laterality in non-human primates may be factors that have been involved in the emergence of human handedness. I found that the actions that induced a strong laterality involved : high postural demands, manipulation, bimanual coordination, tool-use, throwing or gestural communication. Notably, the laterality was particularly marked for the "tube task", the "termite fishing" task and the begging experiment. These findings indicate that the factors involved in these tasks could be important factors regarding laterality, and might have been involved in the emergence of handedness. Since different factors have been found to influence laterality, I suggest that none of the proposed factors, alone, would be "the" selective pressure for the emergence of handedness. Instead, I endorse the view that one function alone could not be responsible for such a sophisticated and important feature as handedness. It seems more likely that laterality would rather result from a combination of factors, acting simultaneously and interactively.

Chapter 4: General conclusion

To summarize, I assessed hand preferences in a large sample of bonobos for a variety of tasks. I found evidence of significant hand preferences in almost all the actions studied. This laterality was not related to artificial biases due to captive settings, experiments or human-rearing, and can possibly reflect a brain lateralization for manual functions. I found no or little effect of sex and age (except the age effect observed in the "tube task"). The laterality was very marked in some cases, with a high proportion of lateralized subjects and preferences that reached extreme values (exclusive use of one hand). However, the proportion of unlateralized subjects was high in many of the actions. Also, the bonobos exhibited individual-level preferences only. No group-level laterality occurred in any of the actions studied (with one exception). The high proportion of unlateralized subjects, as well as the absence of group-level bias, might have been related to small sample size issues in some cases (see section IV.1.2.1). However, the findings can be considered as reliable, because they occurred for many different actions, and with small as well as large samples of subjects and of data points per subject. Moreover, the absence of group-level bias would not be related to the influence of external or internal individual factors (though the effect of age warrants further investigation). Therefore, the absence of group-level bias, demonstrated in this comprehensive study that used a large sample and multi-tasks, is an important finding that suggests that bonobos would display only individual-laterality. My findings thus suggest that this species would not be lateralized at the group-level.

When I compare my results in bonobos with the pattern of laterality observed in humans, the two forms of laterality show marked differences. In humans, the great majority of individuals preferentially use the right hand for most actions, and left-handers and unlateralized subjects are rare (laterality is an extreme 90% group-level right bias) (Annett 1985; Fagard 2004; Faurie 2004; Faurie and Raymond 2004; Vuoksimaa et al. 2009). In bonobos, a significant proportion of individuals were unlateralized (in most of the actions studied). The preferences were only present on an individual basis and they were not necessarily consistent between actions. In fact, I found that none of the actions studied (even the most complex tasks) elicited a laterality that approached the pattern observed in humans. Therefore, my data indicate that the bonobos do not exhibit a laterality that is close to that of humans. These findings are consistent with the previous results in bonobos and other non-human primates species (see section I.3 and review articles : Cashmore et al. 2008; Corballis 1989; Fagard 2004; Fagot and Vauclair 1991; Falk 1987; Harris 2000; Hopkins and Cantalupo 2005; Hopkins 2006; Lehman 1993; McGrew and Marchant 1997a; McNeilage et al. 1987; Papademetriou et al. 2005; Warren 1980). Thus, my results suggest that, despite particular features, bonobos would display a laterality that is not more marked or more similar to human-handedness, compared to other non-human primate species.

My data in bonobos add to the extant database to show that non-human primates exhibit a significant manual laterality, which is however weaker than the extreme form observed in humans. Of course, there are significant methodological differences that must be taken into account (see section I.3.3) as different methods have been used to assess hand preferences in humans and in non-human primates (Harris 2000; Hopkins et al. 1993c). Much simpler tasks are generally used with non-human primates compared to humans, which makes comparisons difficult (Faurie 2004; Uomini 2009). Data suggest that when humans are tested with simple tasks - tasks that are similar to those used with non-human primates -, their preferences are less pronounced (Annett 1985; Fagard 2004; Faurie 2004; Marchant et al. 1995; Seltzer et al. 1990; Steenhuis and Bryden 1989). Within the same line, non-human primates are expected to exhibit a more human-like laterality when they are tested on very complex tasks. My findings (notably studies 2 and 3b), along with previous data (e.g. see section I.3.1) show that, even when tested on complex tasks, non-human primates exhibit a weaker form of laterality compared to that of humans.

Therefore, together my results and previous findings indicate that human right-handedness would have no equivalent in other species, even in bonobos that exhibit relevant close-to-human features (see section I.4.1) (predictions 9, 10 and 11). The lateralities observed in non-human primates may be viewed as incipient forms of handedness (McNeilage 1993). However, my data and previous data - especially that from humans’ closest relatives tested on complex tasks – support the idea that an extreme form of laterality would have developed only in hominids (Byrne and Byrne 1991; Fagard 2004; Marchant and McGrew 2007; McGrew and Marchant 1997a; Warren 1980). Is this outstanding feature related to human-specific traits, such as language, bipedalism, tool-use or release of the hands from postural duties? I investigated this idea in my study using bonobos. I found support for several hypotheses, but none of the hypotheses tested was fully supported by my data, which was also the case with the extant literature in non-human primates. Therefore, whilst my study has provided important new clues to the knowledge, more investigation is necessary to further test these hypotheses and help understanding the evolution of laterality in primates.

Recommendations for future research

This largest and most comprehensive study on laterality in bonobos to date has provided invaluable and so far missing data. These findings yield important new clues for discussing hypotheses on hand preferences in non-human primates and hypotheses on the evolution of human handedness. However, whilst my study answered some questions, several issues remain to be addressed in future studies. In the following paragraph, I propose some recommendations for future research, based on the findings and points raised in this thesis.

- Regarding methodology, there is an ongoing debate over the use of frequency or bouts (see section II.2). I investigated this issue by comparing the two measures (study 2) and found significant differences in laterality between the two techniques : the laterality was stronger with frequency than with bouts (higher ABSHI values and more lateralized subjects). This suggests that the recording method affected laterality (and this effect could not just be related to a sample size difference). Therefore, for future research, I recommend using the conservative approach of analysing independent bouts only. I also underline that using frequency along with bouts, and analyzing bout length, can be a very interesting approach.
- I investigated the effect of the number of data points on individual laterality and found significant effects in some cases (particularly regarding the strength of laterality). Therefore, the sample size is a variable that may influence the results and that should be systematically taken into account when interpreting the data.
- My findings, in accordance with previous results, show that laterality would be sensitive to several factors that are related to the task. This implies that any small between-studies difference in the methods used to assess laterality (e.g. size of the item, posture, other hand activity) can possibly influence the results. I thus strongly emphasize the need to use strictly comparable, standardized measures to allow for comparability between studies and species.

- My data also suggest some influence of factors that are related to the individual (i.e. age), so I highlight the need to systematically take into account the characteristics of the individual when examining laterality.
- In future studies, it would be particularly important to investigate the possible effects of maturation and practise on laterality in growing subjects (using longitudinal approaches). This would provide crucial data to help understanding the mechanisms that underlie laterality.
- My investigation on external factors (i.e. settings and rearing history) yielded negative findings that suggest that these factors did not affect hand preference. Nevertheless, I recommend systematic examination of the possible effect of these factors. I also strongly encourage studies that assess laterality in wild subjects, because comparing captive and wild animals would be essential to definitely prove that the captivity related factors to which the animal is subjected have no effect on its hand preference.
- Previous data and my data show that the hand preferences would be natural biological traits. However, the mechanisms that underlie laterality remain largely unclear. I emphasize the need for more work that investigates whether laterality is based on genes and brain lateralization, is related to practise and learning or results from a combination of genes and learning.
- I particularly encourage studies that examine social learning to investigate recent hypotheses proposing that human right-handedness stems from learning complex technologies (e.g. making and using stone tools) from social partners (Uomini 2009).
- I would like to underline the importance of studying hand performance, as a complementary approach to hand preference. Indeed, comparing the efficiency of the two hands is crucial for determining whether the assumed difference in hand skills is real and whether performance and preference are actually related.
- I investigated the effects of several factors on hand use, but the experimental work allowed at the study sites was limited. I highlight the need for studies using experimental designs that manipulate the factors tested. This would allow disentangling the effects of confounded factors to isolate the role of each one. Notably, it would be important to try to disentangle bimanuality and complexity, which are usually confounded factors. Particularly, there is a need for data on one-handed but complex tasks and on two-handed but simple tasks (Fletcher 2006; Marchant and McGrew 2007). Also, only experiments can allow testing the influence of the factors by grading them (e.g. progressively increasing skillfulness).

- I encourage future studies to use several tasks of varied complexity within the same subjects, as an approach for understanding which factors can elicit laterality.
- My results on the effects of postural demands were rather unclear, while this issue may be key regarding the evolution of laterality in primates. I emphasize the need to collect data for comparing behaviours that are performed on the ground when both hands are freed from postural duties with behaviours that are performed in the trees when postural constraints are high.
- Importantly, I emphasize the need for field studies that would observe the bonobos in natural life conditions. Indeed, comprehensive field studies that encompass a wide range of the behavioural repertoire would be invaluable to the current knowledge.
- Also, experimental work on wild subjects would provide very interesting data.
- I would like to strongly emphasize the need for investigations that aim to demonstrate the advantages of laterality. It is generally admitted that laterality provides important advantages, but the data regarding this issue remain limited. Thus, I encourage studies that compare the efficiency of lateralized and unlateralized subjects. Comparing the efficiency between right-handers and left-handers, and comparing between the minority type and the majority type would also be very important regarding evolutionary hypotheses.
- I also emphasize the need for investigation on the disadvantages and advantages of laterality, which is necessary to investigate the benefits and costs of this feature, and help in understanding the pressures that have acted for and against the emergence of this feature in primates.
- Finally, we have seen that disparity in the methods used to assess hand preference strongly hinders comparison of the findings between humans and non-human primates (Faurie 2004; Uomini 2009). To compare laterality between humans and non-human primates, it is necessary to use comparable measures, which has almost never been done (see Faurie 2004; Westergaard et al. 2000; Uomini 2009). Therefore, future investigations that use the same methods are necessary. In collaboration with Jacqueline Fagard (Université Paris V), we have designed and started an experiment that measured hand preference in human subjects with the "tube task" (Chapelain and Fagard, submitted). This is one of the first times that exactly the same task is used with humans and non-human primates (also see Faurie 2004; Westergaard et al. 2000; Uomini 2009) and this will yield invaluable data for direct comparisons.

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Appendix

Table of contents for the appendix

Table 1app: Review of the previous data in bonobos.

Asterixes indicate experiments. N: number of subjects; Left-handed, Nlat and right-handed: number of subjects that were classified as left-handed, unlateralized and right-handed (when this information was given in the publication); sum lat: number of subjects that were classified as lateralized; B test: p value of the Binomial test that we performed on the numbers of right-handed versus left-handed subjects (whenever possible, i.e. when there was at least 6 lateralized subjects).

authors	task	N	Left handed	Nlat	Right handed	sum lat	B test
Christel et al 1998	* simple reaching for small items with precise grip (posture seated preferred)	3	0	0	3	3	
Christel 1994	* simple reaching for small items with precise grip	5	0	0	5	5	
Colell et al. 1995b	* simple reaching for small items (quadrupedal, seated)	2	0	0	2	2	
De Vleeschouwer et al. 1995	* simple reaching seated. “food thrown on the ground in front of and close to the sitting animal”	5	0	5	0	0	
De Vleeschouwer et al. 1995	* simple reaching tripedal: “food thrown on the ground far from the animal so that it had to walk toward it”	5	0	5	0	0	
De Vleeschouwer et al. 1995	* bipedal reach: posture1: “bipedal standing with support of one hand (food placed 1.5 above the ground)”	5	1	4	0	1	
De Vleeschouwer et al. 1995	* bipedal reach: posture2: “bipedal standing without support (food at the end of a rope, 1.5m above the ground)”	5	3	2	0	3	
De Vleeschouwer et al. 1995	* reach while jumping1: “jumping (food at the end of a rope, 2m above the ground)”	5	2	3	0	2	
De Vleeschouwer et al. 1995	* reach while jumping2 (indirect): “jumping via support on a ridge along the wall (food at the end of a rope, 2.5m above the ground)”	5	1	2	0	1	
De Vleeschouwer et al. 1995	* reach while hanging: posture: “hanging on bars (food at the end of a rope, 2.5m above the ground)”	5	2	2	1	3	
Harrison and Nystrom 2008	“carry and object manipulation: transport an object for at least 3 consecutive steps; manoeuvre an object for some purpose other than feeding or tool use”	22	2	14	5	7	0.453
Harrison and Nystrom 2008	feeding	22	5	8	9	14	0.424
Harrison and Nystrom 2008	gesture: “use hand for communicative purposes towards another (e.g. reconciliatory), keeper or public (e.g. begging)”	22	1	18	2	3	
Harrison and Nystrom 2008	leading limb (hand)	22	1	18	3	4	

table 1app continued	**task**	**N**	**Left handed**	**Nlat**	**Right handed**	**sum lat**	**B test**
Harrison and Nystrom 2008	leading limb (foot)	22	0	15	1	1	
Harrison and Nystrom 2008	scratching itself	22	0	18	3	3	
Harrison and Nystrom 2008	tool use: “use an object to alter more efficiently the form, position or condition of another object, another individual or the users themselves”	22	3	5	4	7	1
Harrison and Nystrom 2008	reaching						
Hopkins and De Waal 1995	bimanual feeding: “feed with one hand, the other hand is holding food”	10					
Hopkins and De Waal 1995	carrying: “the ape uses one or both hands to grasp an object or food item and physically carry it to a different location in the cage. This includes dragging objects such as the plastic drums placed in the cage. A minimum of 3 strides must occur for carrying to be recorded”	10	4	6	0	4	
Hopkins and De Waal 1995	face touching itself	10	2	8	0	2	
Hopkins and De Waal 1995	gestures: “subject uses its hands for communicative purposes. This includes instances in which the subjects clap each other or by themselves. It also includes begging gestures directed toward caretakers or observers”	10	0	5	0	0	
Hopkins and De Waal 1995	leading limb (hand, foot if bipedalism)	10	0	3	7	7	0.016
Hopkins and De Waal 1995	self touching	10	0	8	2	2	
Hopkins and De Waal 1995	simple reaching (tripedal?)	10	3	7	0	3	
Hopkins and De Waal 1995	feeding						
Hopkins et al. 1993	bimanual feeding: “feed with one hand, the other hand is holding food”						
Hopkins et al. 1993	* bipedal reaching for a raisin placed on the cage mesh, both feet on the floor. Food 1.3 to 1.6m above ground.	8					
Hopkins et al. 1993	carrying: “animal uses one or both hands to grasp an object, an infant, or a food item and physically carry it to a different location in the cage. A minimum of 3 strides must occur for carrying to be recorded”	11	3	8	0	3	
Hopkins et al. 1993	face touching itself	11	1	8	2	3	

table 1app continued	**task**	**N**	**Left handed**	**Nlat**	**Right handed**	**sum lat**	**B test**
Hopkins et al. 1993	feeding	11					
Hopkins et al. 1993	gestures: “animal uses its hands for communicative purposes, such as clapping to another animal or by itself and begging toward the caretakers or observers”	11	2	5	2	4	
Hopkins et al. 1993	leading limb	11	0	6	5	5	
Hopkins et al. 1993	self touching	11	2	8	0	2	
Hopkins et al. 1993	simple reaching tripedal (spontaneous)	11	1	8	2	3	
Hopkins et al. 1993	* simple reaching tripedal (experimental): “locomote to the food and reach from triped, food thrown to the ani. Midline”	8					
Shafer 1997	self touching	14	1	9	4	5	
Shafer 1997	touching others	14	2	9	3	5	
Shafer 1997	hitting/knocking	14	1	11	2	3	
Shafer 1997	throwing	14	0	2	0	0	
Shafer 1997	feeding	14	3	3	8	11	0.227
Shafer 1997	object manipulation (large object): “the manipulation of any object (usually large or heavy) with the whole arm or arms, distinguished by elbow flexion, as opposed to finger/wrist flexion”	14	2	5	7	9	0.18
Shafer 1997	object manipulation (small object): “the manipulation of any object with just the hands or fingers, ditinguished by wrist and/or finger flexion. This would include small tool use”	14	2	3	9	11	0.065
Shafer 1997	digging/sifting	14	1	3	3	4	
Shafer 1997	gesture: “any hand motion interpreted as signalling to another bonobo or as solitary gestures. There were many more gestures performed than were scored in this category because behaviors listed in other categories were often used to signal as well. This category deserves a separate study. Gestures that were scored included hand and finger waves, hand flaps, arms sweeps in various directions, "high fives" (clapping one hand with that of another bonobo), begging, and gestures that seemed to say "stop", "go away", or "leave me alone" or, more often "come play" (both playful and sexual solicitation)”	14	0	9	1	1	
Shafer 1997	hanging	14	1	9	3	4	
Shafer 1997	tool use: “using sticks and grass blades to poke into holes in a log occasionally stocked with honey”	2	1	0	0	1	

table 1app continued	**task**	**N**	**Left handed**	**Nlat**	**Right handed**	**sum lat**	**B test**
Shafer 1997	other/miscellaneous: “any hand behaviors not listed above. These included right over left hand or vice versa, chase or catch an insect, water play, water drink, give or accept a food gift, poke fingers into holes or through the mesh of cage or through a toy chain, flexing and extending fingers, catch urine or feces, regurgitate into hand. Bimanual behaviors included standing on hands, a kind of "cartwheel", and "angels in the snow" on the grass”						
Shafer 1997	all spontaneous behaviours together	14	2	1	11	13	0.022
Ingmanson 1998, 2005	picking up an object	?					
Ingmanson 1998, 2005	branch dragging	?					
Ingmanson 1998, 2005	grooming	?					
Ingmanson 1998, 2005	“the peeling of sugar cane, where one hand is used in power grip and the other for small manipulations”.	?					

Table 2app: Study 1: Individual raw data for overall limb use.
This table is given as additional information because overall limb use has sometimes been analyzed in other studies, but these data were not discussed in the thesis because we believe it is difficult to interpret data that combine different actions together (see section I.3.3).
Data for overall limb use: all analyzed non-social actions merged together. Right hand: number of right hand responses, Left hand: number of left hand responses; total: total number of observations. B test: p value of the Binomial test performed on the number of right versus left hand trials. Cat: category in which the individual was classified based on Binomial test: L: left-handed, R: right-handed, Nlat: not lateralized.

		Right hand	**Left hand**	**total**	**HI**	**ABSHI**	**B test**	**cat**
lola	Api	25	66	91	-0,451	0,451	2,00E-05	L
lola	Beni	31	28	59	0,051	0,051	0,795	Nlat
lola	Bili	35	25	60	0,167	0,167	0,245	Nlat
lola	Bisengo	25	12	37	0,351	0,351	0,047	R
lola	Boende	38	61	99	-0,232	0,232	0,027	L
lola	Bolobo	68	48	116	0,172	0,172	0,077	Nlat (R trend)
lola	Dilolo	48	43	91	0,055	0,055	0,675	Nlat
lola	elikia	15	13	28	0,071	0,071	0,851	Nlat
lola	Fizi	42	42	84	0	0	1,087	Nlat
lola	Ilebo	76	69	145	0,048	0,048	0,618	Nlat
lola	Isiro	70	30	100	0,4	0,4	8,00E-05	R
lola	Kalina	39	29	68	0,147	0,147	0,275	Nlat
lola	Kasongo	67	32	99	0,354	0,354	6,00E-04	R
lola	Kikongo	39	53	92	-0,152	0,152	0,175	Nlat
lola	Kubulu	108	22	130	0,662	0,662	8,00E-15	R
lola	Likasi	24	52	76	-0,368	0,368	0,002	L
lola	Lisala	36	22	58	0,241	0,241	0,087	Nlat (R trend)
lola	Lodja	45	30	75	0,2	0,2	0,105	Nlat
lola	Lukaya	43	37	80	0,075	0,075	0,576	Nlat
lola	Luozi	4	7	11	-0,273	0,273	0,549	Nlat
lola	Mabali	25	23	48	0,042	0,042	0,885	Nlat
lola	Maluku (Malou)	28	33	61	-0,082	0,082	0,609	Nlat
lola	Maniema	61	47	108	0,13	0,13	0,211	Nlat
lola	Manono	66	62	128	0,031	0,031	0,791	Nlat
lola	Matadi	47	53	100	-0,06	0,06	0,617	Nlat
lola	Max	62	86	148	-0,162	0,162	0,058	Nlat (L trend)
lola	Maya	55	50	105	0,048	0,048	0,696	Nlat
lola	Mbandaka	32	44	76	-0,158	0,158	0,207	Nlat
lola	Mbano	10	16	26	-0,231	0,231	0,327	Nlat
lola	Mimia (mimi)	9	15	24	-0,25	0,25	0,307	Nlat
lola	Mixa	80	34	114	0,404	0,404	2,00E-05	R
lola	Nioki	17	58	75	-0,547	0,547	2,00E-06	L
lola	Opala	62	42	104	0,192	0,192	0,062	Nlat (R trend)
lola	Pole	31	13	44	0,409	0,409	0,01	R
lola	Salonga	81	74	155	0,045	0,045	0,63	Nlat
lola	Semendwa	29	32	61	-0,049	0,049	0,798	Nlat
lola	Tatango	28	27	55	0,018	0,018	1	Nlat

table 2app continued		**Right hand**	**Left hand**	**total**	**HI**	**ABSHI**	**B test**	**cat**
lola	Tembo	38	39	77	-0,013	0,013	1	Nlat
lola	Tshilomba	19	20	39	-0,026	0,026	1	Nlat
lola	Yolo (Iolo)	62	5	67	0,851	0,851	1,00E-13	R
zoos	Banbo	7	14	21	-0,333	0,333	0,189	Nlat
zoos	Banya	218	61	279	0,563	0,563	7,00E-22	R
zoos	Bokela	78	118	196	-0,204	0,204	0,005	L
zoos	Cheka	82	41	123	0,333	0,333	3,00E-04	R
zoos	Chipita	37	32	69	0,072	0,072	0,63	Nlat
zoos	Daniela	70	62	132	0,061	0,061	0,543	Nlat
zoos	David	61	47	108	0,13	0,13	0,211	Nlat
zoos	Diatou	34	91	125	-0,456	0,456	3,00E-07	L
zoos	Diwani	26	127	153	-0,66	0,66	4,00E-17	L
zoos	Jasiri	337	169	506	0,332	0,332	7,00E-14	R
zoos	Jasongo	124	37	161	0,54	0,54	4,00E-12	R
zoos	Jill	508	317	825	0,232	0,232	3,00E-11	R
zoos	Kakowet	47	167	214	-0,561	0,561	6,00E-17	L
zoos	Keke	100	93	193	0,036	0,036	0,666	Nlat
zoos	Khaya	6	12	18	-0,333	0,333	0,238	Nlat
zoos	Kichele	77	126	203	-0,241	0,241	7,00E-04	L
zoos	Kirembo	95	11	106	0,792	0,792	8,00E-18	R
zoos	Kombote	19	5	24	0,583	0,583	0,007	R
zoos	Kumbuka	236	385	621	-0,24	0,24	2,00E-09	L
zoos	Liboso	239	155	394	0,213	0,213	3,00E-05	R
zoos	Lina	205	54	259	0,583	0,583	7,00E-22	R
zoos	Lingala	262	384	646	-0,189	0,189	2,00E-06	L
zoos	Lomela	326	352	678	-0,038	0,038	0,337	Nlat
zoos	Louisoko	92	26	118	0,559	0,559	8,00E-10	R
zoos	Lucuma	47	45	92	0,022	0,022	0,917	Nlat
zoos	Luo	110	132	242	-0,091	0,091	0,177	Nlat
zoos	Mixi	13	10	23	0,13	0,13	0,678	Nlat
zoos	Mobikisi	147	167	314	-0,064	0,064	0,284	Nlat
zoos	Mwindu	429	278	707	0,214	0,214	1,00E-08	R
zoos	Zorba	7	19	26	-0,462	0,462	0,029	L
zoos	Zuani	165	176	341	-0,032	0,032	0,588	Nlat
	Total	5924	5207	11131				
	Mean			156.775	0,051	0,247		
	SD			175.124	0,32	0,209		
	Minimum			11	-0,66	0		
	Maximum			825	0,851	0,851		

Table 3app: Study 1: Behaviours and behavioural patterns ranked according to their HI values
(lola + zoos sample)

behaviour	condition	mean HI
swinging + hanging	other hand inactive	-0.294
swinging	other hand inactive	-0.209
hanging	other hand inactive	-0.209
crossing arms		-0.055
tripedal movement while feeding with one hand	other hand: postural support	-0.045
reach in the water pond		-0.025
crossing legs		-0.009
tripedal movement holding food/object in one hand	other hand: postural support	0.009
feeding	posture: seated, other hand: holding a food item	0.017
tripedal movement holding food/object in one hand + while feeding	other hand: postural support	0.022
turning (standing)		0.03
quadrupedal movement holding food/object in one hand	other hand: postural support	0.054
feeding	global	0.066
reaching for big items	global	0.078
reaching for small items (seeds)	posture: seated, other hand: inactive	0.086
feeding	posture: triped, other hand: postural support	0.087
inserting a finger (self directed)		0.093
reaching for big items	posture: triped, other hand: postural support	0.103
dragging an object	other hand: postural support	0.107
pulling grass out	global	0.113
feeding	posture: seated, other hand: inactive	0.117
reaching in the fixed object (dipping) (unimanual)		0.138
feeding	posture: seated, other hand: postural support	0.139
reaching for small items (seeds)	global	0.14
foetus position		0.146
reaching for small items (seeds)	posture: seated, other hand: postural support	0.155
reaching for small items (seeds)	posture: triped, other hand: postural support	0.259
pushing an object	other hand: postural support	0.281
reaching for small items (seeds)	global. grip type: lateral grip (1p2mlat)	0.312
raking seeds on the floor	posture: seated	0.403
raking seeds on the floor	global	0.502

Table 4app: Study 1: Results of the comparisons between the main spontaneous non-social actions.
Results of MW tests: p values for the paired comparisons of HI, ABSHI and total (number of data points per subject) between behaviours. Only significant results are shown; all other comparisons yielded non-significant results (MW p>0.05).

Behaviour	MW test
Feeding versus:	- tripedal move U=298, p=0.004 for ABSHI, U=91, p<0.001 for total - quadrupedal move U=582, p<0.001 for ABSHI, U=349 p<0.001 total - push object U=86.5, p<0.001 for ABSHI, U=148.5, p=0.006 for total - reach big U=489.5, p=0.002 for ABSHI, U=213.5, p<0.001 total - reach small U=715, p=0.007 for ABSHI - pull grass U=105, p<0.001 for ABSHI, U=85.5, p<0.001 for total - reach in water U=82, p=0.019 for ABSHI, U=27, p=0.001 for total - inserting finger (self directed) U=88, p=0.027 for ABSHI, U=54, p=0.004 for total - rake seeds U=66, p=0.002 for ABSHI
swinging + hanging versus:	- tripedal move U=71, p=0.032 for ABSHI, U=66.5, p=0.020 for total - quadru move U=154, p=0.049 for HI - reach big U=105, p=0.015 for HI - reach small U=94.5, p=0.001 for HI - pull grass U=28.5, p=0.005 for ABSHI - rake seeds U=15, p=0.008 for HI and ABSHI - reach in fixed object U=21, p=0.012 for HI - feeding U=182, p<0.001 for HI, U=327.5, p=0.049 for total - push object U=39.5, p=0.048 for HI, U=21, p=0.003 for ABSHI
Reach in the fixed object versus:	- rake seeds U=7, p=0.015 for ABSHI - inserting finger (self directed) U=8.5, p=0.045 for ABSHI - pull grass U=16, p=0.020 for ABSHI - push U=11.5, p=0.011 for ABSHI
Rake seeds on the floor versus:	- feed U=66, p=0.002 for ABSHI - quadru move U=45, p=0.014 for ABSHI - swinging+hanging U=15, p=0.008 for ABSHI - reach big U=37, p=0.017 for ABSHI, U=24.5, p=0.003 for total - reach small U=43, p=0.010 for ABSHI - reach in the fixed obj U=7, p=0.015 for ABSHI
Pull grass out versus:	- feed U=105, p<0.001 for ABSHI, U=85.5, p<0.001 total - quadru move U=92, p=0.019 for ABSHI - swinging+hanging U=28.5, p=0.005 for ABSHI - reach big U=74.5, p=0.022 for ABSHI - reach small U=93, p=0.016 for ABSHI - reach in fixed obj U=16, p=0.020 for ABSHI
Push versus:	- feed U=86.5, p<0.001 for ABSHI, U=148.5, p=0.006 for total - quadru move U=74, p=0.011 for ABSHI - swinging+hanging U=21, p=0.003 for ABSHI - reach big U=60.5, p=0.014 for ABSHI - reach small U=77.5, p=0.012 for ABSHI, U=91.5, p=0.034 for total - reach in fixed obj U=11.5, p=0.011 for ABSHI

Table 5app: Study 1: Behaviours and behavioural patterns ranked according to their ABSHI values.
(lola + zoos sample)

behaviour	condition	mean ABSHI
hanging	other hand inactive	0.209
foetus position		0.242
feeding	global	0.27
feeding	posture: seated, other hand: postural support	0.284
feeding	posture: seated, other hand: holding a food item	0.288
swinging	other hand inactive	0.29
swinging + hanging	other hand inactive	0.299
reach in the fixed object (dipping) (unimanual)		0.335
feeding	posture: seated, other hand: inactive	0.363
turning (standing)		0.378
feeding	posture: triped, other hand: postural support	0.415
reaching for small items (seeds)	global	0.43
reaching for small items (seeds)	posture: seated, other hand: inactive	0.433
crossing arms		0.448
reaching for small items (seeds)	posture: triped, other hand: postural support	0.448
reaching for big items	global	0.452
quadrupedal movement holding food/object in one hand	other hand: postural support	0.456
reaching for big items	posture: triped, other hand: postural support	0.463
reaching for small items (seeds)	global. grip type: lateral grip (1p2mlat)	0.464
tripedal movement holding food/object in one hand + while feeding		0.473
dragging an object	other hand: postural support	0.485
reaching for small items (seeds)	posture: seated, other hand: postural support	0.492
crossing legs		0.532
tripedal movement holding food/object in one hand	other hand: postural support	0.55
tripedal movement while feeding with one hand	other hand: postural support	0.567
reach in the water pond		0.569
insert finger (self directed behav)		0.599
pushing an object	other hand: postural support	0.693
pulling grass out	global	0.706
raking seeds on the floor	posture: seated	0.736
raking seeds on the floor	global	0.787

Table 6app: Study 1: Results of the tests on the effect of the posture and action of the other hand for “feeding”.
Results of W tests comparing the HI and ABSHI between postural patterns: p values for the paired comparisons of: Tripedal, other hand postural support (still); Seated, other hand postural support; Seated, other hand holds a food item; Seated, other hand inactive. Significant p values are in bold.

	Tripedal, other hand postural support	**Seated, other hand postural support**	**Seated, other hand holding a food item**
Tripedal, other hand postural support			
Seated, other hand postural support	W, N=30, z=-2.489, p=0.013 for total z=-0.249, p=0.804 for HI, **z=-2.541, p=0.011 for ABSHI**		
Seated, other hand holding a food item	W, N=29, z=-0.633, p=0.527 for total z=-0.40, p=0.689 for HI, z=-1.308, p=0.191 for ABSHI	W, N=38, z=-2.687, p=0.007 for total z=-0.46, p=0.645 for HI, z=-0.807, p=0.420 for ABSHI	
Seated, other hand inactive	W, N=31, z=-2.255, p=0.024 for total z=-0.247, p=0.805 for HI, z=-1.45, p=0.147 for ABSHI	W, N=45 z=-0.133, p=0.894 for HI, z=-1.485, p=0.137 for ABSHI	W, N=37 z=-1.007, p=0.314 for HI, z=-0.713, p=0.476 for ABSHI

Table 7app: Study 1: Descriptive data for each sex, age and rearing group for the main spontaneous non-social actions.

Behaviour	**Group considered**	**Group distribution and B test on R vs L**	**Mean number of data points per subject**	**Mean HI and T test**	**Mean ABSHI**
Overall limb use	Sex male N=37	10R, 5L, 22Nlat p=0.302	122.676	0.067 T p=0.253	0.26
Overall limb use	Sex female N=34	8R, 7L, 19Nlat p=1	193.882	0.033 T p=0.507	0.233
Overall limb use	Age regpt1 gp1 N=31	6R, 3L, 22 Nlat p=0.508	112.258	0.064 T p=0.223	0.223
Overall limb use	Age regpt1 gp2 N=40	12R, 9L, 19Nlat p=0.664	191.275	0.041 T p=0.464	0.265
Overall limb use	Age regpt2 gp1 N=43	10R, 8L, 25Nlat p=0.815	127.419	0.036 T p=0.460	0.250
Overall limb use	Age regpt2 gp2 N=28	8R, 4L, 16Nlat p=0.388	201.857	0.074 T p=0.251	0.242
Overall limb use	Rearing gp1 N=27	11R, 5L, 11Nlat p=0.210	273.852	0.113 T p=0.078	0.260
Overall limb use	Rearing gp 2,3 N=44	7R, 7L, 30Nlat p=1.209	84.932	0.013 T p=0.792	0.239
Overall limb use	Age regpt3 gp1 N=31	6R, 3L, 22Nlat p=0.508	112.258	0.064 T p=0.223	0.223
Overall limb use	Age regpt3 gp2 N=12	4R, 5L, 3Nlat p=1	166.583	-0.035 T p=0.762	0.32
Overall limb use	Age regpt3 gp3 N=28	8R, 4L, 16Nlat p=0.388	201.857	0.074 T p=0.251	0.242
Feeding, general	Sex male N=36	9R, 3L, 24Nlat p=0.146	61.194	0.116 T p=0.064	0.288
Feeding, general	Sex female N=29	3R, 3L, 23Nlat p=1.313	81.035	0.004 T p=0.951	0.249
Feeding, general	Age regpt1 gp1 N=26	**7R, 0L,** 19Nlat **p=0.016**	54.923	0.153 T **p=0.012**	0.256

table 7app continued	**Group considered**	**Group distribution and B test on R vs L**	**Mean number of data points per subject**	**Mean HI and T test**	**Mean ABSHI**
Feeding, general	Age regpt1 gp2 N=39	5R, 6L, 28Nlat	80.128	0.008 T p=0.901	0.28
Feeding, general	Age regpt2 gp1 N=38	8R, 2L, 28Nlat p=0.109	63.053	0.095 T **p=0.047**	0.229
Feeding, general	Age regpt2 gp2 N=27	4R, 4L, 19Nlat p=0.273	79.889	0.025 T p=0.771	0.328
Feeding, general	Rearing gp1 N=24	6R, 1L, 17Nlat p=0.125	91.333	0.095 T p=0.198	0.274
Feeding, general	Rearing gp 2,3 N=41	6R, 5L, 30Nlat p=1	57.585	0.049 T p=0.391	0.268
Feeding, general	Age regpt3 gp1 N=26	**7R, 0L,** 19Nlat **p=0.016**	54.923	0.153 T **p=0.012**	0.256
Feeding, general	Age regpt3 gp2 N=12	1R, 2L, 9Nlat	80.667	-0.031 T p=0.667	0.17
Feeding, general	Age regpt3 gp3 N=27	4R, 4L, 19Nlat p=1.273	79.889	0.025 T p=0.771	0.328
Reaching for small items, general	Sex male N=15	4R, 2L, 9Nlat p=0.688	39.40	0.181 T p=0.199	0.483
Reaching for small items, general	Sex female N=18	6R, 3L, 9Nlat p=0.508	85.278	0.107 T p=0.378	0.387
Reaching for small items, general	Age regpt1 gp1 N=6	1R, 0L, 5Nlat	40.667	0.313 T **p=0.027**	0.339
Reaching for small items, general	Age regpt1 gp2 N=27	9R, 5L, 13Nlat p=0.424	69.704	0.102 T p=0.334	0.451
Reaching for small items, general	Age regpt2 gp1 N=12	3R, 2L, 7Nlat	52.417	0.201 T p=0.169	0.439
Reaching for small items, general	Age regpt2 gp2 N=21	7R, 3L, 11Nlat p=0.344	71.286	0.106 T p=0.368	0.426
Reaching for small items, general	Rearing gp1 N=21	9R, 2L, 10Nlat p=0.065	87.762	0.255 T **p=0.013**	0.394

table 7app continued	**Group considered**	**Group distribution and B test on R vs L**	**Mean number of data points per subject**	**Mean HI and T test**	**Mean ABSHI**
Reaching for small items, general	Rearing gp 2,3 N=12	1R, 3L, 8Nlat	23.58	-0.059 T p=0.727	0.494
Reaching for small items, general	Age regpt3 gp1 N=6	1R, 0L, 5Nlat	40.667	0.313 T p=**0.027**	0.339
Reaching for small items, general	Age regpt3 gp2 N=6	2R, 2L, 2 Nlat	64.167	0.09 T p=0.743	0.539
Reaching for small items, global	Age regpt3 gp3 N=21	7R, 3L, 11Nlat p=0.344	71.286	0.106 T p=0.368	0.426
Quadrupedal movement	Sex male N=17	0R, 2L, 15Nlat	15.88	-0.081 T p=0.487	0.408
Quadrupedal movement	Sex female N=15	4R, 1L, 10Nlat	24.20	0.207 T p=0.174	0.511
Quadrupedal movement	Age regpt1 gp1 N=13	2R, 0L, 11Nlat	10.846	0.141 T p=0.354	0.462
Quadrupedal movement	Age regpt1 gp2 N=19	2R, 3L, 14Nlat	25.895	-0.005 T p=0.966	0.452
Quadrupedal movement	Age regpt2 gp1 N=18	3R, 1L, 14Nlat	15.556	0.105 T p=0.43	0.485
Quadrupedal movement	Age regpt2 gp2 N=14	1R, 2L, 11Nlat	25.214	-0.011 T p=0.934	0.419
Quadrupedal movement	Rearing gp1 N=10	4R, 2L, 4Nlat	40.3	0.171 T p=0.371	0.481
Quadrupedal movement	Rearing gp 3 N=22	0R, 1L, 21Nlat	10.455	0.001 T p=0.993	0.445
Quadrupedal movement	Age regpt3 gp1 N=13	2R, 0L, 11Nlat	10.846	0.141 T p=0.354	0.462
Quadrupedal movement	Age regpt3 gp2 N=5	1R, 1L, 3Nlat	27.80	0.012 T p=0.97	0.545
Quadrupedal movement	Age regpt3 gp3 N=14	1R, 2L, 11Nlat	25.214	-0.011 T p=0.934	0.419

table 7app continued	**Group considered**	**Group distribution and B test on R vs L**	**Mean number of data points per subject**	**Mean HI and T test**	**Mean ABSHI**
Reaching for big items, general	Sex male N=12	1R, 11Nlat	13.167	0.045 T p=0.741	0.372
Reaching for big items, general	Sex female N=14	4R, 2L, 8Nlat p=0.688	17.143	0.107 T p=0.508	0.52
Reaching for big items, general	Age regpt1 gp1 N=8	1R, 7Nlat	7.625	0.093 T p=0.622	0.438
Reaching for big items, general	Age regpt1 gp2 N=18	4R, 2L, 12Nlat p=0.688	18.722	0.072 T p=0.583	0.458
Reaching for big items, general	Age regpt2 gp1 N=13	2R, 11Nlat	8.846	0.023 T p=0.865	0.381
Reaching for big items, general	Age regpt2 gp2 N=13	3R, 2L, 8Nlat p=0.	21.769	0.134 T p=0.425	0.523
Reaching for big items, general	Rearing gp1 N=11	5R, 1L, 5Nlat p=0.219	24.546	0.138 T p=0.399	0.458
Reaching for big items, general	Rearing gp 2,3 N=15	1L, 14Nlat	8.533	0.035 T p=0.808	0.447
Reaching for big items, general	Age regpt3 gp1 N=8	1R, 7Nlat	7.625	0.093 T p=0.622	0.438
Reaching for big items, general	Age regpt3 gp2 N=5	1R, 4Nlat	10.80	-0.089 T p=0.674	0.289
Reaching for big items, general	Age regpt3 gp3 N=13	3R, 2L, 8Nlat	21.769	0.134 T p=0.425	0.523
tripedal movement + while feeding	Sex male N=15	1R, 3L, 11Nlat	9.733	0.008 T p=0.960	0.425
tripedal movement + while feeding	Sex female N=12	3R, 3L, 6Nlat p=1.313	19.167	0.04 T p=0.839	0.532
tripedal movement + while feeding	Age regpt1 gp1 N=12	1R, 1L, 10Nlat	11.583	0.129 T p=0.308	0.318
tripedal movement + while feeding	Age regpt1 gp2 N=15	3R, 5L, 7Nlat p=0.727	15.80	-0.064 T p=0.735	0.596

table 7app continued	**Group considered**	**Group distribution and B test on R vs L**	**Mean number of data points per subject**	**Mean HI and T test**	**Mean ABSHI**
tripedal movement + while feeding	Age regpt2 gp1 N=18	2R, 4L, 12Nlat p=0.688	13.389	-0.030 T p=0.832	0.452
tripedal movement + while feeding	Age regpt2 gp2 N=9	2R, 2L, 5Nlat	15.0	0.126 T p=0.573	0.515
tripedal movement + while feeding	Rearing gp1 N=15	3R, 3L, 9Nlat p=1.313	16.60	0.101 T p=0.536	0.495
tripedal movement + while feeding	Rearing gp 2,3 N=12	1R, 3L, 8Nlat	10.583	-0.078 T p=0.661	0.445
tripedal movement + while feeding	Age regpt3 gp1 N=12	1R, 1L, 10Nlat	11.583	0.129 T p=0.308	0.318
tripedal movement + while feeding	Age regpt3 gp2 N=6	1R, 3L, 2Nlat	17.0	-0.349 T p=0.328	0.718
tripedal movement + while feeding	Age regpt3 gp3 N=9	2R, 2L, 5Nlat	15.0	0.126 T p=0.573	0.515

Table 8app: Study 1: Results of the tests on the effect of the number of data points. Results of Spearman correlations between the number of data points and the HI and ABSHI values; and of MW tests comparing lateralized and unlateralized subjects.

Behaviour	**Spearman test for HI**	**Spearman test for ABSHI**	**MW on total for lateralized versus unlateralized subjects**
Overall limb use	rho=0.096, p=0.425	rho=0.013, p=0.915	p=**0.005** mean total: 110.073 for unlat, 220.60 for lat
Quadrupedal movement N=32	rho=-0.275, p=0.128	rho=-0.194, p=0.287	NA
tripedal movement N=17	rho=0.606, p=**0.010**	rho=0.124, p=0.635	p=0.296
tripedal movement while feeding with one hand N=10	rho=0.710, p=**0.021**	rho=-0.586, p=0.075	NA
tripedal movement + while feeding N=27	rho=0.150, p=0.455	rho=0.025, p=0.90	p=0.163
Feeding, general N=65	rho=0.122, p=0.332	rho=-0.294, **p=0.017**	p=0.379
Feeding, posture: triped, other hand: postural support N=33	rho=0.130, p=0.471	rho=-0.223, p=0.213	p=0.150
Feeding, posture: seated, other hand: hold a food item N=41	rho=0.162, p=0.312	rho=0.052, p=0.745	NA
Feeding, posture: seated, other hand: postural support N=49	rho=-0.081, p=0.578	rho=-0.214, p=0.140	p=0.068
Feeding, posture: seated, other hand: inactive N=54	rho=0.147, p=0.290	rho=-0.041, p=0.770	p=**0.008** mean total: 19.474 for unlat, 34.813 for lat
Pushing an object N=10	rho=-0.269, p=0.452	rho=-0.166, p=0.646	NA
Dragging an object N=11	rho=0.126, p=0.712	rho=-0.120, p=0.726	NA
swinging + hanging N=15	rho=0.406, p=0.134	rho=-0.360, p=0.187	NA
Reaching for big items, general N=26	rho=0.128, p=0.532	rho=0.018, p=0.929	p=**0.003** mean total: 10.0 for unlat, 29.714 for lat
Reaching for big items, posture: triped, other hand: postural support N=21	rho=0.163, p=0.481	rho=-0.074, p=0.748	NA
Reaching for small items, general N=33	rho=0.042, p=0.815	rho=-0.040, p=0.823	p=**0.015** mean total: 43.50 for unlat, 89.533 for lat

table 8app continued	**Spearman test for HI**	**Spearman test for ABSHI**	**MW on total for lateralized versus unlateralized subjects**
Reaching for small items, posture: triped, other hand: postural support N=18	rho=-0.251, p=0.315	rho=-0.117, p=0.645	p=**0.003** mean total: 17.90 for unlat, 73.625 for lat
Reaching for small items, posture: seated, other hand: postural support N=27	rho=0.028, p=0.889	rho=0.036, p=0.860	p=**0.037** mean total: 26.118 for unlat, 32.50 for lat
Reaching for small items, posture: seated, other hand: inactive N=22	rho=-0.057, p=0.801	rho=-0.333, p=0.130	p=**0.337** mean total: 14.133 for unlat, 19.714 for lat
Reaching for small items, (global) grip type: lateral grip (1p2mlat) N=17	rho=0.016, p=0.951	rho=-0.077, p=0.77	p=**0.186** mean total: 51.1 for unlat, 91.571 for lat
Pulling grass out N=11	rho=-0.207, p=0.541	rho=0.329, p=0.322	NA
foetus position N=18	rho=-0.247, p=0.324	rho=-0.096, p=0.704	NA
crossed arms N=18	rho=0.370, p=0.130	rho=-0.013, p=0.958	NA
turning (standing) N=7	rho=-0.667, p=0.102	rho=-0.559, p=0.192	NA
crossed legs N=9	rho=0.586, p=0.097	rho=-0.527, p=0.145	NA
inserting a finger (self directed) N=6	rho=-0.319, p=0.538	rho=0.058, p=0.913	NA
raking seeds on the floor (global) N=7	rho=-0.214, p=0.645	rho=0.198, p=0.67	NA
raking seeds on the floor, seated N=6	rho=0.143, p=0.787	rho=1, p<0.01	NA
reaching in the water pond N=8	rho=-0.119, p=0.779	rho=-0.524, p=0.183	NA

Table 9app: Study 1: Data per subject. Lola ya bonobo (1)

	api	bandundu	beni	bili	bisengo	boende	bolobo	boyoma	dilolo	eleke	elikia	etumbe	fizi	ilebo	isiro	kalina	kasongo
swinging																	
hanging																	
swinging+hanging											Nlat						
feeding, general	L		Nlat	Nlat	R	Nlat	Nlat		Nlat		Nlat		Nlat	Nlat	R	Nlat	R
feeding, tripedal	L		Nlat				R		Nlat				Nlat	Nlat	Nlat	R	R
feeding, seated, other hand in postural support	Nlat			Nlat	Nlat	Nlat	Nlat		Nlat		Nlat		Nlat	R	Nlat	Nlat	R
feeding, seated, other hand holding a food item	Nlat			Nlat		Nlat	Nlat		Nlat				Nlat	Nlat	R	Nlat	Nlat
feeding, seated, other hand inactive	Nlat			Nlat	Nlat	Nlat	Nlat		Nlat				Nlat	Nlat	R	Nlat	Nlat
pulling grass out, general																	
pulling grass out, tripedal																	
pulling grass out, seated, other hand in postural support																	
pulling grass out, seated, other hand inactive																	
quadrupedal movement holding item				Nlat		L			Nlat				Nlat	Nlat	Nlat		Nlat
tripedal movement holding item					Nlat		Nlat										
tripedal movement while feeding	L													Nlat			Nlat
reaching for big items, general	Nlat		Nlat				Nlat						Nlat	Nlat	Nlat		Nlat
reaching for big items, tripedal	Nlat		Nlat				Nlat							Nlat			Nlat
reaching for small items, general																	
reaching for small items, tripedal																	
reaching for small items, seated, other hand in postural support																	
reaching for small items, seated, other hand inactive																	
reaching for small items, lying on the belly																	
reaching for small items with lateral grip type																	

table 9app continued	api	bandundu	beni	bili	bisengo	boende	bolobo	boyoma	dilolo	eleke	elikia	etumbe	fizi	ilebo	isiro	kalina	kasongo
reaching for small items with one finger grip type																	
reaching for small items with dorsal grip type																	
pushing an object																	
dragging an object	L																
pulling water vegetation out, general																	
pulling water vegetation out, tripedal																	
pulling leaves out (bimanual)																	
behaviours related to genitals, general																	
behaviours related to genitals, tripedal																	
inserting a finger (self-directed)																	
inserting hand in throat																	
raking seeds on the floor																	
reaching in water pond																	
chest rubbing																	
reaching in the fixed object (unimanual)																	
reaching in the object (bimanual)																	
catching																	
nut cracking																	
arm around neck posture																	
foetus position																	
turning (standing)													Nlat				
turning (supine)																	
crossing legs		Nlat		Nlat								Nlat					
side of the sexual swellings when seated																	
crossing arms																	
breaking a piece from the food item																	
throwing	R								Nlat								
peeling the fruit																	

Table 10app: Study 1. Data per subject. Lola ya bonobo (2)

	kikongo	kisento	kubulu	likasi	lisala	lodja	lomela 2	lukaya	luozi	mabali	makali	maluku	maniema	manono	matadi
swinging															
hanging															
swinging+hanging				Nlat											
feeding, general	Nlat		R	Nlat	Nlat	Nlat		Nlat	Nlat	Nlat		Nlat	R	Nlat	Nlat
feeding, tripedal	Nlat		Nlat	Nlat				Nlat					R	R	Nlat
feeding, seated, other hand in postural support	Nlat		R	Nlat	Nlat	Nlat		Nlat		Nlat		Nlat	Nlat	Nlat	Nlat
feeding, seated, other hand holding a food item	Nlat		Nlat		Nlat	Nlat		Nlat		Nlat		Nlat	Nlat	Nlat	Nlat
feeding, seated, other hand inactive	Nlat		R	Nlat	Nlat	Nlat		Nlat				Nlat	Nlat	L	Nlat
pulling grass out, general															
pulling grass out, tripedal															
pulling grass out, seated, other hand in postural support															
pulling grass out, seated, other hand inactive															
quadrupedal movement holding item	Nlat							Nlat				Nlat	Nlat	Nlat	Nlat
tripedal movement holding item															
tripedal movement while feeding	L		R												
reaching for big items, general	Nlat							Nlat						Nlat	Nlat
reaching for big items, tripedal	Nlat													Nlat	Nlat
reaching for small items, general														Nlat	

table 10app continued	kikongo	kisento	kubulu	likasi	lisala	lodja	lomela 2	lukaya	luozi	mabali	makali	maluku	maniema	manono	matadi
pushing an object														R	R
dragging an object			R							R		Nlat			
pulling water vegetation out, general															
pulling water vegetation out, tripedal															
pulling leaves out (bimanual)															
behaviours related to genitals, general															
behaviours related to genitals, tripedal															
inserting a finger (self-directed)															
inserting hand in throat															
raking seeds on the floor															
reaching in water pond															
chest rubbing															
chest rubbing (2 hands)													L		
reaching in the fixed object (unimanual)															
reaching in the object (bimanual)															
catching															
nut cracking															
arm around neck posture															
foetus position															
turning (standing)															
turning (supine)															
crossing legs		Nlat													
side of the sexual swellings when seated															
crossing arms															
breaking a piece from the food item															
throwing															
peeling the fruit			Nlat	L		Nlat									

Table 11app: Study 1. Data per subject. Lola ya bonobo (3)

	max	maya	mbandaka	mbano	mimia	mixa	nioki	opala	pole	sake	salonga	semendwa	tatango	tembo	tshilomba	yolo
swinging																
hanging																
swinging+hanging																
feeding, general	L	Nlat	Nlat	Nlat	Nlat	R	L	Nlat	R		Nlat	Nlat	Nlat	Nlat	Nlat	R
feeding, tripedal						Nlat	L	Nlat			Nlat	Nlat		Nlat		
feeding, seated, other hand in postural support	Nlat	Nlat	Nlat	Nlat		R		Nlat	R		Nlat	Nlat	Nlat	Nlat		R
feeding, seated, other hand holding a food item	Nlat	Nlat	Nlat			Nlat	Nlat	Nlat			Nlat	Nlat	Nlat	Nlat		
feeding, seated, other hand inactive	L	R	Nlat	Nlat	Nlat	Nlat	L	Nlat	Nlat		R	Nlat	Nlat		Nlat	R
pulling grass out, general																
pulling grass out, tripedal																
pulling grass out, seated, other hand in postural support																
pulling grass out, seated, other hand inactive																
quadrupedal movement holding item		Nlat	Nlat			Nlat		Nlat			Nlat	Nlat		Nlat	Nlat	Nlat
tripedal movement holding item							L		Nlat							
tripedal movement while feeding							L									
reaching for big items, general								Nlat			Nlat					
reaching for big items, tripedal								Nlat			Nlat					
reaching for small items, general	Nlat	L				Nlat								Nlat		
reaching for small items, tripedal						Nlat										
reaching for small items, seated, other hand in postural support	Nlat	Nlat												Nlat		

table 11 continued	max	maya	mbandaka	mbano	mimia	mixa	nioki	opala	pole	sake	salonga	semendwa	tatango	tembo	tshilomba	yolo
pushing an object	R												L			
dragging an object	R												Nlat			
pulling water vegetation out, general																
pulling water vegetation out, tripedal																
pulling leaves out (bimanual)																
behaviours related to genitals, general																
behaviours related to genitals, tripedal																
inserting a finger (self-directed)																
inserting hand in throat																
raking seeds on the floor																
reaching in water pond																
chest rubbing																
chest rubbing (2 hands)																
reaching in the fixed object (unimanual)																
reaching in the object (bimanual)																
catching																
nut cracking																
arm around neck posture																
foetus position																
turning (standing)				L												
turning (supine)																
crossing legs		Nlat			Nlat			Nlat					Nlat		R	
side of the sexual swellings when seated																
crossing arms																
breaking a piece from the food item											L					
throwing													L			
peeling the fruit			Nlat													

Table 12app: Study 2: raw data for each individual for the “tube task”, for bouts and for frequency.
Italic cases were excluded from the analyses (individuals that had less than 15 data points).
Right: number of right hand responses, Left: number of left hand responses; total: total number of trials. B test: p value of the Binomial test performed on the number of right versus left hand trials. Category: category in which the individual was classified based on Binomial test: L: left-handed, R: right-handed, Nlat: not lateralized.

		Bouts								Frequency						
	individuals	Right	Left	total	HI	ABSHI	B test	category		Right	Left	total	HI	ABSHI	B test	category
lola	Api	*7*	*5*	*12*	*0,167*	*0,167*	*0,77*	*Nlat*		27	50	77	-0,299	0,299	0,012	L
lola	Beni	24	22	46	0,043	0,043	0,883	Nlat		158	142	300	0,053	0,053	0,387	Nlat
lola	Bili	19	21	40	-0,05	0,05	0,875	Nlat		77	134	211	-0,27	0,27	1E-04	L
lola	Bisengo	*5*	*4*	*9*	*0,111*	*0,111*	*1*	*Nlat*		7	10	17	-0,176	0,176	0,629	Nlat
lola	Boende	8	14	22	-0,273	0,273	0,286	Nlat		24	48	72	-0,333	0,333	0,006	L
lola	Bolobo	26	15	41	0,268	0,268	0,117	Nlat		85	29	114	0,491	0,491	1E-07	R
lola	Boyoma	17	1	18	0,889	0,889	1E-04	R		42	1	43	0,953	0,953	1E-11	R
lola	Dilolo	19	12	31	0,226	0,226	0,281	Nlat		74	37	111	0,333	0,333	6E-04	R
lola	Eleke	16	20	36	-0,111	0,111	0,618	Nlat		46	77	123	-0,252	0,252	0,007	L
lola	Fizi	7	11	18	-0,222	0,222	0,481	Nlat		35	83	118	-0,407	0,407	1E-05	L
lola	Ilebo	27	29	56	-0,036	0,036	0,894	Nlat		109	152	261	-0,165	0,165	0,009	L
lola	Isiro	14	6	20	0,4	0,4	0,115	Nlat		135	57	192	0,406	0,406	2E-08	R
lola	Kalina	9	12	21	-0,143	0,143	0,664	Nlat		55	84	139	-0,209	0,209	0,017	L
lola	Kasongo	2	18	20	-0,8	0,8	4E-04	L		9	86	95	-0,811	0,811	7E-17	L
lola	Katako	21	19	40	0,05	0,05	0,875	Nlat		54	86	140	-0,229	0,229	0,009	L
lola	Keza	*10*	*3*	*13*	*0,538*	*0,538*	*0,09*	*Nlat (R trend)*		56	31	87	0,287	0,287	0,01	R
lola	Kikongo	18	15	33	0,091	0,091	0,728	Nlat		88	56	144	0,222	0,222	0,01	R
lola	Kubulu	*0*	*12*	*12*	*-1*	*1*	*0*	*L*		0	60	60	-1	1	2E-18	L
lola	Likasi	2	19	21	-0,81	0,81	2E-04	L		7	61	68	-0,794	0,794	7E-12	L
lola	Lisala	12	3	15	0,6	0,6	0,035	R		123	43	166	0,482	0,482	4E-10	R
lola	Lodja	12	15	27	-0,111	0,111	0,701	Nlat		54	43	97	0,113	0,113	0,31	Nlat
lola	Lomela 2	19	33	52	-0,269	0,269	0,07	Nlat (L trend)		56	118	174	-0,356	0,356	3E-06	L
lola	Lukaya	6	19	25	-0,52	0,52	0,015	L		23	147	170	-0,729	0,729	3E-23	L

		Bouts								**Frequency**						
	individuals	**Right**	**Left**	**total**	**HI**	**ABSHI**	**B test**	**category**		**Right**	**Left**	**total**	**HI**	**ABSHI**	**B test**	**category**
lola	Luozi	21	5	26	0,615	0,615	0,002	R		142	28	170	0,671	0,671	1E-19	R
lola	Mabali	*5*	*6*	*11*	*-0,09*	*0,091*	*1*	*Nlat*		29	14	43	0,349	0,349	0,032	R
lola	Makali	24	12	36	0,333	0,333	0,065	Nlat (R trend)		255	61	316	0,614	0,614	2E-29	R
lola	Maluku	15	28	43	-0,302	0,302	0,066	Nlat (L trend)		62	104	166	-0,253	0,253	0,001	L
lola	Maniema	18	4	22	0,636	0,636	0,004	R		103	11	114	0,807	0,807	7E-20	R
lola	Manono	13	6	19	0,368	0,368	0,167	Nlat		106	32	138	0,536	0,536	2E-10	R
lola	Matadi	2	19	21	-0,81	0,81	2E-04	L		16	143	159	-0,799	0,799	1E-26	L
lola	Max	13	8	21	0,238	0,238	0,383	Nlat		137	43	180	0,522	0,522	1E-12	R
lola	Maya	11	14	25	-0,12	0,12	0,69	Nlat		177	98	275	0,287	0,287	2E-06	R
lola	Mbandaka	20	14	34	0,176	0,176	0,392	Nlat		107	72	179	0,196	0,196	0,011	R
lola	Mbano	*6*	*8*	*14*	*-0,14*	*0,143*	*0,79*	*Nlat*		22	26	48	-0,083	0,083	0,665	Nlat
lola	Mimia	4	15	19	-0,579	0,579	0,019	L		18	243	261	-0,862	0,862	2E-51	L
lola	Mixa	11	16	27	-0,185	0,185	0,442	Nlat		33	170	203	-0,675	0,675	2E-23	L
lola	Mwanda	12	8	20	0,2	0,2	0,503	Nlat		66	19	85	0,553	0,553	3E-07	R
lola	Nioki	*13*	*0*	*13*	*1*	*1*	*0*	*R*		164	0	164	1	1	9E-50	R
lola	Opala	8	13	21	-0,238	0,238	0,383	Nlat		34	73	107	-0,364	0,364	2E-04	L
lola	Sake	20	31	51	-0,216	0,216	0,161	Nlat		45	93	138	-0,348	0,348	5E-05	L
lola	Salonga	14	18	32	-0,125	0,125	0,597	Nlat		89	108	197	-0,096	0,096	0,2	Nlat
lola	Semendwa	23	13	36	0,278	0,278	0,132	Nlat		158	36	194	0,629	0,629	2E-19	R
lola	Tatango	18	21	39	-0,077	0,077	0,749	Nlat		53	108	161	-0,342	0,342	2E-05	L
lola	Tembo	9	13	22	-0,182	0,182	0,523	Nlat		151	181	332	-0,09	0,09	0,111	Nlat
lola	Tshillenge	15	10	25	0,2	0,2	0,424	Nlat		63	35	98	0,286	0,286	0,006	R
lola	Tshilomba	*8*	*3*	*11*	*0,455*	*0,455*	*0,23*	*Nlat*		47	18	65	0,446	0,446	4E-04	R
lola	Vanga	40	10	50	0,6	0,6	2E-05	R		211	26	237	0,781	0,781	3E-37	R
lola	Yolo	15	0	15	1	1	6E-05	R		49	0	49	1	1	4E-15	R
Ap	Jasiri	17	60	77	-0,558	0,558	9E-07	L		65	296	361	-0,64	0,64	2E-36	L
Ap	Jill	66	1	67	0,97	0,97	9E-19	R		651	5	656	0,985	0,985	7E-19	R
Ap	Kumbuka	15	41	56	-0,464	0,464	7E-04	L		32	156	188	-0,66	0,66	9E-21	L
Ap	Liboso	45	15	60	0,5	0,5	1E-04	R		341	51	392	0,74	0,74	9E-54	R

	individuals	Right	Left	total	HI	ABSHI	B test	category		Right	Left	total	HI	ABSHI	B test	category
Ap	Lingala	14	34	48	-0,417	0,417	0,006	L		30	72	102	-0,412	0,412	4E-05	L
Ap	Lomela 1	23	42	65	-0,292	0,292	0,025	L		112	432	544	-0,588	0,588	3E-45	L
Ap	Mwindu	17	16	33	0,03	0,03	1	Nlat		154	85	239	0,289	0,289	1E-05	R
Ap	Zuani	17	34	51	-0,333	0,333	0,024	L		170	450	620	-0,452	0,452	4E-30	L
St	Banbo	9	41	50	-0,64	0,64	6E-06	L		13	74	87	-0,701	0,701	2E-11	L
St	Chipita	21	33	54	-0,222	0,222	0,134	Nlat		86	118	204	-0,157	0,157	0,03	L
St	Daniela	14	1	15	0,867	0,867	0,001	R		214	6	220	0,945	0,945	2E-55	R
St	David	4	37	41	-0,805	0,805	1E-07	L		8	177	185	-0,914	0,914	1E-42	L
St	Diwani	7	60	67	-0,791	0,791	1E-11	L		16	376	392	-0,918	0,918	2E-90	L
St	Khaya	27	43	70	-0,229	0,229	0,072	Nlat (L trend)		74	102	176	-0,159	0,159	0,042	L
St	Kirembo	18	2	20	0,8	0,8	4E-04	R		167	6	173	0,931	0,931	6E-42	R
St	Kombote	20	29	49	-0,184	0,184	0,253	Nlat		101	149	250	-0,192	0,192	0,003	L
St	Lina	7	17	24	-0,417	0,417	0,064	Nlat		51	200	251	-0,594	0,594	5E-22	L
St	Louisoko	15	1	16	0,875	0,875	5E-04	R		132	5	137	0,927	0,927	4E-33	R
St	Lucuma	6	16	22	-0,455	0,455	0,053	Nlat (L trend)		12	35	47	-0,489	0,489	0,001	L
St	Mixi	21	15	36	0,167	0,167	0,405	Nlat		69	52	121	0,14	0,14	0,146	Nlat
St	Zorba	46	1	47	0,957	0,957	7E-13	R		333	6	339	0,965	0,965	4E-90	R
Tw	Banja	57	41	98	0,163	0,163	0,129	Nlat		385	218	603	0,277	0,277	1E-11	R
Tw	Cheka	31	24	55	0,127	0,127	0,419	Nlat		106	130	236	-0,102	0,102	0,134	Nlat
Tw	Diatou	13	32	45	-0,422	0,422	0,007	L		61	212	273	-0,553	0,553	1E-20	L
Tw	Jasongo	25	0	25	1	1	6E-08	R		146	0	146	1	1	2E-44	R
Tw	Kakowet II	18	32	50	-0,28	0,28	0,065	Nlat (L trend)		124	117	241	0,029	0,029	0,699	Nlat
Tw	Keke	53	4	57	0,86	0,86	6E-12	R		328	15	343	0,913	0,913	7E-78	R
Tw	Kichele	40	27	67	0,194	0,194	0,142	Nlat		208	92	300	0,387	0,387	2E-11	R
Tw	Luo	6	10	16	-0,25	0,25	0,455	Nlat		18	45	63	-0,429	0,429	9E-04	L
	Total	1276	1291	2567						7888	7059	14947				
	Mean			37,2	0,026	0,401						194,1	0,034	0,499		
	SD			18,02	0,495	0,287						131,2	0,581	0,293		
	Minimum			15	-0,81	0,03						17	-1	0,029		
	Maximum			98	1	1						656	1	1		

Table 13app: Study 2: Descriptive data for each age, sex and rearing group and settings for the “tube task” (lola + zoos sample) with frequency.

Behaviour	**Group considered**	**Group distribution and B test on R vs L**	**Mean number of data points per subject**	**Mean HI and T test**	**Mean ABSHI**
Lola Ya Bonobo + Zoos - Frequency	Sex male N=40	20R, 15L, 5Nlat p=0.5	161.675	0.111 T p=0.264	0.533
Lola Ya Bonobo + Zoos - Frequency	Sex female N=37	13R, 20L, 4Nlat p=0.296	229.19	-0.048 T p=0.589	0.463
Lola Ya Bonobo + Zoos - Frequency	Age regpt1 gp1 N=36	13R, 19L, 4Nlat p=0.377	128.389	-0.073 T p=0.440	0.483
Lola Ya Bonobo + Zoos - Frequency	Age regpt1 gp2 N=41	20R, 16L, 5Nlat p=0.618	251.829	0.129 T p=0.169	0.514
Lola Ya Bonobo + Zoos - Frequency	Age regpt2 gp1 N=48	16R, 26L, 6Nlat p=0.164	146.667	-0.073 T p=0.382	0.494
Lola Ya Bonobo + Zoos - Frequency	Age regpt2 gp2 N=29	17R, 9L, 3Nlat p=0.169	272.656	0.212 T **p=0.049**	0.508
Lola Ya Bonobo + Zoos - Frequency	Rearing gp1 N=23	9R, 10L, 4Nlat p=1	271.217	0.003 T p=0.981	0.565
Lola Ya Bonobo + Zoos - Frequency	Rearing gp 2,3 N=54	24R, 25L, 5Nlat p=1	161.278	0.048 T p=0.531	0.471
Lola Ya Bonobo + Zoos - Frequency	Age regpt3 gp1 N=36	13R, 19L, 4Nlat p=0.377	128.389	-0.073 T p=0.44	0.483
Lola Ya Bonobo + Zoos - Frequency	Age regpt3 gp2 N=12	3R, 7L, 2Nlat p=0.344	201.50	-0.074 T p=0.698	0.527
Lola Ya Bonobo + Zoos - Frequency	Age regpt3 gp3 N=29	17R, 9L, 3Nlat p=0.169	272.656	0.212 T p=0.049	0.508

Table 14app: Study 2: Descriptive data for each age, sex and rearing group and settings for the “tube task” (lola + zoos sample) with bouts.

Behaviour	**Group considered**	**Group distribution and B test on R vs L**	**Mean number of data points per subject**	**Mean HI and T test**	**Mean ABSHI**
Lola Ya Bonobo + Zoos - Bouts	Sex male N=34	10R, 5L, 19Nlat p=0.302	31.971	0.138 T p=0.153	0.451
Lola Ya Bonobo + Zoos - Bouts	Sex female N=35	4R, 10L, 21Nlat p=0.18	42.286	-0.083 T p=0.247	0.352
Lola Ya Bonobo + Zoos - Bouts	Age regpt1 gp1 N=32	6R, 8L, 18Nlat p=0.607	35.063	-0.052 T p=0.561	0.41
Lola Ya Bonobo + Zoos - Bouts	Age regpt1 gp2 N=37	8R, 6L, 23Nlat p=0.791	39.054	0.093 T p=0.250	0.393
Lola Ya Bonobo + Zoos - Bouts	Age regpt2 gp1 N=42	8R, 10L, 24Nlat p=0.815	35.952	-0.052 T p=0.492	0.398
Lola Ya Bonobo + Zoos - Bouts	Age regpt2 gp2 N=27	6R, 4L, 17Nlat p=0.754	39.148	0.148 T p=0.127	0.405
Lola Ya Bonobo + Zoos - Bouts	Rearing gp1 N=21	6R, 7L, 8Nlat p=1	32.833	0.021 T p=0.751	0.361
Lola Ya Bonobo + Zoos - Bouts	Rearing gp 2,3 N=48	8R, 7L, 33Nlat p=1	47.191	0.037 T p=0.776	0.492
Lola Ya Bonobo + Zoos - Bouts	Age regpt3 gp1 N=32	6R, 8L, 18Nlat p=0.607	35.063	-0.052 T p=0.561	0.41
Lola Ya Bonobo + Zoos - Bouts	Age regpt3 gp2 N=10	2R, 2L, 6Nlat	38.80	-0.053 T p=0.731	0.362
Lola Ya Bonobo + Zoos - Bouts	Age regpt3 gp3 N=27	6R, 4L, 17Nlat p=0.754	39.148	0.148 T p=0.127	0.405

Table 15app: Study 2: Results of the tests on the effect of the number of data points per subject (mini 15 data points per subject). Results of Spearman correlations between the number of data points and the HI and ABSHI values. Results of KW tests comparing right-handed, left-handed and unlateralized individuals and of MW tests comparing lateralized and unlateralized subjects.

		comparison of the number of data points between right-handed, left-handed and unlateralized individuals	**comparison of the number of data points between lateralized and unlateralized individuals**	**correlation between the number of data points and the ABSHI values**	**correlation between the number of data points and the HI values**
Zoos	frequency	*NA*	NA	no correlation. Spearman test, rho=0.108, p=0.578, N=29	no correlation. Spearman test, rho=0.071, p=0.716, N=29
	bouts	*no difference. KW test, H=2.288, df=2, p=0.319*	no difference. MW test, p=0.929, U=100, N1=12, N2=17	no correlation. Spearman test, rho=-0.205, p=0.286, N=29	no correlation. Spearman test, rho=-0.145, p=0.454, N=29
Lola Ya Bonobo	frequency	*no difference. KW test, H=0.047, df=2, p=0.977*	no difference. MW test, p=0.876 U=121 N1=6, N2=42	no correlation. Spearman test, rho=-0.132, p=0.371, N=48	no correlation. Spearman test, rho=0.006, p=0.966, N=48
	bouts	***significant difference. KW test, H=7.304, df=2, p=0.026***	**significant difference. MW test, p=0.007, U=71, Mean=22.91 for lateralized subjects (N=11), 32.207 for unlateralized subjects (N=29)**	**negative correlation. Spearman test, rho=-0.529, p=0.0004, N=40**	no correlation. Spearman test, rho=-0.118, p=0.423, N=40
Lola Ya Bonobo + Zoos	frequency	*no difference. KW test, H=0.109, df=2, p=0.947 N=77*	no difference. MW test, p=0.918 U=299.5 N1=9, N2=68	no correlation Spearman test, rho=0.023, p=0.843, N=77	no correlation. Spearman test, rho=0.042, p=0.716, N=77
	bouts	*no difference. KW test, H=3.144, df=2, p=0.208, N=69*	no difference. MW test, p=0.888, U=562.5 N1=41, N2=28	no correlation. Spearman test, rho=-0.194, p=0.11, N=69	no correlation. Spearman test, rho=-0.174, p=0.153, N=69

Table 16app: Study 3b: Descriptive data for each age, sex and rearing group and settings for the ‘’termite fishing task’’.

Group considered	Group distribution and B test on R vs L	Mean number of data points per subject	Mean HI and T test	Mean ABSHI
Sex male N=8	1R, 1L, 6Nlat	44.750	0.082 T p=0.705 t(7)=0.395	0.368
Sex female N=11	6R, 3L, 2Nlat p=0.508	58.818	0.177 T p=0.452 t(10)=0.783	0.657
Age regpt2 gp1 N=8	3R, 2L, 3Nlat	51.250	0.103 T p=0.714 t(7)=0.382	0.589
Age regpt2 gp2 N=11	4R, 2L, 5Nlat p=0.688	54.091	0.162 T p=0.416 t(10)=0.848	0.496
Rearing gp1 N=12	5R, 3L, 4Nlat p=0.727	58.083	0.069 T p=0.743 t(11)=0.336	0.555
Rearing gp 2 N=7	2R, 1L, 4Nlat	44.0	0.254 T p=0.328 t(6)=1.066	0.50
Setting Stuttgart N=12	5R, 3L, 4Nlat p=0.727	51.0	0.133 T p=0.556 t(11)=0.607	0.618
Setting Twycross N=7	2R, 1L, 4Nlat	56.143	0.144 T p=0.508 t(6)=0.704	0.393

Table 17app: Study 3b: Results of the tests on the effects of sex, age, rearing, settings and number of data points for the "termite fishing" task.
Results of MW tests comparing the different groups.

	MW test for age groups paired comparisons
Age (regpt2)	- gp1 vs gp2: N1=8, N2=11, MW U=40.5, p=0.772 for total, U=39.5, p=0.710 for HI, U=39, p=0.679 for ABSHI
Sex	MW N1=8, N2=11, U=36.5, p=0.536 for HI, U=27, p=0.160 for ABSHI, U=31.5, p=0.302 for total
Rearing	MW N1=7, N2=12, U=33.5, p=0.472 for HI, U=39, p=0.80 for ABSHI, U=, U=30, p=0.310 for total
Settings	MW N1=12, N2=7, U=41, p=0.933 for HI, U=27, p=0.204 for ABSHI, U=37, p=0.672 for total
Effect of the number of data points: correlation between the number of data points and the HI and ABSHI values	Spearman test, rho=-0.73, p=0.766 for HI Rho=-0.048, p=0.844 for ABSHI
Effect of the number of data points: comparisons between lateralized and unlateralized subjects	MW N1=8, N2=11, U=42, p=0.869 for total
Effect of the number of data points: comparisons between right-handed, left-handed and unlateralized subjects	NA

Table 18app: Study 4a: Behavioural patterns ranked according to their HI values.

behaviour	**mean HI**
touching the partner's body	-0.14
holding the partner during ventro-ventral mount	-0.089
touching the genitals of the partner	-0.075
dragging the other	0.016
play related behaviours	0.038
moving with arm around the partner	0.078
playing	0.082
lateral embrace	0.175
holding the hand or foot of the other	0.214
tripedal movement holding the baby under belly with one arm	0.286
inviting related behaviours (global)	0.315
arm held toward the other (invitation)	0.336

Table 19app: Study 4a: Behavioural patterns ranked according to their ABSHI values.

behaviour	mean ABSHI
play related behaviours	0.196
touching the partner's body	0.217
lateral embrace	0.256
moving with arm around the partner	0.257
dragging the other	0.289
playing	0.294
holding the hand or foot of the other	0.303
holding the partner during ventro-ventral mount	0.356
inviting related behaviours (global)	0.365
arm held toward the other (invitation)	0.399
touching the genitals of the partner	0.452
"tripedal movement holding the baby under belly with one arm"	0.748

Table 20app: Study 4a: Results of the comparisons between the main social actions. MW test p values for HI and ABSHI and total paired comparisons for the 12 manual social behaviours. Only significant results are reported here; all other paired comparisons yielded non-significant results (MW p>0.05).

Behaviour	**MW test**
"arm held toward the other (invitation)" versus :	touching the partner's body U=6, p=0.009 for HI
"touching the genitals of the partner" versus :	touching the partner's body U=8, p=0.008 for ABSHI
	moving with arm around the partner U=13, p=0.031 for ABSHI
	lateral embrace U=12.5, p=0.028 for ABSHI
"tripedal movement holding the baby under belly with one arm" versus :	holding the hand or foot of the other U=4, p=0.025 for ABSHI, U=4.5, p=0.030 for total
	touching the genitals of the partner U=6.5, p=0.038 for ABSHI, U=4.5, p=0.018 for total
	dragging the other U=4, p=0.015 for ABSHI, U=5, p=0.022 for total
	playing U=6, p=0.020 for ABSHI, U=6.5, p=0.24 for total
	touching the partner's body U=2, p=0.002 for ABSHI, U=5, p=0.007 for total
	moving with arm around the partner U=1.5, p=0.002 for ABSHI, U=10, p=0.030 for total
	lateral embrace U=6.5, p=0.011 for ABSHI, U=9, p=0.023 for total
	holding the partner during ventro-ventral mount U=7.5, p=0.015 for ABSHI, *U=12.5, p=0.57 for total*

Table 21app: Study 4a: Results of the tests on the effect of the number of data points for spontaneous social actions.

Behaviour	Spearman test for HI	Spearman test for ABSHI
“ play related behaviours ” N=15	rho=-0.105, p=0.711	rho=0.132, p=0.640
“ touching the partner’s body” N=10	rho=0.520, p=0.123	rho=-0.214, p=0.553
“ moving with arm around the partner ” N=10	rho=-0.372, p=0.290	rho=-0.154, p=0.671
“lateral embrace” N=10	rho=-0.426, p=0.220	rho=-0.393, p=0.261
“holding the partner during ventro-ventral mount” N=10	rho=-0.382, p=0.276	rho=-0.079, p=0.829
“suckling from mother’s breast” N=13	rho=-0.063, p=0.837	rho=0.102, p=0.740
“tripedal movement holding the baby under belly with one arm” N=6	rho=0.429, p=0.397	rho=0.60, p=0.208
“arm held towards the other (invitation)” N=6	rho=-0.524, p=0.286	rho=-0.40, p=0.431
“holding the hand or foot of the other” N=6	rho=-0.841, p=0.036	rho=-0.667, p=0.148
“touching the genitals of the partner” N=7	rho=0.255, p=0.582	rho=-0.789, p=0.035
“inviting related behaviours (global)” N=7	rho=-0.585, p=0.167	rho=-0.415, p=0.354
“playing” N=8	rho=0.371, p=0.365	rho=-0.180, p=0.670
“sitting with crossed arms around the baby” N=7	rho=0.036, p=0.933	rho=-0.335, p=0.417
“dragging the other” N=7	rho=-0.714, p=0.071	rho=-0.286, p=0.535

Table 22app: Study 4b: Descriptive data for each sex and age group for the begging experiment.

Group considered	**Group distribution and B test on R vs L**	**Mean number of data points per subject**	**Mean HI and T test**	**Mean ABSHI**
Sex male N=15	6R, 7L, 2Nlat p=1	13.067	**-0.457** T p=0.842 t(14)=-0.204	0.806
Sex female N=9	5R, 2L, 2Nlat p=0.453	16.889	0.381 T p=0.159 t(8)=1.554	0.749
Age regpt1 gp1 N=11	5R, 3L, 3Nlat p=0.727	14.546	0.201 T p=0.427 t(10)=0.828	0.72
Age regpt2 gp2 N=13	6R, 6L, 1Nlat p=1.226	14.462	0.041 T p=0.870 t(12)=0.167	0.839
Age regpt2 gp1 N=15	7R, 5L, 3Nlat p=0.774	14.733	0.149 T p=0.720 t(7)=0.484	0.734
Age regpt2 gp2 N=9	4R, 4L, 1Nlat p=1.273	14.111	0.056 T p=0.860 t(8)=0.182	0.869

Table 23app: Study 4b: Results of tests on the effects of sex and age for the begging experiment.
Results of MW tests comparing the different groups.

	MW test for age groups paired comparisons
Age (regpt1)	- gp1 vs gp2: MW N1=11, N2=13, U=61, p=0.542 for total, U=47.5, p=0.161 for HI, U=64, p=0.658 for ABSHI
Age (regpt2)	- gp1 vs gp2: MW N1=15, N2=9, U=67, p=0.976 for total, U=50, p=0.292 for HI, U=49.5, p=0.274 for ABSHI
Sex	MW N1=14, N2=10, U=67.5, p=0.883 for HI, U=69, p=0.952 for ABSHI, U=38.5, p=0.064 for total