Laterality in Chimpanzees: Links with Behavioural Style and Social Networks

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Declaration

The material being presented for examination is my own work and has not been submitted for an award of this or another HEI except in minor particulars which are explicitly noted in the body of the thesis. Where research pertainingto the thesis was undertaken collaboratively, the nature and extent of my individual contribution has been made explicit.

Sergio Díaz González

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Abstract and thesis structure

This thesis presents a series of studies investigating laterality in chimpanzees and its links with personality examined as behavioural style and social networks. The studies presented in this work were conducted by observing a group of 19 chimpanzees in captivity and present new findings in this species. However, this thesis has a broad evolutionary perspective, addressing important questions regarding personality and laterality that could prove helpful to the understanding of the evolution of laterality in vertebrates. Chapter 1 offers a general review of the three main areas of knowledge investigated: laterality, animal personality and primate social networks. Then, the first study of this project, presented in Chapter 2, began by exploring hand preference in the chimpanzee group, investigating spontaneous actions and unimanual tasks and expanding previous research by studying posture, between-task consistency and temporal stability. Chapter 3 investigated additional measures of motor laterality and proposed a novel way of measuring laterality in primates. Together, Chapters 2 and 3 directly examine laterality in chimpanzees and serve as the base from which to explore the links between laterality, personality and social networks in the subsequent studies. If lateralization is rooted in emotional processing and hemispheric lateralization, then individual differences in behaviour (particularly those that reflect emotional expression) would show a relationship with individual laterality. In order to address this question, Chapter 4 studies behavioural style in chimpanzees and its possible link with laterality. Simultaneously, if intraspecific coordination plays a role in the development of population level laterality, similarly lateralised individuals would likekly have strong bonds to coordinate with each other. Chapter 5 introduces the approach and techniques of social network analysis and uses them to explore and describe the social structure of the group while describing the integration of a new adult chimpanzee. Chapter 6 applies social network analysis to explore if laterality plays a role in the way the group is structured. Lastly, Chapter 7 integrates all empirical chapters and presents the final discussion and conclusions of the thesis.

Chapter 1. Introduction

Laterality

The term laterality, also sometimes alluded to as lateralization, refers to lateral asymmetry in any given function or structure, from motor behaviours to the specialization of sensory information where specific stimuli are processed differently in the left or right hemisphere of the brain (Frasnelli et al., 2012; Wiper, 2017). Laterality is not a single phenomenon; instead, it is an intrinsic characteristic of every asymmetric aspect of an organism. Lateralization of hand function, for example, refers to the systematic use of one hand over the other; while lateralization of hearing function refers to the systematic orientation of one ear when perceiving an acoustic stimulus. Sensory and emotional processes can be lateralised as well. For example, the right hemisphere of the brain is often associated with processing unexpected stimuli (Rogers & Vallortigara, 2015) and emotional expressions (Salva et al., 2012). These functional asymmetries are presumed to reflect neural lateralization of the corresponding function of the opposite brain hemisphere (Fitch & Braccini, 2013). While a great deal can be learned about laterality from studies of neuroanatomy and neuropsychology, it is equally important to understand lateralization of function in behaviour.

Similarly, the study of lateralization can focus on how individuals of a single species are lateralized, or on the biases of lateralization in the whole population. When an individual shows consistent asymmetry in function, this is refered to this as individual level laterality. When more than half of the individuals in a species show the same asymmetries in function or, in other words, when there is a bias towards one side in a population, this is refered to this as population level laterality (Wiper, 2017). This chapter focuses on laterality of motor functions such as hand preference, foot preference and whole-body preference; but also considers laterality in sensory and emotional functions, as often one function cannot be understood without the others. Both individual level and population level laterality are examined, since they present different and interrelated aspects of the evolution of laterality.

Lateral asymmetries are intriguing because they represent a change in the evolutionary tendency of behaviours to be symmetrically distributed. Studying laterality from an evolutionary perspective requires us to consider the costs and benefits associated with the manifestation of lateral assymetries as an evolutionary adaptation (Vallortigara, 2006). Most animals appear to have evolved with a strong tendency to be symmetrical in anatomy and behaviour and, in fact, most living species belong to the order known as the Bilateria, which evolved at least 40 million years before the Cambrian Era (Chen et al., 2004). It has been argued (Corballis, 2012) that animals evolved to have symmetrical bodies in order to interact with the natural world, in which there is no left-right bias, and later started to develop asymmetrical adaptations that do not depend on the external environment. This suggests that lateral asymmetries evolved as a consequence of particular adaptations, which highlights the importance of using an evolutionary perspective to interpret and evaluate the findings in this area.

Early research on laterality was largely focused on humans and, for a time, it was in the centre of the continuity versus dichotomy debate (Corballis, 1989). In the 1980s, a great deal of research on human brain asymmetry and lateralization was based on the presumed uniqueness of lateral asymmetry in humans, based on the strong population level lateralization in both hand preference and language (Fitch & Braccini, 2013). At that time, evidence of population level laterality in non-human animals (hereafter "animals"), for instance, lemurs having a left-hand preference (MacNeilage et al., 1987), was considered too weak to be convincing. In a review of behavioural and archaeological data, Corballis (1985) concluded that human right-handedness was universal and linked to the evolution of tool use, suggesting that it only recently appeared in the *Homo* genus.

Contrary to early knowledge, in the past three decades, evidence of cerebral lateralization in animals has become more abundant (for a review see Vallortigara & Rogers, 2005) which has forced researchers to reconsider many past assumptions on human and animal laterality. Currently, most of the research community agrees that lateralization can no longer be considered an aspect of the uniqueness of one species, but a fundamental property of the vertebrate central nervous system (Atkinson et al., 2016). This accumulation of evidence of lateralization in vertebrates has caused a shift in the position of authors that previously defended the uniqueness of lateralization in the human species. In a recent paper, Corballis (2012) acknowledges the current evidence of laterality in animals, proposing that human asymmetries, even if they were to be considered unique to our species, have roots in systematic asymmetries present in other animals.

The main objectives of laterality research have shifted from trying to explain an assumed "human uniqueness" to studying the similarities and differences in lateralization in a plethora of species in order to understand its evolution. This view requires careful examination of lateralization in light of the specific and natural behaviours of every species. Instead of looking for motor lateralization as the only indication of brain asymmetries, studies have shown that laterality can be manifested in many different forms (Rogers, 2009). This requires us to consider behavioural and sensory asymmetries (such as whole-body-action or eye preference) that might not be as strong in humans, but that can offer invaluable information in other animals. However, hand preference, once considered the "go-to" sign of lateralization, is still widely studied in humans as well as in non-human primates (hereafter primates).

Evidence of Individual Level Laterality

Research in laterality in animals has accumulated a vast collection of evidence showing individual lateralization in a remarkably broad range of species. In mammals, studies show that rats (*Rattus norvegicus domestica*) have a consistent preference to use one paw over the other when picking up pieces of food, even if half of them have a preference to use the left while the other half prefer to use the right (Güven et al., 2003). Cats (*Felis catus*) are also known to have a paw preference when catching moving objects (Fabre-Thorpe et al., 1993). Even animals without limb preferences can show strong individual whole-body asymmetries: horses (*Equus caballus*) show tendencies to shorten distances consistently towards their preferred side (Lucidi et al., 2012), while marine mammals have very strong preferences when turning and swimming laterally (MacNeilage, 2014). In birds, there is evidence that chicken (*Gallus gallus domesticus*) show individual lateralization (Rogers, 2000; Rogers et al., 2004), parrots (multiple species) show strong foot preferences (Magat & Brown, 2004) and magpies (*Gymnorhina tibicen*) have eye preferenes (Hoffman et al., 2006; Koboroff et al., 2008). There are also studies with reptiles, amphibians and fish investigating motor laterality (Bisazza et al., 1998; Vallortigara et al., 1998). All this evidence seems to imply that lateralization cannot be attributed to a single function or behaviour and instead can evolve in similar ways even in radically different species and evolutionary contexts.

Research in primates has contributed greatly to the field, since individuals of many species consistently show hand preference, even if there is no clear bias in the overall population. Marmosets (*Callithrix jacchus*) have a preferred hand to grab pieces of food from the ground and, although half of them are left-handed and half are right-handed, their individual preferences are strong and stable across the lifespan (Cameron & Rogers, 1999). Different tasks can be lateralized in different hemispheres and, as a result, hand preference can change depending on the nature of the task. Hook and Rogers (2008) studied individual hand preferences in a group of 21 common marmosets across four visuospatial reaching tasks and found that, in one of the tasks, a third of the group changed their preferred hand, without changing the overall group bias. Llorente et al. (2009) found somewhat similar data when studying hand preference in simple reaching and an experimental bimanual task in chimpanzees (*Pan troglodytes*): while most of the individuals showed strong preferences, 6 out of the 14 chimpanzees showed a different hand preference depending on the task. These results indicate that even a specific type of lateralization such as hand preference is not a single phenomenon. Instead, each hemisphere seems to specialize in carrying out certain tasks, which highlights the importance of carefully considering the details of every specific behaviour.

The fact that lateralization is apparent in such a wide range of species suggests that it offers some kind of evolutionary advantage. Hemispheric specialization may offer an increase in neural capacity (Vallortigara & Rogers, 2005), avoiding unnecessary and inefficient duplication of functions in the two hemispheres. There is plenty of evidence that lateralized animals have increased fitness when carrying out two tasks at the same time. Rogers et al. (2004) found that lateralization is associated with an enhanced ability to perform two tasks simultaneously in chicken: when compared in their ability to feed while watching out for predators, lateralized birds detected the model predator faster than non-lateralized birds. Similar results have been found with fish; Dadda and Bisazza (2006) selectively bred strongly-lateralized and weakly-lateralized fish (*Girardinus falcatus*) and compared them in a dual-task situation: strongly lateralized fish were twice as fast at feeding in the presence of a predator, using one eye to monitor the predator and the other eye for catching prey. Finally, Piddington and Rogers (2013) tested a group of common marmosets to see if there was a relationship between hand preference and dual-task performance and found that marmosets with stronger hand preferences detected the model predator sooner than those with weaker hand preferences. This indicates that lateralization improves the ability to process two types of information simultaneously.

Evidence of Population Level Laterality

The general consensus of the first investigations examining the possibility of laterality in primates was that individuals that had a right-hand and left-hand preference were equally abundant, indicating that only humans showed population level laterality (Warren, 1980). This quickly changed when MacNeilage et al. (1987), in a now classic paper on hand preference, re-examined evidence of hand preference in primates and determined that population level preference was present in different primate species. According to their reasoning, there was a bias to use the right hand for body support and the left hand for catching insects in early primates, which led to a specialization of the left hand in tasks that require catching moving objects in all modern primates; while changes in the style of locomotion freed the right hand from its supporting role and allowed it to specialize in manipulation of objects and tool use (MacNeilage et al., 1987). Supporting evidence for this theory, known as the Postural Origins Theory, includes studies showing that prosimians have a population level left hand preference for insect-catching (Ward et al., 1993) and chimpanzees show a population level right hand preference for bimanual tool use (Hopkins et al., 2004; Llorente et al., 2011).

Nevertheless, population level hand preference in primates remains inconclusive, with just as many studies not reporting a population bias towards either side in chimpanzees (McGrew & Marchant, 2001). The reasons for these inconsistences, as Fitch and Braccini (2013) suggest, is likely to be the influence of context and task on the manifestation of laterality. Chimpanzee right-handedness is most evident in experimental contexts, and often a minor change in body posture or in the position of the target object can induce changes in the direction of the hand preference, making replication of studies hard to achieve (McGrew & Marchant, 1997). All in all, the Postural Origins Theory created a lot of interest in the area of hand preference and offered an explanation for population level similarities in hand preference but, three decades after its appearance, it is evident that it has limitations, as it does not account for hand preference (or lack thereof) in all possible contexts.

While the Postural Origins Theory only accounted for motor preferences in primates, the study of non-primate species has also shed some light on lateralization as a population phenomenon. Reports of population level limb preferences are not uncommon amongst non-primate species, albeit that the biases towards one side are often lower than for hand preference in humans. Cats tend to use the left paw to stop moving objects (Fabre-Thorpe et al., 1993) while toads have a right foot preference to push objects (Bisazza et al., 1998). Some of the most remarkable preferences at a population level come from parrots: most studied species show a strong bias towards the use of their left foot to hold and manipulate objects (Magat & Brown, 2004). However, if the effect of context and posture can create difficulties when comparing results in primates, comparisons of limb preferences in animals as different as toads and parrots present even more challenges.

Of course, limb preference is not the only manifestation of hand preference. Species that rarely use their limbs for object or terrain manipulation, and even species without limbs, show motor preferences too. In fact, MacNeilage (2014) found what he considered to be “the strongest vertebrate rightward action asymmetries” alongside human handedness in marine mammals (p. 1). Whales and dolphins tend to turn to their right when feeding, with population biases between 85% and 95% for some species (MacNeilage, 2014). Strong population level laterality is also present in swim positions between mother and calf, where calves show strong preferences to keep their mothers on their left side in belugas (*Delphinapterus leucas*, Hill et al., 2017; Karenina et al., 2013) and orcas (*Orcinus orca*, Karenina et al., 2013). Likewise, fish can show directional preferences when initiating a movement behaviour. Bisazza et al. (2000) studied turning responses in 16 species of fish and found that 10 of them showed a clear population level preference towards one side, with preferences being more similar amongst species of the same family. Similar results have been found in land animals for whole-body actions. Eye preference in fish has also been studied in different species, finding a left eye preference when inspecting social stimuli (Sovrano et al., 1999) and a right eye preference for predator vigilance (Facchin et al., 1999). Lucidi et al. (2013) studied the tendency of young horses to “derail” when following their mothers from behind and found that 95% of them showed a propensity towards cutting towards the right side. While whole-body movements of marine mammals and derailment in horses are very different behaviours, both have the potential to show a lateral bias and the fact that most individuals of a species show the same directional bias is remarkable.

Sensory lateralization has also been studied in animals, but it is generally more difficult to study outside of experimental conditions and tends to be conducted on small species such as fish (*Gambusia holbrooki,* Bisazza et al., 1997) and toads (multiple species, Rogers, 2002). Especially interesting are the results found by Hook-Costigan and Rogers (1998) when testing the eye preference of 21 common marmosets: 20 of the monkeys used their right eye consistently when looking through a hole when looking at a piece of food. Common marmosets do not show population level hand preference in any known task (Cameron & Rogers, 1999; Hook & Rogers, 2008), which makes this finding fascinating, since it suggests that sensory lateralization could reveal more about brain lateralization in species that do not show clear hand preference at the population level.

Early Sensory Lateralization and Hemispheric Specialization

Having a lateralized brain has a clear series of advantages in terms of information processing (Vallortigara & Rogers, 2005), which would explain why it is such a common phenomenon. However, these advantages do not require individuals to be lateralized in the same direction, which means that populations would be expected to show distributions of roughly equal percentage of left- and right-lateralized individuals. In reality, population level preferences are not uncommon. Authors such as Rogers (2009) or Fitch and Braccini (2013) have proposed an explanation for the appearance of population level lateralization, suggesting that it may be reflecting early asymmetries in vertebrate evolution. According to this view lateralization in any particular behaviour is not a recent evolutionary characteristic. Instead, current behaviours, such as human handedness or the lateralization of language, have evolved in a previously lateralized brain (Fitch & Braccini, 2013). Rogers (2009) suggests that asymmetries in sensory processing were likely to exist in early vertebrates, creating sensory lateralization, and many of its features have been retained, even in humans. This perspective shares some common elements with the Postural Origins Theory, but encompasses all vertebrates and has a higher emphasis on sensory lateralization. Rogers (2009) states that the Postural Origins Theory (MacNeilage et al., 1987) implies that motor biases evolved prior to brain lateralization for sensory processing. In contrast with this, Rogers (2009) proposes that limb/hand preferences – and implicitly other kinds of motor lateralization too - are influenced by each hemisphere’s sensory specialization.

The origin for this sensory processing specialization could be found in the fact that early vertebrates were physically asymmetrical (Andrew, 2002) and, having the mouth on the right side of the head, developed an asymmetrical central nervous system. Additionally, the evolution of two eyes might have also played an important role in the development of a lateralised brain. Since feeding behaviours had to be done with the right side of the body, the left eye could have a more predominant role in vigilance for predators (Andrew, 2002). The early nervous system, according to this theory, specialised the left hemisphere of the brain for categorizing familiar stimuli such as food, as well as approaching behaviours, while the right hemisphere became specialised in managing responses to unexpected stimuli (Wiper, 2017).

There is evidence of the left hemisphere specialising in dealing with social and expected stimuli in primates, as Japanese macaques (*Macaca fuscata*) discriminate social stimuli when presented to the right ear (Petersen et al., 1978) and chimpanzees tend to produce social gestures more often with their right hand (Hopkins et al., 1998). Similarly, motor control of facial movements associated with the production of intentional, learned sounds is lateralized on the left hemisphere (Losin et al., 2008).

Interestingly, the role of the right hemisphere in dealing with unexpected stimuli has often been linked to higher emotional responses and avoidance behaviours. For example, left-handed individuals take longer to explore novel environments and interact less often with new objects than right-handers in both common marmosets (Cameron & Rogers, 1999) and chimpanzees (Hopkins & Bennet, 1994). Similarly, it has also been observed that species-typical vocalizations are associated with a stronger emotional expression on the left side of the mouth, which authors have interpreted as an indication of a higher control of the right hemisphere in emotional responses (Fernández-Carriba et al., 2002). These results indicate that lateralization can be related to, or reflect, differences in general patterns of behaviour, with the right hemisphere being associated with intense reactive emotions that induce withdrawal. The section on personality of this chapters goes into more detail about the link between hemispheric lateralization and personality. The link between laterality and personality is still not fully understood, although research in this area has grown in popularity in the last decade (Fernández-Lázaro et al., 2019; Rogers, 2009; Tomassetti et al., 2019).

Laterality and Intraspecific Coordination

While the link between laterality and personality is an interesting field to explore, there are certain questions that are still unanswered. First, species that are phylogenetically close to each other can show differences in terms of population level lateralization for the same task: Rogers (1980) investigated foot preference in nine species of Australian parrots and found that eight showed a left foot population level preference and one showed a right foot population level preference. This indicates that there might be mechanisms of selection for lateralization that are more recent in their evolutionary history. Furthermore, there is evidence of population level lateralization in invertebrates including honeybees (*Apis mellifera,* Letzkus et al., 2006), cockroaches (*Periplaneta americana,* Cooper et al., 2010) and ants (*Formica rufa* and *Formica polyctera*, Heuts et al., 2003) among others (Frasnelli et al., 2012) that cannot be explained by a common starting point in neural processing. Second, even in the strongest population level preference, there is often a minority of individuals lateralized in the opposite direction to the population bias (Ghirlanda et al., 2009). These questions require an examination of the evolutionary implications of population level lateralization.

The work of Vallortigara (2006) offered a careful examination of the evolutionary costs and benefits of having a lateralized brain at a population level and arrived at the conclusion that the direction of the lateralization can be understood as an evolutionarily stable strategy. Evolutionarily stable strategies are sets of behavioural patterns that, if adopted by a critical proportion of the population, allow no alternative strategy to compete (Dominey, 1984). Vallortigara (2006) argues that lateralization at the population level can not be explained as a simple by-product of individual lateralization and that direct genetic mechanisms are insufficient to explain this common phenomenon, given that strength of lateralization can be naturally selected without favouring one direction over the other. According to this view, if the fitness of an individual is affected by its aligning with the direction of the laterality of the majority of the group, then the direction of lateralization will be a frequency-dependent characteristic (Ghirlanda & Vallortigara, 2004).

For example, fish show a preference towards the side they choose when swimming away from a predator (Bisazza et al., 2000). When a predator attacks, the fitness of an individual fish will depend on whether or not it starts swimming in the same initial direction as the rest of the group, in other words, it will depend on the direction of its lateralization. Fish that have a preference aligned with the rest of the shoal will have a better chance of survival. This particular example can be backed by the evidence that shoaling fishes show population level bias when faced with a dummy predator, while non-shoaling fishes do not show any population preferences towards a side (Bisazza et al., 2000).

The notion of population level lateralization as an evolutionarily stable strategy has been explained using game theory (Vallortigara, 2006) to predict the effect of predation on lateralization; and mathematical models (Ghirlanda et al., 2009). These theoretical models can explain how population level lateralization can arise when asymmetrical organisms need to adapt their behaviour with other asymmetrical individuals by examining the role of inter and intraspecific cooperation and competition. The usefulness of these models is that they can also explain the small percentage of individuals lateralized in the other direction, since those individuals would be using frequency-dependant strategies such as the ability to surprise predators that anticipate a lateral bias in their prey.

These models prove the theoretical viability of the explanation of lateralization as an evolutionarily stable strategy and there is some evidence that indicates that cooperation and competition may play a role, since social species have stronger biases than non-social ones (in fish Bisazza et al., 2000; in invertebrates Frasnelli et al., 2013). However, finding evidence in other animal species with more complex social dynamics can present a challenge. The section on social networks of this chapter introduces a potential approach to explore this area in social animals such as primates.

Animal Personality

The systematic study of animal personality dates back to the landmark studies of Pavlov (in Carere & Locurto, 2011), where he developed the first typology of behaviour for dogs (*Canis lupus familiaris*). After these influential studies, little systematic research was conducted in animal personality. However, in the past three decades biologists and psychologists have been taking more interest in animal personality and research has been rapidly growing in associated fields such as animal cognition (Carere & Locurto, 2011), neuroendocrinology (Koolhaas et al., 2010) and evolutionary ecology (Réale et al., 2010). There is evidence of personality in domestic animals (Gosling & Bonnenberg, 1998); primates (for a review, see Freeman & Gosling, 2010); birds (Mettke-Hofmann et al., 2005) and even fish (Millot et al., 2014) among many other species. Gosling (2001), in the first systematic review of animal personality, encountered a very broad field with a great diversity of traits and species studied and with reports of validity and reliability comparable to those in human personality research.

This increase in popularity may be due to the importance of understanding individual differences in behaviour in order to better understand different aspects of the range of behaviour of a given species. Research in animal personality tackles behavioural plasticity, attempting to explain how and why individual differences in behaviour emerge and are maintained within a species (Koski, 2014). The study of consistent differences in behaviour that are consistent across contexts, from an evolutionary point of view, can have notable consequences in fitness (Carere et al., 2010). As an example, some individuals are consistently more proactive than others, and this is reflected in the frequency and style of exploration in new surroundings, leading to a better adaptation to changing environments (Carere & Locurto, 2011). The fitness consequences for different individuals will depend on their environment, but also on their specific personalities, making the study of animal personality an important topic in animal research.

In the specific area of primate personality, Freeman and Gosling (2010) reviewed 210 different articles of personality in primates and found that most studies addressed categories such as Sociability, Confidence/Aggression and Fearfulness; with other categories such as Extraversion and Dominance also showing high values of reliability and validity. However, it is hard to discuss broad categories that could fit every primate species and some of them, like Conscientiousness, have only been found in chimpanzees (Freeman & Gosling, 2010). In addition to the uneven study between different species -with macaques and chimpanzees being widely studied while other species are virtually unexplored-, differences in methods and analyses used also made findings difficult to compare. In this review (Freeman & Gosling, 2010) there is a call for researchers to create a new framework that allows for the description and comparison of personality between species. Although methods have been continuously improving since the first comprehensive review in the field (Gosling, 2001), the need for a unified framework and better tools for assessing personality in different species is still vital.

Defining Personality

As is to be expected from an area that spans research in such a wide range of disciplines, finding a specific definition of personality has proven a difficult task. Researchers from various fields have used different terminology to refer to the same or very similar concepts such as predispositions, behavioural profiles, syndromes, temperament or coping styles (Carere & Locurto, 2011). Fortunately, in the last decade there has been a considerable effort to unify terminology and the term personality is now mostly described using two main definitions (Réale et al., 2010): a broad-sense definition that encompasses any behaviour across any context and a narrow-sense definition that focuses on individual differences in novel or challenging contexts.

The broad-sense definition was initially proposed by Gosling (2001) and describes personality as consistent patterns of behaviour and emotion characteristic of individuals. This broad definition of personality has the advantage of being able to study any behaviour and, since it focuses on patterns of behaviour across different contexts, facilitates comparison between species. It includes research using earlier terminology with a broad sense, such as temperament and behavioural profiles. The narrow sense definition describes personality as the differences in behaviour in a single, well-studied and usually controlled, environment. It captures more details about specific behaviours and often underlines the importance of emotion when dealing with a novel or potentially dangerous stimulus. It includes a plentiful number of studies in behavioural neuroendocrinology, where the preferred term for this narrow sense of personality is still coping styles (Koolhaas et al., 2010). This thesis will use the broad sense definition of personality, although it will also incorporate studies that use a narrower interpretation when they can be useful in the study of individual differences in behaviour.

Personality and Hemispheric Specialization

Behaviour and emotion are deeply interlinked in the study of personality, both in humans and animals (Carver et al., 2000). In humans, neuroticism is typically characterised by expressions of emotion, while descriptors of extraversion such as energy and spontaneity could be considered as positive emotional tendencies (Carver et al., 2000). In animals, the connection between emotion and personality is even more evident, judging by the most used dimensions: dominance, emotionality and novelty seeking are some of the proposed dimensions for primates (Freeman & Gosling, 2010). In a review of human personality, Carver et al. (2000) closely examine this relationship between personality and emotion, and propose an approach based on two basic emotional responses that serve as building blocks for personality: approach and avoidance. This review (Carver et al., 2000) is mostly centred on aspects of human personality such as motivation, self-discrepancy and attitudes, concepts rarely studied in animals. Nevertheless, this approach fits perfectly with some of the most common studies in animal personality, especially when considering its narrow-sense definition. The study of personality in this sense (Koolhaas et al., 2010) is largely based on approach-oriented individuals, sometimes called bold, and avoidance-oriented individuals, also called shy.

There is some evidence in primates that hand preference is associated with differences in personality. For example, in the first study measuring laterality and personality, Hopkins and Bennet (1994) used this approach to personality and presented two sets of novel objects to a total of 49 chimpanzees and recorded latency to enter the room and to touch the object. Left-handed chimpanzees were less bold in these situations, taking more time before entering the room and exploring the object (Hopkins & Bennet, 1994). Similar results have also been found in two species of marmosets, with left-handed individuals taking more time and being less likely to explore new objects in both common marmosets (Cameron & Rogers, 1999) and Geoffroy's marmosets (*Callithrix geoffroyi* Braccini & Caine, 2009). This evidence suggests that the specialization of the right hemisphere in the control of avoidance behaviour is reflected in the dominance of lateralized behaviours. Similar results have also been reported in social environments in rhesus macaques (*Macaca mulatta*), as left-handed individuals tend to react more submissively than right-handed macaques (Westergaard et al., 2003). In a similar line of work, Lindell (2013) reviewed the current evidence in emotional processing and expression in primates and concluded that emotion was lateralized in remarkably similar ways in all primate species studied. Thanks to the current knowledge of neuroendocrinology and neuroanatomy in animals, it is clear that the right hemisphere is related to both cortisol and fear level (Kalin et al., 1998). These specializations in emotional processing of the hemispheres fit well with Rogers' (2009) proposal of the sensory lateralization of early vertebrates. The left hemisphere of the brain of early vertebrates would be in charge of approach behaviours while the right hemisphere would specialize in vigilance and predator avoidance behaviours (Rogers, 2009).

Interestingly, while this emotional lateralization seems to be present in domestic animals as well as in primates (Leliveld et al., 2013), evidence regarding a link between motor laterality and emotional lateralization is less clear in non-primate species. The direction of paw preference in dogs does not seem to be associated with personality, although lateralized dogs displayed more stranger-directed aggression than non-lateralized dogs (Schneider et al., 2013). Similarly, when measuring motor laterality when passing an obstacle, lateralised sheep (*Ovis aries*) spent more time approaching others during separation, which the authors interpret as a sign of distress (Barnard et al., 2016). Data is sparse in regards to the link between laterality and personality, and the disparity in laterality measures in different species makes contributions in different species difficult to compare. While data in primate and non-primate species generally indicates that motor lateralization can be an indicator of lateralization in emotional processing, more research is needed to investigate the extent and characteristics of the relationship between laterality and personality.

Social Network Theory

Social network theory (SNT) is an approach to study social groups using matrix-based data to study the relationships (edges) between two or more individuals (nodes), forming a network (Wey et al., 2008). Each node can have attributes, such as age, sex or different personality traits. Edges link nodes together and can represent a number of variables, from kinship relations to frequencies of behaviour. This approach has been widely used in social sciences for many decades and has proved to be a valuable tool for studying human interactions and groups (Sih et al., 2009). A crucial aspect of SNT is that it does not constitute a given methodology or a group of analyses. Instead, it is a perspective that views groups as structures defined by the relationships of individual actors (Borgatti et al., 2013): the base of SNT are the nodes, or actors that form the network, and the relationships between them. Nodes can be anything, from individual humans to cities (Wey et al., 2008). Relationships can be similarly varied, from physical proximity to trade activity. In the study of animal behaviour, however, nodes are typically individual animals while relationships can vary from familiar ties to behavioural measures. Social network analysis can be centred in how the attribute of a node influences its position on the network (node level); for example, this can allow researchers to study if early maternal deprivation causes chimpanzees to hold less central positions in the grooming network (Kalcher-Sommersguter et al., 2015). It can also be focused on qualities of the whole network; for instance, group metrics can be used to compare different species of macaques in order to better investigate how different levels of tolerance in the dominance hierarchy affect centrality in the group (Sueur et al., 2011). Lastly, hypothesis testing tools allow researchers to investigate complex questions such as if tool-using dolphins preferentially associate with other tool-users (Mann et al., 2012).The fact that SNT is equally useful in so many different contexts and allows for node, network and dyad level of analysis makes it an efficient and elegant approach to the study of social groups in animals.

Until recently, researchers in the field of animal behaviour had not paid much attention to the SNT approach. However, even before the appearance of SNT, research in animals has always examined different aspects of social structure. Hinde (1976) created an extensive conceptual framework to study a social group of baboons, including aspects such as interactions, relationships and social structure. This work is considered a cornerstone in the study of animal social groups and offers a comprehensive integration of instances of behavioural interactions, family ties, age and sex to create a complex multileveled structure. The main differences between Hinde's (1976) approach and SNT is that the former creates a structure by incorporating different elements of relationships and interactions to different levels while the latter uses quantitative measures of the relationship between the nodes to form the network.

The main difference of SNT from traditional perspectives is that the analysis focuses on relationships, rather than on individuals. Notably, SNT allows the analysis of relationships by using techniques that bypass the assumption of independence of data points that traditional statistics make (i.e. the relationship of A with B cannot be independent from the relationship of A with C since both contain information about A). This makes it a useful tool for analysing the role of individuals within a group, the structure of the group and the presence of subgroups and clusters (Farine & Whitehead, 2015). In the past decade, numerous methodological advances have been developed to study network data past the descriptive level, integrating powerful inferential statistics with matrix-data such as Multiple Regression Quadratic Assignment Procedure (MRQAP) and Network-Based Diffusion Analysis (NBDA) (Pinter-Wollman et al., 2014).

While certain aspects of the social structure such as family ties and group size have always been studied in animal behaviour, the tools offered by SNT had not gathered much attention until Wey et al., (2008) strongly advocated using social network analysis and emphasized the advantages of using this framework. This was soon followed by another review in which Sih et al. (2009) wrote a comprehensive article discussing key points of SNT, metrics based on it and how they can be used to enrich different fields in ecology and animal behaviour. Sih et al. (2009) propose four key aspects to understand SNT: (1) within a group, differences among individuals affect both group and individual outputs; (2) indirect connections also affect individuals; (3) individuals differ in their position and importance inside a group; and (4) characteristics of a social network are often stable across different contexts. Since then, the use of social network analysis has become more popular, particularly among primatologists (Brent et al., 2011).

These tools allow researchers to not only study the network and every individual position in it, but also important factors that influence it. Animal personality is one such factor, as the network position of an individual is both a consequence of and a force of influence on personality (Krause et al., 2010). While this area has been widely studied in humans (Burt et al., 1998; Schaefer et al., 2008 in Krause et al., 2010), researchers have only recently begun exploring how personality and social networks interface in animals. In particular, previous research has investigated how certain personality aspects influence the position of individuals within their networks. Research in fish has found that bolder individuals have fewer social interactions than shy individuals (Pike et al., 2008), although the opposite has been found in mammals (Best et al., 2015). Research in birds has found that individuals with more central positions tend to be more proactive (Alpin et al., 2013) and explore faster

(Snidjers et al., 2014) than those with lower centralities. Also, studies in reptiles have found that less aggressive males have a tendency to avoid other individuals (Sih et al., 2018) but less aggressive males are more strongly connected to females than aggressive males (Godfrey et al., 2012). In addition to studying the position of individuals in the group structure, another application of SNA is the study of homophily, the tendency to form social ties between individuals with similar traits. While studies in primates have yet to employ SNA for this purpose, the study of homophily of personality is rapidly gaining popularity among primatologists. Past studies have mainly focused on investigating how individuals with similar levels of sociability/gregariousness have stronger relationships (Ebenau et al., 2019; Massen & Koski, 2014; Morton et al., 2015; Ebenau et al., 2019). While homophily can be studied without employing techniques specifically created for SNA, these techniques facilitate the analysis and help bypass some of the common problems encountered in this area such as non-independent data points. Thus, the use of SNA can help advance the current knowledge regarding the interaction between personality and social interactions.

Current Knowledge of Social Networks in Primates

The many applications of social network analysis can contribute to ecology (Croft et al., 2011), ethology (Makagon, 2012), animal conservation (Snijders et al., 2017) and captive management (Rose & Croft, 2017). Although it is a new approach in animal research, studies have already explored numerous animal species, from birds (*Phoenicopterus roseus*, Frumkin et al., 2016; Rose & Croft, 2017, 2018; *Parus major*, Aplin et al., 2013; Firth et al., 2017) to mammals (*Capra hircus*, Stanley & Dunbar, 2013; *Equus caballus*, Stanley et al., 2018; *Zalophus wollebaeki*, Wolf et al., 2007; *Crocuta crocuta*, Ilany et al., 2015). Primatology in particular has extensively used social network theory to study diverse species (Sueur et al., 2011). Primates are known to form relationships in a non-random way (in capuchin (*Sapajus apella*) and squirrel monkeys (*Saimiri sciureus*): Dufour et al., 2011; in Japanese macaques: Koyama, 2003; in chimpanzees: Hobaiter et al., 2014; in humans: Molho et al., 2016). The study of patterns of association can provide invaluable data about how social groups are formed and persist, as well as the advantages and disadvantages they carry in the evolution of many different species. Behavioural ecologists have used SNT to predict infectious disease risk in wild chimpanzees (Rushmore et al., 2013), showing that individuals with large families and, to a lesser extent, high ranking individuals, have the highest risk of infection. This study is an illustration of real management uses of SNT, as it helps identify the most important individuals to target for intervention strategies.

New tools developed to test hypotheses allow researchers to use social network analysis to investigate how different factors influence social behaviour in primates. One of the main uses of social network analysis in the study of primate behaviour is to inform and improve management in captivity (Rose & Croft, 2015). For example, this perspective has been applied in order to identify predictors of social aggression in a sample of 1300 rhesus macaques, using the findings to allow for a better manipulation of group composition in order to reduce aggressiveness (McCowan et al., 2008). Similarly, network metrics allow researchers to test the impact that changes in the social and physical environment have on Sulawesi crested macaques (*Macaca nigra*), identifying the introduction of new members as the most disruptive change (Cowl et al., 2020). In chimpanzees, it has been used to document changes in group dynamics during the integration of two groups of adult chimpanzees, identifying which individuals play a key role in creating links between the groups (Schel et al., 2013). Additionally, this approach has also been used to explore other aspects of primate sociality, such as social play (Lutz et al., 2019), communication (Roberts & Roberts, 2018a,b) or the impact of environment on behaviour (Koyama & Aureli, 2019). Overall, this approach has proven to be useful in any area that involves the study of social interactions. It is clear that social network theory is a powerful framework to study social relationships in animals, and in primates in particular. The more complex and intricate a social structure is, the more necessary it is for researchers to quantify different aspects of it. Investigating the social roles of each individual, group structure and the importance of specific behaviours such as grooming is vital to fully understand behaviour in social species. Finally, the value of SNT as a management tool both for primates in the wild and in captivity has been proven, making it not only useful for researchers, but also for all professionals involved in conservation and management of primates.

Networks and Intraspecific Coordination

Mathematical models can account for the benefits of population level laterality as a consequence of intraspecific coordination: when a high percentage of individuals of a species are lateralised to the same side, they would benefit from a faster coordinated response, being able to better predict their conspecifics' behaviour (Vallortigara, 2006; Vallortigara & Rogers, 2005). Evidence for these models that propose population level laterality as an evolutionarily stable strategy has thus far come from studies of escape responses in fish using predator-prey situations (Ghirlanda & Vallortigara, 2004; Ghirlanda et al., 2009). However, these models would greatly benefit from further empirical research that investigates if such advantages are present in other social contexts. In particular, primate species present the opportunity of exploring possible advantages of intraspecific coordination in complex social systems, where the link between lateralization and behavioural responses is not as clear as in fish. For example, Vallortigara (2006) suggests that data indicating population level laterality in chimpanzees, particularly considering how biases seem to be inherited from mother to offspring (Lonsdorf & Hopkins, 2005) can be a valuable source of new information regarding how social roles might influence laterality, which would be consistent with laterality as an evolutionarily stable strategy.

Studying intraspecific coordination in primates, particularly in apes, requires an approach that can better account for their social systems. Frequency dependant models operate on the basis that the behaviour of one individual is expected to change depending on the frequency of other behaviours of other individuals within the population (Voelkl & Kasper, 2009). An assuption of these models is that individuals interact at random with other group members (Voelkl & Kasper, 2009). On the contrary, individuals usually interact only with a portion of the population, and these interactions will shape their experience and their behaviour (Sih et al., 2009). In order to address the complex web of interactions that form a group, social network theory offers us tools to quantify certain aspects of it. These tools can offer new insights into the evolution of behaviours and strategies and how they are affected by social interaction (Krause et al., 2007). While direct investigation of lateralization as an evolutionarily stable strategy would require research in frequency-dependent effects between species, it is possible to shed some light into the link between laterality and intraspecific coordination by using social network analysis to examine if laterality can explain association, affiliation or aggressive interactions in primates.

Overview and Integration of Both Perspectives

The notion that current displays of lateralization are somehow influenced or built upon early sensory lateralization has deep implications in terms of emotional information processing, crossing paths with the study of personality. Meanwhile, intraspecific coordination and competition models seem to be able to explain certain aspects of population level laterality that would otherwise prove difficult to study. Each of these two theories offer different rationales as to why lateralization could evolve as a population level phenomenon, but they should not be seen as complete explanations that are incompatible with one another. Certainly, they can complement each other and could be operating simultaneously. Early sensory lateralization can help to explain the origin of brain lateralization and why behavioural and sensory lateralization can be deeply connected to personality but it is not enough to explain why population level lateralization is so widely extended, even across invertebrate species, and why it is more prevalent among social species. Intraspecific coordination models can better explain these aspects, but not why vertebrate brains seem to have such similarities when processing information, e.g. right hemisphere more involved in reactive responses and left hemisphere in proactive behaviours. The theoretical basis for this thesis lies in the integration of both of these perspectives, trying to offer a comprehensive explanation for the evolution of lateralization.

References

Aplin, L. M., Farine, D. R., Morand-Ferron, J., Cole, E. F., Cockburn, A., & Sheldon, B. C. (2013). Individual personalities predict social behaviour in wild networks of great tits (*Parus major*). *Ecology Letters, 16*(11), 1365–1372. https://doi.org/10.1111/ele.12181

Andrew, R. J. 2002 Behavioral development and lateralization. In L. J. Rogers & R. J. Andrew (Ed.), *Comparative vertebrate lateralization* (pp. 157–205). Cambridge, United Kingdom: Cambridge University Press.

Atkinson, E. G., Rogers, J., & Cheverud, J. M. (2016). Evolutionary and developmental implications of asymmetric brain folding in a large primate pedigree. *Evolution*, *70*(3), 707–715.

Barnard, S., Matthews, L., Messori, S., Podaliri-Vulpiani, M., & Ferri, N. (2016). Laterality as an indicator of emotional stress in ewes and lambs during a separation test. *Animal Cognition*, *19*(1), 207–214. https://doi.org/10.1007/s10071-015-0928-3

Best, E. C., Blomberg, S. P., & Goldizen, A. W. (2015). Shy female kangaroos seek safety in numbers and have fewer preferred friendships. *Behavioral Ecology, 26*(2), 639–646. https://doi.org/10.1093/beheco/arv003

Bisazza, A., Cantalupo, C., Capocchiano, M., & Vallortigara, G. (2000). Population lateralisation and social behaviour: A study with 16 species of fish. *Laterality: Asymmetries of Body, Brain and Cognition*, *5*(3), 269–284.

Bisazza, A., Pignatti, R., & Vallortigara, G. (1997). Detour tests reveal task- and stimulus-specific behavioural lateralization in mosquitofish (*Gambusia holbrooki*). *Behavioural Brain Research*, *89*, 237–242.

Bisazza, A., Rogers, L. J., & Vallortigara, G. (1998). The origins of cerebral asymmetry: A review of evidence of behavioural and brain lateralization in fishes, reptiles and amphibians. *Neuroscience and Biobehavioral Reviews*, *22*(3), 411–426.

Borgatti, S. P., Everett, M. G., & Johnson, J. C. (2013). *Analyzing social networks*. London, United Kingdom: SAGE.

Braccini, S. N., & Caine, N. G. (2009). Hand preference predicts reactions to novel foods and predators in marmosets (*Callithrix geoffroyi*). *Journal of Comparative Psychology*, *123*(1), 18–25.

Brent, L. J. N., Lehmann, J., & Ramos-Fernández, G. (2011). Social network analysis in the study of nonhuman primates: A historical perspective. *American Journal of Primatology*, *73*(8), 720–730. https://doi.org/10.1002/ajp.20949

Burt, R. S., Jannotta, J. E., & Mahoney, J. T. (1998). Personality correlates of structural holes. *Social Networks*, *20*(1), 63-87.

Cameron, R., & Rogers, L. J. (1999). Hand preference of the common marmoset (*Callithrix jacchus*). Problem solving and responses in a novel setting. *Journal of Comparative Psychology*, *113*(2), 149–157.

Carere, C., Caramaschi, D., & Fawcett, T. W. (2010). Covariation between personalities and individual differences in coping with stress: Converging evidence and hypotheses. *Current Zoology*, *56*(6), 728–740.

Carere, C., & Locurto, C. (2011). Interaction between animal personality and animal cognition. *Current Zoology*, *57*(4), 491–498.

Carver, C. S., Sutton, S. K., & Scheier, M. F. (2000). Action, emotion and personality: Emerging conceptual integration. *Personality and Social Psychology Bulletin*, *26*, 741–751.

Chen, J.Y., Bottjer, D. J., Oliveri, P., Dornbos, S. Q., Gao, F., Ruffins, S., Huimei, C., & Davidson, E. H. (2004). Small bilaterian fossils from 40 to 55 million years before the Cambrian. *Science*, *305*, 218–222. https://doi.org/10.1126/science.1099213

Collins, R. L. (1969). On the inheritance of handedness. *Journal of Heredity*, *59*(1), 9–12.

Cooper, R., Nudo, N., González, J. M., Vinson, S. B., & Liang, H. (2011). Side-dominance of *Periplaneta americana* persists through antenna amputation. *Journal of Insect Behavior*, *24*(3), 175–185. https://doi.org/10.1007/s10905-010-9246-4

Corballis, M. C. (1989). Laterality and human evolution. *Psychological Review*, *96*(3), 492–505. https://doi.org/10.1037/0033-295X.96.3.492

Corballis, M. C. (2012). Lateralization of the human brain. *Progress in Brain Research, 195,* 103–121. https://doi.org/10.1016/B978-0-444-53860-4.00006-4

Croft, D. P., Madden, J. R., Franks, D. W., & James, R. (2011). Hypothesis testing in animal social networks. *Trends in Ecology and Evolution*, *26*(10), 502-507.

Dadda, M., & Bisazza, A. (2006). Does brain asymmetry allow efficient performance of simultaneous tasks? *Animal Behaviour*, *72*(3), 523-529.

Dominey, W. J. (1984). Alternative mating tactics and evolutionarily stable strategies. *American Zoologist*, *24*(2), 385–396. https://doi.org/10.1093/icb/24.2.385

Dufour, V., Sueur, C., Whiten, A., & Buchanan-Smith, H. M. (2011). The impact of moving to a novel environment on social networks, activity and wellbeing in two new world primates. *American Journal of Primatology*, *73*, 1–10.

Ebenau, A., von Borell, C., Penke, L., Ostner, J., & Schülke, O. (2019). Personality homophily affects male social bonding in wild Assamese macaques, *Macaca assamensis*. *Animal Behaviour, 155*, 21–35. https://doi.org/10.1016/j.anbehav.2019.05.020

Fabre-Thorpe, M., Fagot, J., Lorincz, E., Levesque, F., & Vauclair, J. (1993). Laterality in cats: paw preference and performance in a visuomotor activity. *Cortex*, *29*(1), 15–24.

Facchin, L., Bisazza, A., & Vallortigara, G. (1999). What causes lateralization of detour behavior in fish? Evidence for asymmetries in eye use. *Behavioural Brain Research*, *103*(2), 229–234. https://doi.org/10.1016/S0166-4328(99)00043-1

Farine, D. R., & Whitehead, H. (2015). Constructing, conducting and interpreting animal social network analysis. *Journal of Animal Ecology*, *84*(5), 1144–1163. https://doi.org/10.1111/1365-2656.12418

Fernández-Carriba, S., Loeches, Á., Morcillo, A., & Hopkins, W. D. (2002). Asymmetry in facial expression of emotions by chimpanzees. *Neuropsychologia*, *40*(9), 1523–1533.

Fernández-Lázaro, G., Latorre, R., Alonso-García, E., & Barja Núñez, I. (2019). Nonhuman primate welfare: Can there be a relationship between personality, lateralization and physiological indicators? *Behavioural Processes*, *166*, 103897. https://doi.org/10.1016/j.beproc.2019.103897

Firth, J. A., Voelkl, B., Crates, R. A., Aplin, L. M., Biro, D., Croft, D. P., & Sheldon, B. C. (2017). Wild birds respond to flockmate loss by increasing their social network associations to others. *Proceedings of the Royal Society B: Biological Sciences, 284*(1854), 20170299. https://doi.org/10.1098/rspb.2017.0299

Fitch, W. T., & Braccini, S. N. (2013). Primate laterality and the biology and evolution of human handedness: A review and synthesis. *Annals of the New York Academy of Sciences*, *1288*(1), 70–85.

Frasnelli, E., Vallortigara, G., & Rogers, L. (2012). Left-right asymmetries of behaviour and nervous system in invertebrates. *Neuroscience and Biobehavioral Reviews*, *36*, 1273–1291.

Freeman, H. D., & Gosling, S. D. (2010). Personality in nonhuman primates: a review and evaluation of past research. *American journal of primatology*, *72*(8), 653-671.

Frumkin, N. B., Wey, T. W., Exnicios, M., Benham, C., Hinton, M. G., Lantz, S., Atherton, C., Forde, D., & Karubian, J. (2016). Inter-annual patterns of aggression and pair bonding in captive American flamingos (*Phoenicopterus ruber*). *Zoo Biology, 35*(2), 111–119. https://doi.org/10.1002/zoo.21274

Ghirlanda, S., Frasnelli, E., & Vallortigara, G. (2009). Intraspecific competition and coordination in the evolution of lateralization. *Philosophical Transactions of the Royal Society*, *364*, 861–866.

Ghirlanda, S., & Vallortigara, G. (2004). The evolution of brain lateralization: A game- theoretical analysis of population structure. *The Royal Society*, *271*, 853–857.

Godfrey, S. S., Bradley, J. K., Sih, A., & Bull, C. M. (2012). Lovers and fighters in sleepy lizard land: Where do aggressive males fit in a social network? *Animal Behaviour, 83*(1), 209–215. https://doi.org/10.1016/j.anbehav.2011.10.028

Goodall, J. (1986). *The chimpanzees of Gombe: Patterns of behavior*. Cambridge, MA: Harvard University Press.

Gosling, S. D. (2001). From mice to men: What can we learn about personality from animal research? *Psychological Bulletin*, *127*(1), 45-86.

Gosling, S. D., & Bonnenburg, A. V. (1998). An integrative approach to personality research in anthrozoology: Ratings of six species of pets and their owners. *Anthrozoös*, *11*(3), 148-156.

Güven, M., Elalmis, D., Binokay, S., & Tan, Ü. (2003). Population level right-paw preference in rats assessed by a new computerized food-reaching test. *International Journal of Neuroscience*, *113*, 1675–1689.

Heuts, B. A., Cornelissen, P., & Lambrechts, D. Y. M. (2003). Different attack modes of Formica species in interspecific one-on-one combats with other ants [*Hymenoptera: Formicidae*]. *Annales Zoologici*, *53*(2), 205–216.

Hill, H. M., Guarino, S., Calvillo, A., Gonzalez, A., Zuniga, K., Bellows, C., Polasek, L., & Sims, C. (2017). Lateralized swim positions are conserved across environments for beluga (*Delphinapterus leucas*) mother–calf pairs. *Behavioural Processes*, *138*, 22–28.

Hinde, R. A. (1976). Interactions, relationships and social structure. *Man*, *11*(1), 1–17.

Hirnstein, M., Hausmann, M., & Lewald, J. (2007). Functional cerebral asymmetry in auditory motion perception. *Laterality*, *12*(1), 87-99.

Hobaiter, C., Poisot, T., Zuberbühler, K., Hoppitt, W., & Gruber, T. (2014). Social network snalysis shows direct evidence for social transmission of tool use in wild chimpanzees. *PLoS Biology*, *12*(9): e1001960. https://doi.org/10.1371/journal.pbio.1001960.

Hoffman, A. M., Robakiewicz, P. E., Tuttle, E. M., & Rogers, L. J. (2006). Behavioural lateralisation in the Australian magpie (*Gymnorhina tibicen*). *Laterality*, *11*(2), 110–121. https://doi.org/10.1080/13576500500376674

Hook, M. A., & Rogers, L. J. (2008). Visuospatial reaching preferences of common marmosets (*Callithrix jacchus*): An assessment of individual biases across a variety of tasks. *Journal of Comparative Psychology*, *122*(1), 41–51.

Hook-Costigan, M. A., & Rogers, L. J. (1998). Eye preferences in common marmosets (*Callithrix jacchus*): Influence of age, stimulus, and hand preference. *Laterality*, *3*(2), 109–130

Hopkins, W. D., & Bennett, A. J. (1994). Handedness and approach-avoidance behavior in chipanzees (*Pan*). *Journal of Experimental Psychology: Animal Behavior Processes*, *20*(4), 413–418.

Hopkins, W. D., & Leavens, D. A. (1998). Hand use and gestural communication in chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, *112*(1), 95–99.

Hopkins, W. D., Wesley, M. J., Kay Izard, M., Hook, M., & Schapiro, S. J. (2004). Chimpanzees (*Pan troglodytes*) are predominantly right-handed: replication in three populations of apes. *Behavioural Neuroscience*, *118*(3), 659–663.

Ilany, A., Booms, A. S., & Holekamp, K. E. (2015). Topological effects of network structure on long-term social network dynamics in a wild mammal. *Ecology Letters, 18*(7), 687–695. https://doi.org/10.1111/ele.12447

Kalcher-Sommersguter, E., Preuschoft, S., Franz-Schaider, C., Hemelrijk, C. K., Crailsheim, K., & Massen, J. J. M. (2015). Early maternal loss affects social integration of chimpanzees throughout their lifetime. *Scientific Reports*, *5*(1), 16439. https://doi.org/10.1038/srep16439

Kalin, N. H., Larson, C., Shelton, S. E., & Davidson, R. J. (1998). Asymmetric frontal brain activity, cortisol, and behavior associated with fearful temperament in rhesus monkeys. *Behavioral Neuroscience*, *112*(2), 286–292.

Karenina, K., Giljov, A., Glazov, D., & Malashichev, Y. (2013). Social laterality in wild beluga whale infants: Comparisons between locations, escort conditions, and ages. *Behavioral Ecology and Sociobiology*, *67*(7), 1195–1204. https://doi.org/10.1007/s00265-013-1545-2

Karenina, K., Giljov, A., Ivkovich, T., Burdin, A., & Malashichev, Y. (2013). Lateralization of spatial relationships between wild mother and infant orcas, *Orcinus orca*. *Animal Behaviour*, *86*(6), 1225–1231. https://doi.org/10.1016/j.anbehav.2013.09.025

Krause, J., Croft, D. P., & James, R. (2007). Social network theory in the behavioural sciences: Potential applications. *Behavioral Ecology and Sociobiology*, *62*, 15–27.

Koboroff, A., Kaplan, G., & Rogers, L. J. (2008). Hemispheric specialization in Australian magpies (*Gymnorhina tibicen*) shown as eye preferences during response to a predator. *Brain Research Bulletin*, *76*(3), 304–306.

Koyama, N. F. (2003). Matrilineal cohesion and social networks in *Macaca fuscata*. *International Journal of Primatology*, *24*(4), 797-811.

Koyama, N. F., & Aureli, F. (2019). Social network changes during space restriction in zoo chimpanzees. *Primates*, *60*(3), 203–211. https://doi.org/10.1007/s10329-018-0675-6

Koolhaas, J.M., de Boer, S. F., Coppens, C. M., & Buwalda, B. (2010). Neuroendocrinology of coping styles: Towards understanding the biology of individual variation. *Frontiers in Neuroendocrinology*, *31*, 307–321.

Koski, S. E. (2014). Broader horizons for animal personality research. *Frontiers in Ecology and Evolution*, *2*, 1-6. https://doi.org/10.3389/fevo.2014.00070

Krause, J., James, R., & Croft, D. P. (2010). Personality in the context of social networks. *Philosophical Transactions of the Royal Society B: Biological Sciences, 365*(1560), 4099–4106. https://doi.org/10.1098/rstb.2010.0216

Leliveld, L. M. C., Langbein, J., & Puppe, B. (2013). The emergence of emotional lateralization: Evidence in non-human vertebrates and implications for farm animals. *Applied Animal Behaviour Science*, *145*(1), 1–14. https://doi.org/10.1016/j.applanim.2013.02.002

Letzkus, P., Ribi, W. A., Wood, J. T., Zhu, H., Zhang, S.-W., & Srinivasan, M. V. (2006). Lateralization of Olfaction in the Honeybee *Apis mellifera*. *Current Biology*, *16*(14), 1471–1476. https://doi.org/10.1016/j.cub.2006.05.060

Lindell, A. K., Hopkins, W., & Scott, A. (2013). Continuities in emotion lateralization in human and non-human primates. *Frontiers in Human Neuroscience*, *7*, 1–9. https://doi.org/10.3389/fnhum.2013.00464

Llorente, M., Riba, D., Palou, L., Carrasco, L., Mosquera, M., Colell, M., & Feliu, O. (2011). Population level right-handedness for a coordinated bimanual task in naturalistic housed chimpanzees:

Replication and extension in 114 animals from Zambia and Spain. *American Journal of Primatology*, *73*, 281–290.

Llorente, M., Mosquera, M., & Fabré, M. (2009). Manual laterality for simple reaching and bimanual coordinated task in naturalistic housed *Pan troglodytes*. *International Journal of Primatology*, *30*, 183–197.

Losin, E. A. R., Russell, J. L., Freeman, H., Meguerditchian, A., & Hopkins, W. D. (2008). left hemisphere specialization for oro-facial movements of learned vocal signals by captive chimpanzees. *PLoS ONE*, *3*(6).

Lucidi, P., Bacco, G., Sticco, M., Mazzoleni, G., Benvenuti, M., Bernabò, N., & Trentini, R. (2013). Assessment of motor laterality in foals and young horses (*Equus caballus*) through an analysis of derailment at trot. *Physiology and Behavior*, *109*, 8–13.

Lutz, M. C., Ratsimbazafy, J., & Judge, P. G. (2019). Use of social network models to understand play partner choice strategies in three primate species. *Primates*, *60*, 247–260. https://doi.org/10.1007/s10329-018-00708-7

MacNeilage, P. F. (2014). Evolution of the strongest vertebrate rightward action asymmetries: Marine mammal sidedness and human handedness. *Psychological Bulletin*, *140*(2), 587–609.

MacNeilage, P. F., Studdert-Kennedy, M. G., & Lindblom, B. (1987). Primate handedness reconsidered. *Behavioral and Brain Sciences*, *10*, 247–303.

Magat, M., & Brown, C. (2009). Laterality enhances cognition in Australian parrots. *Proceedings of the Royal Society of London B: Biological Sciences*, *276*(1676), 4155-4162.

Makagon, M. M., McCowan, B., & Mench, J. A. (2012). How can social network analysis contribute to social behavior research in applied ethology? *Applied Animal Behaviour Science*, *138*, 152–161.

Mann, J., Stanton, M. A., Patterson, E. M., Bienenstock, E. J., & Singh, L. O. (2012). Social networks reveal cultural behaviour in tool-using dolphins. *Nature Communications*, *3*(1), 980. https://doi.org/10.1038/ncomms1983

Massen, J. J. M., & Koski, S. E. (2014). Chimps of a feather sit together: Chimpanzee friendships are based on homophily in personality. *Evolution and Human Behavior, 35*(1), 1–8. https://doi.org/10.1016/j.evolhumbehav.2013.08.008

McCowan, B., Anderson, K., Heagarty, A., & Cameron, A. (2008). Utility of social network analysis for primate behavioral management and well-being. *Applied Animal Behaviour Science*, *109*, 396–405.

McGrew, W. C., & Marchant, L. F. (1997). On the other hand: current issues in and meta-analysis of the behavioral laterality of hand function in nonhuman primates. *American Journal of Physical Anthropology*, *40*, 201–232.

McGrew, W. C., & Marchant, L. F. (2001). Ethological study of manual laterality in the chimpanzees of the Manale Mountains, Tanzania. *Behaviour*, *138*(3), 329–358.

Mettke-Hofmann, C., Ebert, C., Schmidt, T., Steiger, S., & Stieb, S. (2005). Personality traits in resident and migratory warbler species. *Behaviour*, *142*, 1357–1375.

Millot, S., Péan, S., Labbé, L., Kerneis, T., Quillet, E., Dupont-Nivet, M., & Bégout, M. L. (2014). Assessment of genetic variability of fish personality traits using rainbow trout isogenic lines. *Behavior Genetics*, *44*(4), 383-393.

Molho, C., Roberts, S. G. B., de Vries, R. E., & Pollet, T. V. (2016). The six dimensions of personality (HEXACO) and their associations with network layer size and emotional closeness to network members. *Personality and Individual Differences*, *99*, 144–148.

Morton, F. B., Weiss, A., Buchanan-Smith, H. M., & Lee, P. C. (2015). Capuchin monkeys with similar personalities have higher-quality relationships independent of age, sex, kinship and rank. *Animal Behaviour, 105*, 163–171. https://doi.org/10.1016/j.anbehav.2015.04.013

Petersen, M. R., Beecher, M. D., Zoloth, Moody, D. B., & Stebbins, W. C. (1978). Neural lateralization of species-specific vocalizations by Japanese macaques (*Macaca fuscata*). *Science*, *202*(4365), 324–327. https://doi.org/10.1126/science.99817

Piddington, T., & Rogers, L. J. (2013). Strength of hand preference and dual task performance by common marmosets. *Animal Cognition*, *16*(1), 127-135.

Pike, T. W., Samanta, M., Lindström, J., & Royle, N. J. (2008). Behavioural phenotype affects social interactions in an animal network. P*roceedings of the Royal Society B: Biological Sciences, 275*(1650), 2515–2520. https://doi.org/10.1098/rspb.2008.0744

Pinter-Wollman, N., Hobson, E. A., Smith, J. E., Edelman, A. J., Shizuka, D., de Silva, S., Waters, J. S., Prager, S. D., Sasaki, T., Wittemyer, G., Fewell, J., & McDonald, D. B. (2014). The dynamics of animal social networks: Analytical, conceptual, and theoretical advances. *Behavioral Ecology*, *25*(2), 242–255. https://doi.org/10.1093/beheco/art047

Réale, D., Dingemanse, N. J., Kazem, A. J., & Wright, J. (2010). Evolutionary and ecological approaches to the study of personality. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1560), 3937-3946.

Roberts, A. I., & Roberts, S. G. B. (2018). Intentional gestures predict complex sociality in wild chimpanzee. *bioRxiv*, 365858. https://doi.org/10.1101/365858

Roberts, A. I., & Roberts, S. G. B. (2018). Persistence in gestural communication predicts sociality in wild chimpanzees. *Animal Cognition*, *22*(5), 605-618. https://doi.org/10.1007/s10071-018-1219-6

Rogers, L. J. (1980). Lateralisation in the avian brain. *Bird Behavior*, *2*(1), 1-12.

Rogers, L. J. (2000). Evolution of hemispheric specialization: advantages and disadvantages. *Brain and Language*, *73*(2), 236-253.

Rogers, L. J. (2002). Lateralised brain function in anurans: Comparison to lateralisation in other vertebrates. *Laterality*, *7*(3), 219–239.

Rogers, L. J. (2009). Hand and paw preferences in relation to the lateralized brain. *Philosophical Transactions of the Royal Society*, *364*, 943–954.

Rogers, L. J., Zucca, P., & Vallortigara, G. (2004). Advantages of having a lateralized brain. *Proceedings of the Royal Society of London B: Biological Sciences*, *271*(6), 420-422.

Rose, P. E., & Croft, D. P. (2015). The potential of social network analysis as a tool for the management of zoo animals. *Animal Welfare*, *24*, 123–138.

Rose, P. E., & Croft, D. P. (2017). Social bonds in a flock bird: Species differences and seasonality in social structure in captive flamingo flocks over a 12-month period. *Applied Animal Behaviour Science, 193*, 87–97. https://doi.org/10.1016/j.applanim.2017.03.006

Rose, P. E., & Croft, D. P. (2018). Quantifying the social structure of a large captive flock of greater flamingos (*Phoenicopterus roseus*): Potential implications for management in captivity. *Behavioural Processes, 150*, 66–74. https://doi.org/10.1016/j.beproc.2018.03.002

Rushmore, J., Caillaud, D., Matamba, L., Stumpf, R. M., Borgatti, S. P., & Altizer, S. (2013). Social network analysis of wild chimpanzees provides insights for predicting infectious disease risk. *Journal of Animal Ecology*, *82*, 976–986.

Schel, A. M., Rawlings, B., Claidière, N., Wilke, C., Wathan, J., Richardson, J., Pearson, S., Herrelko, E.S., Whiten, A., & Slocombe, K. (2013). Network analysis of social changes in a captive chimpanzee community following the successful integration of two adult groups. *American Journal of Primatology*, *75*, 254–266.

Schneider, L. A., Delfabbro, P. H., & Burns, N. R. (2013). Temperament and lateralization in the domestic dog (*Canis familiaris*). *Journal of Veterinary Behaviour*, *8*(3), 124–134. https://doi.org/doi:10.1016/j.jveb.2012.06.004

Sih, A., Hanser, S. F., & McHugh, K. A. (2009). Social network theory: New insights and issues for behavioral ecologists. *Behavioral Ecology and Sociobiology*, *63*, 975–988.

Sih, A., Spiegel, O., Godfrey, S., Leu, S., & Bull, C. M. (2018). Integrating social networks, animal personalities, movement ecology and parasites: A framework with examples from a lizard. *Animal Behaviour, 136*, 195–205. https://doi.org/10.1016/j.anbehav.2017.09.008

Snijders, L., Blumstein, D. T., Stanley, C. R., & Franks, D. W. (2017). Animal social network theory can help wildlife conservation. *Trends in Ecology & Evolution*, *32*(8), 567-577.

Snijders, L., van Rooij, E. P., Burt, J. M., Hinde, C. A., van Oers, K., & Naguib, M. (2014). Social networking in territorial great tits: Slow explorers have the least central social network positions. *Animal Behaviour, 98*, 95–102. https://doi.org/10.1016/j.anbehav.2014.09.029

Sovrano, V. A., Rainoldi, C., Bisazza, A., & Vallortigara, G. (1999). Roots of brain specializations: Preferential left-eye use during mirror-image inspection in six species of teleost fish. *Behavioural Brain Research*, *106*(1), 175–180.

Stanley, C. R., & Dunbar, R. I. M. (2013). Consistent social structure and optimal clique size revealed by social network analysis of feral goats, *Capra hircus*. *Animal Behaviour, 85*(4), 771–779. https://doi.org/10.1016/j.anbehav.2013.01.020

Stanley, C. R., Mettke-Hofmann, C., Hager, R., & Shultz, S. (2018). Social stability in semiferal ponies: Networks show interannual stability alongside seasonal flexibility. *Animal Behaviour, 136*, 175–184. https://doi.org/10.1016/j.anbehav.2017.04.013

Sueur, C., Jacobs, A., Amblard, F., Petit, O., & King, A. J. (2011). How can social network analysis improve the study of primate behavior? *American Journal of Primatology*, *73*, 703–719.

Sueur, C., Petit, O., De Marco, A., Jacobs, A. T., Watanabe, K., & Thierry, B. (2011). A comparative network analysis of social style in macaques. *Animal Behaviour*, *82*(4), 845-852. https://doi.org/10.1016/j.anbehav.2011.07.020

Vallortigara, G., & Rogers, L. J. (2005). Survival with an asymmetrical brain: Advantages and disadvantages of cerebral lateralization. *Behavioral and Brain Sciences*, *28*, 575–633.

Vallortigara, G. (2006). The evolutionary psychology of left and right: Costs and benefits of lateralization. *Developmental Psychobiology*, *48*, 418–427.

Vallortigara, G., Rogers, L. J., Bisazza, A., Lippolis, G., & Robins, A. (1998). Complementary right and left hemifield use for predatory and agonistic behaviour in toads. *NeuroReport*, *9*(14), 3341-3344.

Voelkl, B., & Kasper, C. (2009). Social structure of primate interaction networks facilitates the emergence of cooperation. *Biology Letters*, *5*(4), 462–464. https://doi.org/10.1098/rsbl.2009.0204

Ward, J. P., Milliken, G. W., & Stafford, D. K. (1993). Patterns of lateralized behavior in prosimians. In J.P. Ward, & W.D. Hopkins (Eds.) *Primate laterality: Current Behavioral Evidence of Primate Asymmetries*, (pp. 43-74) New York, NY: Springer-Verlag.

Westergaard, G. C., Chavanne, T. J., Lussier, I. D., Houser, L., Cleveland, A., Suomi, S. J., & Higley, J. D. (2003). Left-handedness is correlated with csf monoamine metabolite and plasma cortisol concentrations, and with impaired sociality, in free-ranging adult male rhesus macaques (*Macaca mulatta*). *Laterality: Asymmetries of Body, Brain and Cognition*, *8*(2), 169–187. https://doi.org/10.1080/713754484

Wey, T., Blumstein, D. T., Shen, W., & Jordán, F. (2008). Social network analysis of animal behaviour: a promising tool for the study of sociality. *Animal Behaviour*, *75*, 333–344.

Wiper, M. L. (2017). Evolutionary and mechanistic drivers of laterality: A review and new synthesis. *Laterality*, *22*(6), 740–770. https://doi.org/10.1080/1357650X.2017.1291658

Wolf, J. B. W., Mawdsley, D., Trillmich, F., & James, R. (2007). Social structure in a colonial mammal: Unravelling hidden structural layers and their foundations by network analysis. *Animal Behaviour, 74*(5), 1293–1302. https://doi.org/10.1016/j.anbehav.2007.02.024

Chapter 2. Precision Hand Use in Chimpanzees.

Summary

This chapter presents the first empirical study of the thesis. Hand preference is the most common measure for assessing laterality in primates, and chimpanzee research in this topic is extensive and complex. This chapter builds on past research of hand preference in chimpanzees to present a study that examines hand use in different behaviours while considering important factors such as between-task consistency, posture and temporal stability. The objective of this chapter is to explain important aspects of hand preference in chimpanzees while presenting data for simple reach and spontaneous hand use from the Chester group. This will serve as a base for future chapters that will present additional ways of measuring laterality (Chapter 3) and examine possible links between hand preference and both personality (Chapter 4) and social networks (Chapter 6).

Introduction

Hand preference is often defined as an individual bias to carry out a particular task with either the left or right hand (MacNeilage et al., 1987; McGrew & Marchant, 1997b) and has to be understood as part of the larger phenomena of hand laterality. Hand preference has been widely studied in chimpanzees and other primates (Fitch & Braccini, 2013; Meguerditchian et al., 2013), largely due to the strong right-handedness shown in humans (Rogers, 2009), and it is often focused on investigating the evolutionary origins of lateralization. Understanding hand preference can create new knowledge regarding lateralization in primates (MacNeilage et al., 1987; Rogers, 2009). For example, the common left-hand preference in grabbing moving objects in primates has led authors to propose that the right hand might have played an important role in body support (MacNeilage et al., 1987). Given the wide range and complexity of behaviours involving hand use in chimpanzees, this species presents an excellent candidate to investigate finer details of hand preference, such as the possible effect of posture on the manifestation of hand preference.

Although research into hand preference might use the term as a synonym of handedness, the two concepts indicate different manifestations of laterality in hand use. Marchant and McGrew (2013) describe four categories of hand laterality: hand preference, task specialization, manual specialization and handedness. These categories are based on whether the lateralization occurs at the individual or at the population level, and whether it involves one or multiple tasks. Hand preference and manual specialization refer to an individual bias on one and multiple tasks, respectively, whereas task specialization and handedness refer to a population bias in a single task, and across different tasks, respectively (Marchant & McGrew, 2013).

These categories are useful to facilitate comparison between studies and to avoid confusion. However, it is important not to consider them independent phenomena, as often there are no clear cut-offs between categories and these terms are often used interchangeably by some authors (Meguerditchian et al., 2015). For example, it is difficult to define how many tasks are sufficient to constitute handedness instead of task specialization. Similarly, some population biases in lateralized behaviours are stronger in some species than in others; for example, humans show a stronger population bias in hand preference than other primate species such as chimpanzees (Fitch & Braccini, 2013). Differences not only in the existence of population bias, but also in the strength of those biases indicate underlying divergences in the evolutionary processes of laterality even within the same category. The aim of this study is not to use these categories to argue that human handedness is unique as Marchant and McGrew (2013) do. Instead, this study will use them as a way to structure the current knowledge of chimpanzee hand laterality to facilitate the understanding of hand laterality across different tasks, both naturalistic and experimental, that might explain its evolution.

Chimpanzees have demonstrated Marchant and McGrew's (2013) first category, hand preference, in a wide range of tasks. In the wild, individual hand preference has been reported for nutcracking (Boesch, 1991; Humle & Matsuzawa, 2009), bimanual actions (Corp & Byrne, 2004) and termite-fishing (McGrew & Marchant, 1992). In captivity, there is evidence of hand preference in clapping (Fletcher, 2006), reaching for objects in water (Fletcher & Weghorst, 2005), bipedal tool use (Braccini et al., 2010) and experimental tasks that require precision grips (Colell et al., 1995). Grooming, however, is one of the few behaviours studied that does not seem to elicit individual hand preference, neither in captivity (Hopkins et al., 2007) nor in the wild (Boesch, 1991; Marchant & McGrew, 1996; McGrew & Marchant, 2001). On the other hand, evidence regarding simple reaching tasks that do not require precision grips or bimanual actions is inconclusive, with studies in captivity reporting individual hand preferences (Hopkins, 1995a; Llorente et al., 2009) while studies in the wild have failed to find preferences (Mosquera et al., 2007). In spite of this, individual hand preference can exist without a clear population bias, potentially eliciting strong individual preferences leading half of the population to display a left-hand preference and the other half to show a right-hand preference.

However, for some particular tasks, chimpanzees have shown clear population level biases towards the use of one hand. Studies have also shown evidence of task specialization, that is, population biases towards the use of one hand for a particular task. Table 1 shows a summary of research studies of hand use in chimpanzees, detailing significant individual and population level preferences found. In the wild, chimpanzees have shown a right-hand task preference for ant-dipping and extraction of oil-palm heart (Humle & Matsuzawa, 2009). An initial study showed evidence of left-hand task preference for termite fishing (Lonsdorf & Hopkins, 2005), although further investigation failed to find significant biases for either hand (Bogart et al., 2012; Sanz et al., 2016). The majority of the evidence of task specialization, however, comes from studies in captivity, where a right-hand bias has been found for infant cradling and throwing (Hopkins et al., 1993), bipedal reaching (Hopkins, 1993), gesture production (Hopkins & Cantero, 2003, Prieur et al., 2016), clapping (Meguerditchian et al., 2012) and digging (Motes-Rodrigo et al., 2019). Interestingly, behaviours that might not be significantly lateralized at the individual level can show an overall population bias. Grooming, a behaviour usually conducted using both hands where one is considered more dominant, shows a small but significant population bias towards the use of the right hand even though most individuals do not display a significant hand preference (Hopkins et al., 2007). Similarly, simple reaching tasks have also shown a right-hand task specialization (Meguerditchian et al., 2015) at a population level, particularly when directed at inanimate objects (Forrester et al., 2012).

Table 1

Summary of research on hand laterality in chimpanzees.

Authors	Year	Setting	Sample size	Tasks	Posture	Findings
Boesch	1991	Wild	20	Simple reach, grooming, wadge-dipping and nut-cracking	---	Individual hand preference in wadge-dipping, but not in simple reach and grooming. There is no population level preference.
McGrew & Marchant	1992	Wild	15	Termite fishing	---	Individual hand preferences but no population level preference.
Hopkins	1993	Captive	40	Simple reach	Quadrupedal and supported bipedal	Population level right-hand preference for the bipedal supported posture, but not for the quadrupedal posture.
Hopkins et al.	1993	Captive	36	Throwing and infant cradling	Quadrupedal and bipedal postures for throwing	Individual hand preferenes for both tasks. Significant population level right-hand preferences for throwing. Males tended to be more right-handed when trowing bipedally.
Hopkins	1995a	Captive	110	Tube task	---	Strong individual hand preference and right-hand population preference.
Hopkins	1995b	Captive	51	Simple reach	---	Individual hand preferences but no population level preference. Males were significantly more right-handed than females.
Colell et al.	1995	Captive	24	Four experimental tasks manipulating objects	---	Individual hand preference that was consistent across tasks requiring precision grip.
Marchant & McGrew	1996	Wild	42	Spontaneous hand use	Arboreal and non-arboreal	No population level preference, did not assess individual hand preference for each task.
Hopkins & Pearson	2000	Captive	187	Simple reach in different postures, bimanual feeding and bimanual tasks	Quadrupedal and bipedal	Significant correlations between the tasks and overall significant population level right-hand preference.
McGrew & Marchant	2001	Wild	44	Spontaneous hand use	---	Individual hand preferences wer uncommon, no population level preference.

Hopkins et al.	2002	Captive	140	Simple reach	---	Thum-index grip use is related to right-handedness in chimpanzees.
Hopkins & Cantero	2003	Captive	73	Manual gestures	---	Individual and population level preference towards to use of the right hand when gesturing to a human experimenter.
Hopkins et al.	2004	Captive	467	Tube task	---	Three different colonies of chimpanzees showed significant population level right-handedness.
Corp & Byrne	2004	Wild	42	Bimanual food manipulation	---	Individual hand preferences but no population level preference.
Hopkins, Cantalupo et al.	2005	Captive	180	Tube task	---	Individual and population level preference towards to use of the right hand when gesturing to a human experimenter.
Hopkins, Russel et al.	2005	Captive	282	Simple reach	---	Most chimpanzees show individual hand preference but there is no population level preference.
Fletcher & Weghorst	2005	Captive	28	Spontaneous hand use	---	Half of the chimpanzees showed individual hand preferences for foraging behaviours, including simple reach. No population level preference.
Lonsdorf & Hopkins	2005	Wild	17	Termite fishing	---	Individual hand preferences and population level left-hand preference.
Fletcher	2006	Captive	26	Clapping	---	Individual hand preferences but no population level preference.
Mosquera et al.	2006	Captive	10	Spontaneous hand use	---	Few significant individual hand preferences, no population level preference.
Hopkins et al.	2007	Captive	215	Grooming	---	Most chimpanzees did not show strong hand preference but there is a significant population level right-hand preference in bimanual grooming
Humle & Matsuzawa	2009	Wild	13	Nut-cracking, pestle-pounding, ant-dipping and algae-scooping	---	Individual hand preferences for all tasks, population level right-hand preference for ant-dipping.

Llorente et al.	2009	Captive	14	Simple reach and tube task	---	Individual hand preferences, no population level preference in either task but a significant population level right-hand preference when considering both tasks together.
Braccini et al.	2010	Captive	46	Tool use	Sitting, bipedal, supported bipedal	Individual hand preferences but no population level preference. Bipedal posture increases the strength of the preference.
Llorente et al.	2011	Captive	120	Tube task	---	Individual hand preferences and population level right-hand preference.
Bogart et al.	2012	Wild	27	Termite fishing	---	Individual hand preferences but no population level preference.
Forrester et al.	2012	Captive	9	Reaching for innanimate and animate targets	---	Significant population level right-hand preference for animate targets.
Meguerditchian et al.	2012	Captive	94	Clapping	---	Individual hand preferences, there was a trend indicating a population level right-hand preference.
Hopkins et al.	2013	Captive	300	Manual gestures, tool use, simple reach and tube task	---	Individual hand preferences for all tasks, population level right-hand preference for manual gestures and tube tasks.
Hopkins et al.	2015	Captive	34	Manual gestures, simple reach and tube task	---	Individual hand preferences for all tasks, population level right-hand preference for manual gestures and tube tasks.
Meguerditchian et al.	2015	Captive	354	Simple reach and tube task	---	Individual hand preferences and right-hand population level preference for simple reach and tube task.
Prieur et al.	2016	Captive	39	Gestures	---	Individual preferences in only a third of the sample, but significant right-hand population level lateralization for most gestures.
Sanz et al.	2016	Wild	89	Termite fishing	---	Individual preference but no population level preference.
Motes-Rodrigo et al.	2019	Captive	9	Digging	---	Individual hand preference. No population level analysis due to small sample.
Padrell et al.	2019	Captive	19	Simple reach and tube task	---	Individual preferences but no population level preference. Scores were stronger in the tube task.

Furthermore, some of the strongest biases for right-hand task preferences in chimpanzees come from tube tasks in captivity (Hopkins, 1995b, Hopkins et al., 2004; Hopkins et al., 2005; Llorente et al., 2009; Llorente et al., 2011). The tube task is an experimental bimanual task first introduced by Hopkins (1995b) that involves holding a tube with one hand while reaching inside it for food with the other. While it is an artificial task only feasible in captive settings, it allows the study of the coordinated and complementary use of both hands simultaneously. Hopkins (2006) has argued that the strong right-hand bias for reaching for the food in the tube task, in comparison with other measures studied in the wild such as simple reaching, might be due to a better control over factors that have an important effect over hand use, such as grip morphology (Hopkins et al., 2002) and posture (Hopkins, 1993).

The predominance of evidence for right-hand biases in different tasks raises the possibility of chimpanzees exhibiting what McGrew and Marchant (2013) refer to as “true handedness”. However, evidence of handedness would need to show not only a population right-hand bias on different tasks, but also individual consistency between tasks. Verifying that individuals do not change their hand preference between tasks is important, since there is evidence in other primate species (Hook & Rogers, 2008) that population bias can remain the same even though some individuals change their preference from one task to another. Evidence of between task consistencies is scarce, as studies often report only one behaviour, or a few similar tasks. Hopkins and Pearson (2000) evaluated six tasks in a group of 187 captive chimpanzees and found consistency between feeding behaviours and reaching behaviours in three different postures, as well as consistency between two types of bimanual actions, including the tube task and a similar task where the instrument used was shaped as a ball. While there was evidence of right-hand population level preference in both bimanual tasks as well as feeding and reaching in a bipedal posture, individual preferences for bimanual tasks did not correlate with preferences in feeding and reaching. A more recent study by Hopkins et al. (2013) investigated between-task consistency using a bigger sample size, including 300 captive chimpanzees, and a more diverse set of behaviours, assessing hand preference for simple reach, tool use, manual gestures and the tube task. Hopkins et al. (2013) found that only the tube task and manual gestures showed a significant right-hand population bias although, interestingly, the four tasks were significantly correlated between each other, showing clear evidence of between-task consistency. This evidence of between task consistency, together with the extensive research showing right hand biases in different tasks, seems to point to the existence of chimpanzee handedness, which is likely the result of evolutionary pressures similar to those that caused human handedness (MacNeilage, 2014, Corballis, 2012).

The number and diversity of tasks used to assess hand use in chimpanzees requires not only comparisons between tasks, but also a careful examination of different aspects of the tasks and the actions performed during the tasks. Tasks are not only different in their actions, but also in the complexity of those actions, and task requirements and complexity are critical aspects in the assessment of hand preference in primates (Hopkins et al., 2015). For example, reaching for a piece of fruit on the ground requires a less complex action than manipulating an object with two hands and using precise movements to extract food from a tube. While task complexity might not necessarily facilitate the expression of population level hand preferences (Rogers, 2009), complex tasks increase the strength of the lateralization of hand use in chimpanzees (Boesh, 1991; Mosquera et al., 2012). According to Mosquera et al. (2012), tasks can be categorized based on their increasing difficulty in three categories: unimanual spontaneous tasks (such as scratching actions), unimanual precision tasks (such as simple reaching) and, finally, bimanual complementary tasks (such as the tube task).

Similarly, tasks can involve complexity in the body posture that it requires. Reaching for an object while in a bipedal posture will likely be more challenging than when sitting for a chimpanzee. Indeed, studies that examined the effects of posture on hand use have found similar results to those that study task complexity. In is important to note that research studying posture has focused on its effects on either unimanual precision tasks or bimanual complementary tasks due to the overall weaker preferences found in unimanual spontaneous tasks and their lower motor demands.

Chimpanzees show stronger hand preferences when using tools in a bipedal posture rather than sitting (Braccini et al., 2010). Interestingly, chimpanzees show stronger hand preferences when doing simple reaching tasks from a sitting posture, compared to a quadrupedal posture (Llorente et al., 2009). This may not be due to the task difficulty, but to situational convenience. For example, when approaching the object or piece of food, one hand might be closer to it due to the asymmetric nature of quadrupedal locomotion. While previous studies have investigated the effects of bipedal posture (Braccinni et al., 2010; Hopkins, 1993) and sitting (Llorente et al., 2009), other less common postures such as climbing still require further investigation. Lastly, a task can sometimes be performed in different ways, with slightly altered actions. Chimpanzees can do a simple reach action by grasping small objects between the index and middle finger, between their index and thumb or pressing the object with one finger against the ground until it gets stuck on the tip of the finger. Out of these three grip types, using the thumb and index is more common than the other grips and it is associated with the use of the right hand (Hopkins et al., 2005; Llorente et al., 2009; Meguerditchian et al., 2015), which has been attributed to a specialization of the right hand in motor skills (Hopkins et al., 2002).

Furthermore, an aspect often overlooked in hand preference research is its stability over time. Hopkins (1995a) observed that hand preference for simple reach was stable for juvenile chimpanzees over a period of one year. On the other hand, juvenile chimpanzees often show weaker hand preferences (Hopkins, 1995b), which suggests that hand preference for simple reach consolidates with maturity. Despite this assumption of hand preference consolidating in adulthood, temporal stability in adult life has not been commonly researched. Only one recent study, by Padrell et al. (2019), has investigated temporal stability of hand preference in adult chimpanzees. Padrell et al., (2019) found that hand preference for simple reach in chimpanzees correlated when comparing measures from 2008 and 2011, as well as when comparing measures from 2008 and 2018. However, there was no correlation in hand preference between 2007 and 2018, and three out of the 12 chimpanzees studied showed a different hand preference after 10 years. The authors (Padrell et al., 2019) suggest that this lack of correlation might be a consequence of the chimpanzees getting used to interacting with and manipulating the tubes between the periods, as they were occasionally provided as enrichment. It is also important to consider that, despite obtaining non-significant results, the small sample size of the study makes their statistical tests have low power, indicating that more research is needed in order to understand the changes over time in hand preference.

While many of the aspects previously described, such as the consideration of task complexity and the investigation of between-task and temporal stability, appear particularly suitable for studies in a controlled environment, it is also important to consider them when investigating hand use in a spontaneous context. Studies of unimanual precision and spontaneous hand use in the wild (Marchant & McGrew, 1996) and in captivity (Fletcher & Weghorst, 2005) have used extensive ethograms to describe hand use in fine detail, but often do not investigate some of these important aspects of hand use. Additionally, this study includes an examination of the possible effect effect of rearing history in hand preference, although past studies have not shown such an effect in chimpanzees (Hopkins & Wesley, 2002; Hopkins et al., 2003; 2004). The objective of the present study is to assess hand use in chimpanzees in captivity in a range of spontaneous and unimanual precision tasks, studying individual- and group-level laterality, while paying careful attention to postural variables and between-task consistency. This study contributes to previous research by expanding the investigation of posture, in particular, exploring the effects of climbing posture in hand preference, as well as by examining temporal stability between precision tasks in different postures. This study proposes four working hypotheses: 1) more demanding postures result in stronger preferences (Braccinni et al., 2010; Hopkins, 1993; Llorente et al., 2009), therefore climbing should result in stronger preferences than sitting and quadrupedal, and sitting postures should result in stronger preferences than quadrupedal postures; 2) hand indices of precision tasks will show positive relationships between tasks (Hopkins et al., 2013); 3) hand indices of precision tasks in 2017 will show positive relationships with indices in 2019 (Padrell et al., 2019); and 4) the strength of hand preference of precision tasks will be higher than the strength of spontaneous tasks (Mosquera et al., 2012).

Method

Sample and Housing

Subjects were 19 chimpanzees (Table 2) housed together at the chimpanzee colony of Chester Zoo in the United Kingdom. The exhibit consists of two enclosures: the indoor breeding centre and the outdoor island. The breeding centre is an indoor enclosure (approximately 13 meters high and 4.3 meters in diameter) containing climbing structures with resting sites, ropes and nets. The island is an outdoor area of approximately 0.2 hectares connected with the breeding centre, with wide vegetation patches and climbing posts connected with ropes and nets. Feeding involves scattering food on the indoor and outdoor areas, hiding food in the vegetation on the outdoor area in the morning, and food distribution in the indoor area between 1pm and 3pm each day. Additional enrichment food was occasionally offered in the form of yogurt or honey inside small holes on a wall, which the chimpanzees could access by using thin branches to “fish” the food. Known relatedness is included in Appendix I. Further details on rearing history for hand-reared chimpanzees are provided in Appendix II.

Table 2

Chimpanzees at Chester Zoo, UK, indicating sex, age and rearing history (2017).

Name	Sex	Age (years)	Rearing
Carlos	M	12	Mother-reared
Eric	M	14	Mother-reared
Dylan	M	30	Mother-reared
Friday	M	41	Hand-reared
Nicky	M	48	Hand-reared
Wilson	M	49	Hand-reared
Boris	M	51	Hand-reared
Tina	F	8	Mother-reared
Pattie	F	20	Mother-reared
Chrissie	F	21	Mother-reared
Vila	F	22	Mother-reared
Zee Zee	F	23	Mother-reared
Layla	F	25	Mother-reared
Alice	F	26	Mother-reared
Sally	F	29	Mother-reared
Sarah	F	31	Mother-reared

Mandy	F	40	Hand-reared
Farthing	F	42	Mother-reared
Rosie	F	44	Hand-reared

Ethical Note

The study was approved by the Ethics Committee of the School of Psychology at the University of Chester and the Research Committee of Chester Zoo. The study required only observational data; no manipulation of the animals or their environment was needed, and animals were observed only during their normal display hours at the zoo.

Procedure

Data collection for the study was conducted by the author of the thesis from January to April 2017, with additional data collected from June to August 2019 to assess temporal stability. Data were collected both indoors and outdoors using focal subject sampling of 10 minutes. Data were collected both indoors and outdoors using focal subject sampling of 10 minutes, switching focal subject when an animal moved out of sight in the outdoor enclosure to maximize data collection. Focals that were stopped this way were resumed later when the individual was visible again to achieve the total 10 minutes of observation. Focal subjects were chosen in a pseudo-random manner from those that were clearly visible, balancing the amount of total observed time. Focal subjects were switched when they moved out of sight in order to maximize data collection. All observations were collected from approximately 10am until 3pm, during standard zoo opening hours.

Table 3 shows the hand use ethogram, detailing 20 categories of spontaneous hand use. The ethogram was created by adapting existing ethograms of hand use published in studies in the wild (Marchant & McGrew, 1996) and naturalistic captivity (Fletcher & Weghorst, 2005). Although reliability is not often reported in hand use studies, given the easy discrimination between left- and right-hand use (McGrew & Marchant, 1997a), it was informally tested in January 2017 at the commencement of data collection with two additional observers in order to assure that all behavioural categories were sufficiently defined in the ethogram.

Table 3
Categories of hand use

Hand Use	Description
Back Reach	Rest a hand on another's back or shoulder
Cradle	Cradle an infant with one arm
Eat	Place object in mouth
Carry	Transport an object, without further acting on it
Clap	Bring one hand forcefully downwards to strike other hand
Drum	Rapid, forceful blow of hand on inanimate object
Environment-Directed Behaviour	All behaviours directed to the environment when no other category defines them better
Fish in hole	Insert stick inside a hole and pull it out
Genital touching	Repeatedly touch and inspect genitals
Grooming	Grooming or body cleansing of other individual (including both hands)
Hold	Grab and hold a part (hand, foot, chin, etc.) of another individual
Object manipulation	Manually interact with an object
Resting	Rest with arms crossed or holding a body part with one hand
Scratching	Rake rigidly and partly flexed digits over own body surface
Self-Directed Behaviour	All behaviours directed to the subject when no other category defines them better
Self-Grooming	Grooming directed towards the subject
Social Contact	Behaviours directed towards other subjects when no other category defines them better
Solicit Support	Extend an arm with the palm up to another individual
Simple Reach	Pick up an object
Throw	Hurl an object from the hand in a sudden motion

The total number of categories was reduced, excluding some behaviours that were reported as infrequent in the literature (Marchant & McGrew, 1996) such as “suck” or “hat”. Other behaviours were combined into a single category; for example, chin rest and idle are both recorded as rest.

Postural information was collected for simple reach and fish in hole, as these behaviours require precition reaching and manipulation that could be influenced by the position of the body, recording if the animal was in a quadrupedal position, sitting, standing bipedally or climbing with two legs and one arm for support. Information on grip morphology (Llorente et al., 2009; Meguerditchian et al., 2015) was not collected due to the difficulty of observing enough detail in hand use caused by the distance between the observer and the focal animals, as well as obstructions in visibility caused by high grass. Additionally, both simple reach and fish in hole were recorded as events and bouts to address possible problems of non-independence in the data (Hopkins, 1999; Marchant & McGrew, 1997). Events were recorded for simple reach each time an object was picked up, and for fish in hole each time the stick was introduced in the hole. Bouts in both behaviours were separated by: i) another behaviour (for example, if a chimpanzee is using the right hand to pick up objects, then scratches with the right hand, then resumes picking up, that would be considered as two bouts of picking up with the right hand), by ii) the use of the opposite hand (if a chimpanzee is picking up objects with the right, then starts picking up with the left, that would be considered as one bout with either hand) or by iii) a period of inactivity of five or more seconds. All other behaviours were recorded only as bouts.

A common occurrence when collecting data on spontaneous hand use is that often, most observations recorded belong to only a few categories, while other categories will often have a very low number of observations. For example, Marchant and McGrew (1996) studied 36 categories of spontaneous hand use and found that 89% of the observations were included in the 10 most common behaviours, while the remaining 26 categories were pooled together as “miscellaneous hand use”. This creates questions regarding when does a category have too few observations for analysis; for example, if an animal has been observed eating only twice, both times using their left hand, most researchers would agree that there were insufficient data to claim that the animal is completely left-handed when eating. Experimental studies, as well as studies that investigate simple reach, do not have this problem, since they can set a minimum number of trials for the animals to perform. Llorente et al. (2009), for example, scattered food directly on the ground and observed each animal for at least 100 manual events. Studies that employ extensive ethograms on hand use, however, must decide how to handle and potentially exclude categories with low numbers of observations. Boesch (1991) used data for an individual when seven or more behaviours had been observed, while Fletcher and Weghorst (2005) used eight as the minimum per individual. Mosquera et al. (2007) do not state a minimum number of observations required per individual, although they exclude a category where only 13 observations had been made for the full group. To my knowledge, there is no established statistical criteria on the minimum number of observations needed per animal in order to calculate their handedness index (Hopkins, 1999).

As this study is investigating the same chimpanzee group as Fletcher and Weghorst (2005), as well as using an ethogram adapted from that study, the minimum number of observations per animal used was eight. The following categories had fewer than eight behaviours observed for any individual and were not used in the analysis: fish in hole from a bipedal posture (FH3), clap, drum, genital touching, throw, suspensory, hold, back reach, solicit support and hit. While there is no minimum sample size to calculate the statistics used in this study, sample sizes of less than six are often considered extremely small (Bishara & James, 2012; Winter et al., 2016). Categories where more than eight behaviours were observed for only six or fewer chimpanzees were also excluded from the analysis: simple reach from a bipedal posture (SR3), fish in hole from a quadrupedal posture (FH1), fish in hole from a sitting posture (FH2), object manipulation, rest, self-directed behaviour, self-grooming, turn and cradle.

Data Analysis

Individual hand preferences were assessed by calculating binomial tests on the data for each individual, obtaining z-scores to evaluate if they were significantly lateralized (Fletcher & Weghorst, 2005; Hopkins, 1999; Padrell et al., 2019). Handedness indices (HI) were computed for each behavioural category using the formula HI = (R – L) / (R + L) (Hopkins, 1995), where R was the frequency of right-hand use and L was the frequency of left-hand use. HI ranges from -1, indicating a left-hand preference through to 1, indicating a right-hand preference, with values close to 0 indicating no particular preference. Absolute measures for HI (Wiper, 2017) were used to study strength of hand preference, independent of the direction of the preference.

Non-parametric statistics were used based on the small sample sizes and exploration of histograms and Q-Q plots. In order to address the possible differences between events and bouts, data for simple reach were recorded in both categories, as this task offers clear delimitations between events and is also frequently performed in bouts. Spearman's *rho* was used to investigate the relationship between events and bouts in the two most commonly observed behaviours were chimpanzees performed bouts of a behaviour in succession: quadrupedal and sitting simple reach. One sample t-tests were used to investigate group-level preferences by testing whether the mean laterality indices were significantly different from 0 (Llorente et al., 2011; Mosquera et al., 2007), using Bonferroni's correction to avoid increasing the type-1 error. Mann-Whitney U tests were used to examine differences between hand-reared and mother-reared chimpanzees in hand preference and strength of hand preference for simple reach in sitting and quadrupedal postures, using Bonferroni's correction to avoid increasing the type-1 error.

Simple reach was used in order to evaluate the effect of posture and temporal stability as it is a unimanual precision task, requiring higher motor demands than spontaneous tasks. Fishing behaviours were initially going to be used for posture and temporal stability but could not due to a lack of sufficient data. HI obtained from bouts for simple reach in quadrupedal and sitting postures were correlated using Spearman's *rho* to evaluate if individuals showed similar preferences using both measurements. Friedman's test was used to investigate differences between strength of HI between postures for simple reach. Spearman's *rho* was used to investigate inter-task consistency by correlating HI between simple reach and fish in hole as well as to assess temporal stability by correlating HI in simple reach measures obtained in 2017 and 2019. Simple reach measures were used to assess temporal stability as most individuals had enough observations in both periods. Finally, Friedman's test was used to evaluate differences in strength of HI between a precision unimanual task (simple reach) and spontaneous unimanual tasks (scratch, eat). Alpha level was 0.05 for all tests. Data analysis was carried out in SPSS v. 26.

Results

Data Used

The categories used in the analysis (Table 4) were: simple reach (quadrupedal, sitting and climbing), fish in hole while climbing, eat, carry, environment-directed behaviour, groom, scratch and total social contact.

Table 4
Number of chimpanzees used and total number of observations per behaviour

	Number of chimpanzees with 8 or more observations	Total number of bouts
Quadrupedal	19	2342
Sitting	19	2424
Climbing	8	190
Fish in hole Climbing	9	406
Eat	17	463
Carry	10	138
Environment-directed behaviour	16	229
Groom	14	206
Scratch	19	640
Social contact	19	218

Events vs Bouts

A Spearman correlation test was conducted in order to evaluate the choice of using bouts or events of behaviours. The Spearman's correlation analyses revealed significant, strong positive relationships between individual chimpanzees' HI for events and bouts of quadrupedal simple reach ($r(17) = .963$, $p < .001$) and between events and bouts for sitting simple reach ($r(17) = .886$, $p < .001$). These results indicate that measures are similar. This study proceeded to use bouts to calculate hand indices and z-scores in all behaviours where it was relevant.

Individual and Population Level Laterality

The majority of the chimpanzees were significantly lateralised in simple reaching behaviours in quadrupedal and sitting position, while only half of the chimpanzees showed a significant lateralization for simple reach when climbing and a third were lateralised for fishing (Table 5). Most chimpanzees were not significantly lateralised in spontaneous hand use (Table 6). Individual lateralization is shown in Table 7. T-tests adjusted using Bonferroni correction ($p < .005$) did not find significant population level laterality in any of the variables (Tables 5 and 6).

Table 5

Precision hand use measures, showing the number of lateralised individuals, the mean handedness index (HI) for the group as well as the result for the t-test.

	Simple Reach			Fish in Hole
	Quadrupedal (n=19)	Sitting (n=19)	Climbing (n=8)	Climbing (n=9)
Lateralised individuals	14	12	4	3
Mean HI (SD)	0.028 (0.533)	-0.095 (0.607)	0.41 (0.361)	0.109 (0.309)
T	0.229	-0.679	3.218	1.065
P	.821	.506	.015	.318

Table 6

Spontaneous hand use measures, showing the number of lateralised individuals, the mean handedness index (HI) for the group as well as the result for the t-test.

	Eat (n=17)	Carry (n=10)	Environment -directed behaviour (n=16)	Grooming (n=14)	Scratching (n=19)	Social contact (n=19)
Lateralised individuals	3	3	3	4	1	0
Mean HI (SD)	-0.029 (0.412)	0.126 (0.498)	0.039 (0.374)	0.124 (0.37)	0.043 (0.96)	0.068 (0.277)
t	-0.279	0.802	0.409	1.248	0.958	1.012
p	.784	.443	.689	.234	.351	.327

The Mann-Whitney U tests did not find significant differences between hand-reared and mother-reared chimpanzees when correcting for Bonferroni ($p < .015$) for quadrupedal simple reach (*U*(N=19)=16, *p*= .046), sitting simple reach *(U*(N=19)=26, *p*= .282), strength of quadrupedal simple reach (*U*(N=19)=60, *p*= .072) or strength of sitting simple reach (*U*(N=19)=52, *p*= .244).

Posture

A Friedman's test was conducted in order to see if the strength of hand preference (absolute value of the handedness indices) varied in simple reach depending on the posture. The test did not find significant differences between the strength of hand preference in simple reach using quadrupedal, sitting or climbing postures ($\chi^2(2) = 4.75$, *p*= .093).

Between-task Consistency

Table 7 shows the individual classification of hand preference for unimanual precision tasks. Of the 19 individuals, six showed perfect consistency, using the same preferred hand, although only five were measured in quadrupedal and sitting simple reach, and one, Farthing, was consistent in quadrupedal and sitting simple reach as well as climbing fish in hole. Of the remaining individuals, twelve were measured in at least three tasks and were consistent in at least two of them. One individual, Nicky, was measured in quadrupedal and sitting simple reach but was not consistent in his preferred hand.

Table 7
Between-task consistency for simple reach and fish in hole.

	Simple Reach			Fish in hole	Consistency
	Quadrupedal	Sitting	Climbing		
Carlos	L	R	L		2/3
Eric	L	L		R	2/3
Dylan	L	L			2/2
Friday	L	L			2/2
Nicky	L	R			0/2
Wilson	R	R			2/2
Boris	L	L			2/2
Tina	R	R	R	L	3/4
Patti	R	L	R	R	3/4
Chrissie	R	R	L		2/3
Vila	R	L	R	R	3/4
ZeeZee	R	R	R	L	3/4
Layla	R	L	R		2/3
Alice	R	R		L	2/3
Sally	R	L		R	2/3
Sarah	R	L		R	2/3
Mandy	L	L			2/2
Farthing	R	R		R	3/3
Rosie	L	L	R		2/3

R: right hand preference, L: left hand preference

Table 8 shows the results for the Spearman correlations investigating between-task consistency in precise unimanual actions. Simple reach in quadrupedal position showed a moderate positive correlation with simple reach while seating (*r*(17)= .661, *p*= .001) and a strong positive correlation with simple reach in climbing posture (*r*(6)= .881, *p*= .002).

Table 8
Spearman's correlation coefficients for simple reach in quadrupedal, sitting and climbing position and fish in hole.

	Simple reach sitting	Simple reach climbing	Fish in hole
Simple reach quadrupedal	.661*	.881*	-.25
Simple reach sitting		.119	-.483
Simple reach climbing			0

* Indicates significant correlations at $p < .01$, adjusting using a Bonferroni correction.

Temporal Stability

Table 9 shows the individual classification of hand preference for quadrupedal and sitting simple reach in 2017 and 2019. Ten individuals showed temporal stability in both postures, eight showed stability in only one posture and one individual, Nicky, did not show stability in either posture. The Spearman's tests revealed significant, strong positive relationships between the HI of quadrupedal simple reach in 2017 and 2019 ($r(15) = .735$, $p = .001$) as well as between the HI of sitting simple reach in 2017 and 2019 ($r(13) = .849$, $p < .001$).

Table 9

Temporal stability of simple reach in quadrupedal and sitting simple reach.

	Quadrupedal		Sitting		Stability
	2017	2019	2017	2019	
Carlos	L	L	R	L	1/2
Eric	L	L	L	L	2/2
Dylan	L	L	L	L	2/2
Friday	L	L	L	A	1/2
Nicky	L	R	R	L	0/2
Wilson	R	R	R	R	2/2
Boris	L	R	L	L	1/2
Tina	R	R	R	R	2/2
Patti	L	R	R	R	1/2
Chrissie	R	R	R	R	2/2
Vila	R	R	L	R	1/2
ZeeZee	R	R	L	R	1/2
Layla	R	R	L	L	2/2
Alice	R	R	R	R	2/2
Sally	R	R	L	R	1/2
Sarah	R	R	R	L	1/2
Mandy	L	L	L	L	2/2
Farthing	R	R	R	R	2/2
Rosie	L	L	L	L	2/2

Note: R: right hand preference, L: left hand preference, A: ambipreferent, indicating exactly the same number of left and right behaviours.

Differences Between Precision and Spontaneous Tasks

A Friedman's test was conducted to test for for differences between prevision tasks (simple reach) and spontaneous tasks (eat and scratch). The test found a significant difference in the strength of the hand preference between simple reach (sitting), eat and scratch ($\chi^2(2) = 6.5$, $p = .038$). Post Hoc Wilcoxon tests were carried out to investigate the differences between each action, using a Bonferroni correction to adjust the alpha level to $p < .0167$. There were no differences between simple reach and eat ($p = .196$) or between eat and scratch ($p = .034$). However, there was a significant difference between the strength of simple reach and the strength of scratch ($p = .004$).

Discussion

This study presents a comprehensive study of hand preference in captive chimpanzees, building upon previous studies (Fletcher & Weghorst, 2005; Marchant & McGrew, 1996) and adding important considerations such as posture, between-task consistency and temporal stability. The data do not show significant population level laterality for any task, and there is no significant effect of rearing history on hand preference. The results show no significant influence of posture on precision tasks, but they indicate temporal stability and between-task consistency in simple reach. Additionally, results also show that precision tasks elicit stronger hand preference than spontaneous tasks.

The first hypothesis of this study proposed that more demanding postures such as climbing would result in stronger hand preferences. This is based on past research that indicates that posture has an important effect in the strength, but not the direction, of hand preference. Llorente et al., (2009) found stronger hand preferences in sitting simple reach than in quadrupedal simple reach, while Hopkins (1993) found stronger hand preferences in bipedal postures than in quadrupedal simple reach. Similarly, Braccini et al., (2010) reported stronger hand preferences in a bipedal posture compared to sitting when using tools with one hand. Fletcher and Weghorst (2005) measured climbing postures but do not include an analysis of their effect on the strength or direction of hand preference. The current study attempted to account for these four postures (quadrupedal, sitting, bipedal and climbing) although bipedal posture was not considered in the analysis due to its infrequent observation. The results of the present study fail to replicate past findings, as there was no significant difference in the strength of hand preference between quadrupedal, sitting and climbing simple reach. A possible interpretation of the results might be that climbing does not present the same challenging postural demands as bipedalism has been suggested to do in previous studies (Braccini et al., 2010; Hopkins, 1993). These results could challenge the notion that more complex postures elicit stronger hand preferences, although they must be interpreted with caution due to the small number of observations of climbing simple reach, in comparison to quadrupedal and sitting simple reach. Further studies comparing climbing with bipedal postures might shed more light on the demands of both postures and how they impact hand preference.

The second hypothesis related to between-task consistency and proposed that there would be a positive relationship between the different simple reach tasks and fish in hole. The results show a positive relationship between quadrupedal and sitting simple reach, as well as between quadrupedal and climbing simple reach, although climbing and sitting simple reach did not have a significant correlation. More interestingly, fish in hole did not significantly correlate with any of the other tasks and most individuals did not display a significant hand preference in this task. This is also reflected in individual classification based on the polarity of the HI, which indicates that some individuals were lateralised to the opposite hand in fishing behaviours. Fish in hole is a behaviour where the chimpanzees at Chester Zoo use a flexible stick to extract yogurt or honey from small holes on a wall of their enclosure and is meant to replicate ant and termite fishing behaviours that are commonly observed in the wild. In the wild, termite fishing behaviours often elicit strong hand preferences (McGrew & Marchant, 1992) and population level left-hand preference (Lonsdorf & Hopkins, 2005). However, the artificial context in which this behaviour is emulated at Chester Zoo might constrain important aspects of the behaviour. For example, although studies of termite-fishing in the wild often do not give details of posture during the behaviour (Lonsdorf & Hopkins, 2005; McGrew & Marchant, 1992), the position and distribution of termite holes on the ground make them easily accessible from a sitting or quadrupedal posture. In contrast with this, the positioning of the holes at Chester Zoo often made it difficult for all individuals to access them at once unless they climbed on a nearby net, and it is possible that a climbing posture requires the use of the right hemisphere for keeping a more balanced posture (Rogers & Vallortigara, 2015), constraining the use of the left hand that would otherwise be used for fishing. Overall, correlations indicate consistency in hand preference between quadrupedal and sitting simple reach, as well as quadrupedal and climbing simple reach, but not between simple reach and fish in hole.

Regarding the third hypothesis and temporal stability, results are similar to those recently published by Padrell et al., (2019), showing strong correlations between handedness indices from simple reach measures in 2017 and 2019. Importantly, 10 out of the 19 chimpanzees show a preference towards using the same hand in all simple reach behaviours. While nine out of 19 show a change in their preferred hand in either quadrupedal or sitting posture it is worth noting that, whenever a posture elicited an opposite preference, the HI indicated weak lateralization.

Finally, the fourth hypothesis of this study proposed that the strength of hand preference in precision tasks would be stronger than the strength of hand preference for spontaneous tasks, based on the increased difficulty of precision movements (Mosquera et al., 2012). Results partially support this hypothesis, as simple reaching behaviours significantly elicited stronger preferences than scratching. It is interesting to note, however, that laterality in eating behaviours were not significantly different from laterality in either simple reach or scratching, pointing to a continuity between spontaneous and precision tasks, rather than a strict categorical distinction.

However interesting the current findings are, there are some limitations in the present study that require careful consideration. First, this study did not account for grip morphology due to the difficulty of assessing during the observations. Grip morphology is known to play an important role in hand use and hand preference, as right-handed chimpanzees tend to use precise grips more often, using their index finger and thumb (Hopkins et al., 2002; Meguerditchian et al., 2015). However, Llorente et al., (2009) failed to find a difference in hand preference between grip types and, following those findings, subsequent studies investigating simple reach with their chimpanzees do not consider grip types (Padrell et al., 2019). Nonetheless, it would be valuable to investigate grip morphology in future research conducted with the chimpanzee group at Chester Zoo since, to my knowledge, no data has been published on it to date.

A more general limitation is the use of simple reach as a way of characterising hand preference for chimpanzees. Vauclair et al., (2005) consider that simple reach requires minimal motor and cognitive demands, making it a less appropriate task to assess hand preference, since it seems to elicit weaker lateral asymmetries when compared to bimanual experimental tasks. Similarly, experimental studies of hand preference often use simple reach only as a “low-level” or control task to compare to bimanual tasks (Llorente et al., 2009; Padrell et al., 2019). A counter-argument to this characterization of simple reach as a less valuable measure comes from its ecological validity (Marchant & McGrew, 2013) and from the fact that tasks without strong constraints in the use of a particular specialization of a hemisphere can be more valuable when investigating an overall population level bias (Rogers, 2009). Following this rationale, certain specialised bimanual tasks might require the use of a function lateralised in a particular hemisphere. For example, the tube task might have an extensive use of cognitive resources in focused attention, a process that is lateralised in the left hemisphere (Rogers & Vallortigara, 2015), which could be the root of its population bias towards the right hand. Simple reach, with its simpler motor and cognitive requirements, might be more appropriate for the study of the influence of laterality in other aspects of behaviours such as personality (Rogers, 2009).

Lastly, it is worth discussing the use of events and bouts in the observation of hand use, since this has been a topic of debate in the past. It is important to mention that McGrew and Marchant (1997b) have criticised the use of frequency of events, as they argue that events are not independent, and they artificially increase the number of behaviours observed. On the other hand, Hopkins (1999) responded to these criticisms by encouraging the use of HI instead of z-scores, which will not be affected by bigger numbers of behaviours, and by pointing out that frequency of events might better reflect the amount of time each hand is used. For example, if a chimpanzee picks up nine pieces of food continuously with the right hand and then picks up one piece with the left, this would count as one bout with each hand, even though the right hand was used for longer. These arguments are further supported by research (Hopkins, 2001; Hopkins et al., 2013) that shows that the use of events and bouts to create HI do not produce different results, as both types of measures correlate strongly. The present study recorded simple reach both as frequency of events and bouts and the results show extremely high significant correlations between both, supporting Hopkins’ (1999) position.

In conclusion, this study assessed hand use in chimpanzees in a range of spontaneous and unimanual precision tasks, contributing to previous research by expanding the investigation of the effects of posture in hand preference and examining temporal stability and between-task consistency. The findings show that simple reach elicits stronger hand preference than some spontaneous behaviours such as scratching, but not stronger than eating behaviours, although there was no population level preference for any behaviour. Interestingly, the data showed no difference in strength of hand preference based on posture, indicating that climbing postures do not elicit stronger hand preferences in unimanual precision tasks. Finally, the findings of this study show temporal stability in simple reach, although only partial between-task consistency. In conclusion, this is the first study to combine the study of posture and temporal stability in hand preference in chimpanzees, while simultaneously offering a comprehensive investigation of spontaneous behaviours in chimpanzees, contributing to previous research by examining climbing posture and temporal stability, as well as between-task consistency and points towards additional aspects that can be valuable to study in the future, such as the influence of climbing postures in hand use.

References

Bishara, A. J., & Hittner, J. B. (2012). Testing the significance of a correlation with nonnormal data: Comparison of Pearson, Spearman, transformation, and resampling approaches. *Psychological Methods, 17*(3), 399–417. https://doi.org/10.1037/a0028087

Boesch, C. (1991). Handedness in wild chimpanzees. *International Journal of Primatology*, *12*(6), 541–558. https://doi.org/10.1007/BF02547669

Bogart, S. L., Pruetz, J. D., Ormiston, L. K., Russell, J. L., Meguerditchian, A., & Hopkins, W. D. (2012). Termite fishing laterality in the fongoli savanna chimpanzees (*Pan troglodytes verus*): Further evidence of a left hand preference. *American Journal of Physical Anthropology*, *149*, 591–598. https://doi.org/10.1002/ajpa.22175

Braccini, S., Lambeth, S., Schapiro, S., & Fitch, W. T. (2010). Bipedal tool use strengthens chimpanzee hand preferences. *Journal of Human Evolution*, *58*, 234–241. https://doi.org/10.1016/j.jhevol.2009.11.008

Cochet, H. (2012). Development of hand preference for object-directed actions and pointing gestures: A longitudinal study between 15 and 25 months of age. *Developmental Psychobiology*, *54*(1), 105–111. https://doi.org/10.1002/dev.20576

Colell, M., Segarra, M. D., & Sabater-Pi, J. (1995). Manual laterality in chimpanzees (*Pan troglodytes*) in complex tasks. *Journal of Comparative Psychology*, *109*(3), 298–307.

Corp, N., & Byrne, R. W. (2004). Sex difference in chimpanzee handedness. *American Journal of Physical Anthropology*, *123*, 62–68. https://doi.org/10.1002/ajpa.10218

Fitch, W. T., & Braccini, S. N. (2013). Primate laterality and the biology and evolution of human handedness: A review and synthesis. *Annals of the New York Academy of Sciences*, *1288*(1), 70–85. https://doi.org/10.1111/nyas.12071

Fletcher, A. W. (2006). Clapping in chimpanzees: Evidence of exclusive hand preference in a spontaneous, bimanual gesture. *American Journal of Primatology*, *68*, 1081–1088. https://doi.org/10.1002/ajp.20308

Fletcher, A., & Weghorst, J. (2005). Laterality of hand function in naturalistically housed chimpanzees (*Pan troglodytes*). *Laterality: Asymmetries of Body, Brain and Cognition*, *10*(3), 219–242. https://doi.org/10.1080/13576500442000049

Forrester, G. S., Quaresmini, C., Leavens, D. A., Spiezio, C., & Vallortigara, G. (2012). Target animacy influences chimpanzee handedness. *Animal Cognition*, *15*(6), 1121–1127. https://doi.org/10.1007/s10071-012-0536-4

Hill, E. L., & Khanem, F. (2009). The development of hand preference in children: The effect of task demands and links with manual dexterity. *Brain and Cognition*, *71*(2), 99–107. https://doi.org/10.1016/J.BANDC.2009.04.006

Hook, M. A., & Rogers, L. J. (2008). Visuospatial reaching preferences of common marmosets (*Callithrix jacchus*): An assessment of individual biases across a variety of tasks. *Journal of Comparative Psychology*, *122*(1), 41–51. https://doi.org/10.1037/0735-7036.122.1.41

Hopkins, W. D. (1993). Posture and reaching in chimpanzees (*Pan*) and orangutans (*Pongo*). *Journal of Comparative Psychology*, *107*(2), 162–168.

Hopkins, W. D. (1995a). Hand preferences for a coordinated bimanual task in 110 chimpanzees (*Pan troglodytes*): Cross-sectional analysis. *Journal of Comparative Psychology*, *109*(3), 291–297.

Hopkins, W. D. (1995b). Hand preferences for simple reaching in juvenile chimpanzees (*Pan troglodytes*): Continuity in development. *Developmental Psychology*, *31*(4), 619–625.

Hopkins, W. D. (1999). On the other hand: Statistical issues in the assessment and interpretation of hand preference data in nonhuman primates. *International Journal of Primatology*, *20*(6), 851–866.

Hopkins, W. D. (2006). Comparative and familial analysis of handedness in great apes. *Psychological Bulletin*, *132*(4), 538–559. https://doi.org/10.1037/0033-2909.132.4.538

Hopkins, W. D., Bard, K. A., Jones, A., & Bales, S. L. (1993). Chimpanzee hand preference in throwing and infant cradling: Implications for the Origin of Human Handedness. *Current Anthropology*, *34*(5), 786–790.

Hopkins, W. D., Cantalupo, C., Freeman, H., Russel, J., Kachin, M., & Nelson, E. (2005). Chimpanzees are right-handed when recording bouts of hand use. *Laterality*, *10*(2), 121–130.

Hopkins, W. D., Cantalupo, C., Wesley, M. J., Hostetter, A. B., & Pilcher, D. L. (2002). Grip morphology and hand use in chimpanzees (*Pan troglodytes*): Evidence of a left hemisphere specialization in motor skill. *Journal of Experimental Psychology: General*, *131*(3), 412–423. https://doi.org/10.1037//0096-3445.131.3.412

Hopkins, W. D., & Cantero, M. (2003). From hand to mouth in the evolution of language: The influence of vocal behavior on lateralized hand use in manual gestures by chimpanzees (*Pan troglodytes*). *Developmental Science*, *6*(1), 55–61. https://doi.org/10.1111/1467-7687.00254

Hopkins, W. D., Gardner, M., Mingle, M., Reamer, L., & Schapiro, S. J. (2013). Within- and between-task consistency in hand use as a means of characterizing hand preferences in captive chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, *127*(4), 380–391. https://doi.org/10.1037/a0031071

Hopkins, W. D., Hook, M., Braccini, S., & Schapiro, S. J. (2003). Population-Level Right Handedness for a Coordinated Bimanual Task in Chimpanzees: Replication and Extension in a Second Colony of Apes. *International Journal of Primatology,* *24*(3), 677–689. https://doi.org/10.1023/A:1023752816951

Hopkins, W. D., & Pearson, K. (2000). Chimpanzee (*Pan troglodytes*) handedness: Variability across multiple measures of hand use. *Journal of Comparative Psychology*, *114*(2), 126–135.

Hopkins, W. D., Russell, J. L., Hook, M., Braccini, S., & Schapiro, S. J. (2005). Simple reaching is not so simple: Association between hand use and grip preferences in captive chimpanzees. *International Journal of Primatology*, *26*(2), 259–277. https://doi.org/10.1007/s10764-005-2924-y

Hopkins, W. D., Russell, J. L., Remkus, M., Freeman, H., & Schapiro, S. J. (2007). Handedness and grooming in *Pan troglodytes*: Comparative analysis between findings in captive and wild individuals. *International Journal of Primatology*, *28*(6), 1315–1326. https://doi.org/10.1007/s10764-007-9221-x

Hopkins, W. D., & Wesley, M. J. (2002). Gestural communication in chimpanzees (Pan troglodytes): The influence of experimenter position on gesture type and hand preference. *Laterality, 7*(1), 19–30. https://doi.org/10.1080/13576500143000113

Hopkins, W. D., Wesley, M. J., Kay Izard, M., Hook, M., & Schapiro, S. J. (2004). Chimpanzees *(Pan troglodytes*) are predominantly right-handed: Replication in three populations of apes. *Behavioural Neuroscience*, *118*(3), 659–663. https://doi.org/10.1037/0735-7044.118.3.659

Humle, T., & Matsuzawa, T. (2009). Laterality in hand use across four tool-use behaviors among the wild chimpanzees of Bossou, Guinea, West Africa. *American Journal of Primatology*, *71*, 40–48. https://doi.org/10.1002/ajp.20616

Llorente, M., Mosquera, M., & Fabré, M. (2009). Manual laterality for simple reaching and bimanual coordinated task in naturalistic housed *Pan troglodytes*. *International Journal of Primatology*, *30*, 183–197. https://doi.org/10.1007/s10764-009-9338-1

Lonsdorf, E. V, & Hopkins, W. D. (2005). Wild chimpanzees show population level handedness for tool use. *Proceedings of the National Academy of Sciences*, *102*(35), 12634–12638.

MacNeilage, P. F. (2014). Evolution of the strongest vertebrate rightward action asymmetries: Marine mammal sidedness and human handedness marine mammals. *Psychological Bulletin*, *140*(2), 587–609. https://doi.org/10.1037/a0034298

Macneilage, P. F., Studdert-Kennedy, M. G., & Lindblom, B. (1987). Primate handedness reconsidered. *Behavioural and Brain Sciences*, *10*, 247–303. Retrieved from http://journals.cambridge.org

Marchant, L. F., & Mcgrew, W. C. (1996). Laterality of limb function in wild chimpanzees of Gombe National Park: Comprehensive study of spontaneous activities. *Academic Press Limited Journal of Human Evolution*, *30*, 427–443.

Marchant, L. F., & McGrew, W. C. (2013). Handedness is more than laterality: Lessons from chimpanzees. *Annals of the New York Academy of Sciences*, *1288*(1), 1–8. https://doi.org/10.1111/nyas.12062

McGrew, W. C., & Marchant, L. F. (1992). Chimpanzees, tools and termites: Hand preference or handedness? *Current Anthropology*, *33*(1), 114–119.

McGrew, W. C., & Marchant, L. F. (1997a). Using the tools at hand: Manual laterality and elementary technology in *Cebus* spp. and *Pan* spp. *International Journal of Primatology*, *18*(5), 787–810.

McGrew, W. C., & Marchant, L. F. (1997b). On the other hand: Current issues in and meta-analysis of the behavioral laterality of hand function in nonhuman primates. *American Journal of Physical Anthropology*, *40*, 201–232.

McGrew, W. C., & Marchant, L. F. (2001). Ethological study of manual laterality in the chimpanzees of the Manale Mountains, Tanzania. *Behaviour*, *138*(3), 329–358.

Meguerditchian, A., Gardner, M. J., Schapiro, S. J., & Hopkins, W. D. (2012). The sound of one-hand clapping: Handedness and perisylvian neural correlates of a communicative gesture in chimpanzees. *Proceedings of the Royal Society B: Biological Sciences*, *279*, 1959–1966. https://doi.org/10.1098/rspb.2011.2485

Meguerditchian, A., Phillips, K. A., Chapelain, A., Mahovetz, L. M., Milne, S., Stoinski, T., Bania, A., Lonsdorf, E., Schaeffer, J., Russell, J., & Hopkins, W. D. (2015). Handedness for unimanual grasping in 564 great apes: The effect on grip morphology and a comparison with hand use for a bimanual coordinated task. *Frontiers in Psychology*, *6*, 1–9. https://doi.org/10.3389/fpsyg.2015.01794

Meguerditchian, A., Vauclair, J., & Hopkins, W. D. (2013). On the origins of human handedness and language: A comparative review of hand preferences for bimanual coordinated actions and gestural communication in nonhuman primates. *Developmental Psychobiology*, *55*(6), 637–650. https://doi.org/10.1002/dev.21150

Molesti, S., Vauclair, J., & Meguerditchian, A. (2016). Hand preferences for unimanual and bimanual coordinated actions in olive baboons (*Papio anubis*): Consistency over time and across populations. *Journal of Comparative Psychology*, *130*(4), 341–350. https://doi.org/10.1037/com0000040

Mosquera, M., Geribàs, N., Bargalló, A., Llorente, M., & Riba, D. (2012). Complex tasks force hand laterality and technological behaviour in naturalistically housed chimpanzees: Inferences in hominin evolution. *The Scientific World Journal*, *2012*, 1–12. https://doi.org/10.1100/2012/514809

Mosquera, M., Llorente, M., Riba, D., Estebaranz, F., González-Brao, M., Lorenzo, C., Sanmartí, N., Toll, M., Carbonell, E., & Feliu, O. (2007). Ethological study of manual laterality in naturalistic housed chimpanzees (*Pan troglodytes*) from the Mona Foundation Sanctuary (Girona, Spain). *Laterality*, *12*(1), 19–30. https://doi.org/10.1080/13576500600886754

Motes-Rodrigo, A., Hernandez-Aguilar, R. A., & Laska, M. (2019). Preferential hand use by captive chimpanzees (*Pan troglodytes*) in manual and tool digging. *Primates*, *60*(4), 367–373. https://doi.org/10.1007/s10329-019-00727-y

Padrell, M., Gómez-Martínez, C., & Llorente, M. (2019). Short and long-term temporal consistency of hand preference in sanctuary chimpanzees (*Pan troglodytes*) for unimanual and bimanual coordinated tasks. *Behavioural Processes*, *167*, 103911. https://doi.org/10.1016/J.BEPROC.2019.103911

Prieur, J., Pika, S., Barbu, S., & Blois-Heulin, C. (2016). A multifactorial investigation of captive chimpanzees' intraspecific gestural laterality. *Animal Behaviour*, *116*, 31–43. https://doi.org/10.1016/j.anbehav.2016.03.024

Rogers, L. J. (2009). Hand and paw preferences in relation to the lateralized brain. *Philosophical Transactions of the Royal Society*, *364*, 943–954. https://doi.org/10.1098/rstb.2008.0225

Rogers, L., & Vallortigara, G. (2015). When and why did brains break symmetry? *Symmetry*, *7*(4), 2181–2194. https://doi.org/10.3390/sym7042181

Sanz, C. M., Morgan, D. B., & Hopkins, W. D. (2016). Lateralization and performance asymmetries in the termite fishing of wild chimpanzees in the Goualougo Triangle, Republic of Congo. *American Journal of Primatology*, *78*(11), 1190–1200. https://doi.org/10.1002/ajp.22574

Vauclair, J., Meguerditchian, A., & Hopkins, W. D. (2005). Hand preferences for unimanual and coordinated bimanual tasks in baboons (*Papio anubis*). *Cognitive Brain Research*, *25*(1), 210–216. https://doi.org/10.1016/J.COGBRAINRES.2005.05.012

de Winter, J. C., Gosling, S. D., & Potter, J. (2016). Comparing the Pearson and Spearman correlation coefficients across distributions and sample sizes: A tutorial using simulations and empirical data. *Psichological Methods, 21*(3), 273–290.

Chapter 3. Sidedness and Motor Laterality in Chimpanzees

Summary

This chapter follows from Chapter 2 by examining additional measures of laterality in chimpanzees. While Chapter 2 focuses on the most commonly used measure of laterality, hand preference, Chapter 3 investigates the less common measures of locomotion laterality, both when moving quadrupedally and climbing. More importantly, this chapter introduces a novel measure of laterality in primates: sidedness, which measures laterality in the way chimpanzees move around conspecifics. As sidedness is a measure of social laterality, the study presented in this chapter seeks to explain the role of the right hemisphere in the brain when processing social stimuli and researches its possible involvement in sidedness. The topics covered here serve a dual purpose: to introduce a novel measure of laterality and to present the link between laterality and general behaviour, serving a bridge between Chapter 2, which revolves around technical and methodological aspects of laterality, and Chapter 4, which examines the link between laterality and personality.

Introduction

Laterality encompasses different behavioural and sensorial asymmetries including, but not limited to, hand preference, footedness and eye preference that reflect neural lateralization of functions on the contra-lateral brain hemisphere (Fitch & Braccini, 2013). The study of motor laterality in non-human primates has extensively focused on hand preference (Marchant & McGrew, 2013; Meguerditchian et al., 2013), possibly due to obvious comparisons with hand preference in humans, as it is probably the most evident lateral asymmetry in our species (Corballis, 2009). Laterality research in multiple primate species has found ample evidence that individuals show asymmetries in hand use (Fitch & Braccini, 2013) and it is known to be task-dependant, with some individuals switching their preferred hand for different tasks (in common marmosets: Hook & Rogers, 2008; in chimpanzees: Lonsdorf & Hopkins, 2005), which indicates that laterality is not a single process but a complex multi-faceted phenomenon. This study aims to offer an overview of lateralised processes that go beyond hand preference. With this objective, this introduction addresses the current knowledge regarding the advantages of lateralization and hemispheric specialization and focuses more specifically on the link between the right-hemisphere and sociality. Drawing from literature in other species, this study investigates lateral biases in locomotion and on the way chimpanzees move around their conspecifics, hereafter referred to as "sidedness".

Studying laterality across multiple actions can generate deeper knowledge about the evolution of lateralization, helping to shed some light on how different processes have lateralised during the evolutionary history of a species. For example, individual hand preferences in simple reach are common in chimpanzees (Hopkins, 1995; Llorente et al., 2009), with most studies reporting no findings of population level biases (Hopkins et al., 2013). A phenomenon that is as widespread as laterality may offer evolutionary advantages that can explain its prevalence amongst individuals, even in the absence of population level lateralization. Lateralization of different processes in each hemisphere of the brain reduces parallel processing and duplication of function and is associated with an increase in neural processing capacity (Corbalis, 2014; Vallortigara, 2000; Vallortigara & Rogers, 2005). However, these advantages in individual neural processing cannot, on their own, explain the existence of population level laterality.

In order to understand laterality as a population level phenomenon, it is important to recognise laterality as a manifestation of functional asymmetries of the brain. In vertebrates, including primates, each hemisphere of the brain is specialized for different functions (Rogers & Vallortigara, 2015), which are displayed as asymmetries not only in behaviours, but also in processes of perception. Furthermore, lateral specializations in sensory and emotional processing might be at the base of some population level asymmetries in some motor behaviours (Rogers, 2009; Rogers, 2017). A clear example of this is the continuity of laterality in emotional expression in primates, as both human and non-human primates show more marked displays of emotion in the left side of the face (Lindell, 2013) as well as a bias towards inspecting the left side of the face for longer (Guo et al., 2009). In many vertebrate species, including birds, mammals and fish, the left hemisphere is heavily involved in categorising stimuli and focused attention (Rogers & Vallortigara, 2015) while the right hemisphere is involved in rapid processing of social stimuli and processing emotional expressions (Salva et al., 2012). Social stimuli might be especially relevant in facilitating population level laterality. While solitary animals might gain the above-mentioned advantages in neural processing by having lateralised behaviours, social animals have to interact and coordinate with lateralised conspecifics (Ghirlanda et al., 2009; Ghirlanda & Vallortigara, 2004), and showing a similar lateral bias to others can lead to easier and more precise coordination.

Right Hemisphere and Social Stimuli

The link between population level laterality and sociality was hypothesised by Rogers (1989), who proposed that a shared lateral bias in a group might influence group structure. Early research of laterality and sociality in multiple fish species supported this idea, showing that social species were more likely to show a population level bias than solitary species (Bisazza et al., 2000). Social interactions and, in particular, aggressive behaviour towards conspecifics are highly lateralised at the group level, with most individuals of teleost fish (*Gambusia, holbrooki, Xenotoca eiseni* and *Betta splendens*) preferring to initiate attacks and displays while facing rivals with their right eye (Bisazza & de Santi, 2003), while other species (*Danio rerio*) prefer to use their left eye (Ariyomo & Watt, 2013). Similarly, group biases can arise from a need to coordinate escape responses from predators. For example, Yellow-and-Black fusiliers (*Caesio teres*) show a group bias towards turning to the right, keeping the predator on their left side, and individuals that show an opposite preference have decreased escape performance (Chivers et al., 2016). Conspecific aggression and escape behaviours require a quick response in processing social and potentially dangerous stimuli and, although there are exceptions to this (Bisazza & de Santi, 2003), would require the use of the right hemisphere, facilitating faster responses to stimuli in the left visual field (Salva et al., 2012).

Research in non-primate mammals suggest a right hemisphere dominance for escape responses, showing that horses (Austing & Rogers, 2007) and dunnarts (Lippolis et al., 2005) show faster and more marked escape reactions when detecting threats approaching from the left side. In addition to escape reactions, research in non-primate mammals has also focused on the right-hemisphere dominance for processing social stimuli, particularly in mother-infant situations. In marine mammals, infants show a population level preference to swim on their mother's right side, which allows them to monitor them with their left eye (Hill et al., 2017; Karenina, Giljov, Glazov, & Malashichev, 2013; Karenina, Giljov, Ivkovich, et al., 2013), although in potentially threatening situations, mothers actively move to the right side to better monitor the calf (Karenina, Giljov, Ivkovich et al., 2013). Interestingly, other mammals, including humans (Sieratzki & Woll, 1996), non-human primates (Hopkins, 2004), elephants (*Elephas maximus*, Karenina et al., 2018) and flying mammals like bats (*Pteropus giganteus*, Giljov et al., 2018) keep their infants to their left, which allows them to better monitor the needs of their infants and indicates a right hemisphere dominance for social processing (Karenina et al., 2017).

Sidedness

Studies in sheep have found a population level bias to pass obstacles while keeping them on the left visual hemifield (Barnard et al., 2016; Versace et al., 2007). Versace et al. (2007) propose that this lateral bias towards monitoring obstacles is likely a by-product of the right-hemisphere bias in response to conspecifics (in sheep Pierce et al., 2000; in primates Guo et al., 2009; in birds Vallortigara 1992; Vallortigara & Andrew, 1994; in tadpoles Dadda et al., 2003). While passing near inanimate objects might not necessarily elicit the same bias as a social stimulus, both might reflect a general tendency to keep stimuli on a particular side when passing, a bias in "sidedness". Primates have also shown a bias towards keeping conspecifics on their left side. Baboons tend to position themselves in a way such that conspecifics are kept on their left side during fights although, interestingly, after a conflict, the retreating baboon did not show a left-side visual preference (Casperd & Dunbar, 1996). Casperd and Dunbar (1996) explain that, in most cases, the dominant baboons walked away from threats and suggest that, as conflicts did not escalate, this reflects a lack of interest and concern by the dominant in the conflict.

Research into chimpanzee laterality has focused to a large extent on hand preference (Fletcher & Weghorst, 2005; Hopkins et al., 1993; McGew & Marchant, 1992; Mosquera et al., 2006), although there is evidence of continuity in hemispheric lateralization of other behaviours that is consistent with other vertebrates such as birds and fish (Rogers, 2017). The left hemisphere shows a specialization in precise motor skills (Hopkins et al., 2002) and the right hemisphere is specialised in processing social stimuli such as emotion expression (Fernández-Carriba et al., 2002), vocal communication (Reynolds Losin et al., 2007; Wallez et al., 2012) and infant cradling (Hopkins, 2004). More recently, research by Quaresmini et al. (2014) considered the idea that social stimuli are essential in eliciting laterality and incorporated it in a study of hand preference, finding that captive gorillas have a significant preference for keeping conspecifics on their left side, and chimpanzees show a similar trend, although it was not statistically significant. It is important to consider that Quaresmini and colleagues (2014) use manual activities such as picking up food from the ground as referential events to assess social laterality, as opposed to assessing laterality in a social behaviour, which allows them to assess the positioning of chimpanzees with respect to their conspecifics. Conversely, this also creates questions regarding the lateralisation of social behaviours, such as gestures or social positioning during locomotion. For example, if chimpanzees have a preference towards keeping their conspecifics on their left side, this might be more evident in the side they keep conspecifics on when walking past them or when sitting next to them.

An important factor to consider when investigating social positioning is lateralization of locomotion itself. Versace et al. (2007) propose a bias in sidedness could be accounted for by an overall lateral bias in locomotion. For example, bottlenose dolphins (*Tursiops truncatus*) in captivity have a tendency to swim in counter-clockwise circles (Sobel et al., 1994), which could affect their movement in the group, and facilitate the positioning of adults on the right side of infants. Some species of primates have shown a population level bias towards initiating quadrupedal movement using their right hand (Regaiolli et al., 2016). There is some evidence of locomotion preferences in chimpanzees in captivity. Morcillo et al. (2006) studied the leading arm during different types of locomotion in captive chimpanzees, including quadrupedal, climbing and descending movement, and found a group-level right-hand preference in quadrupedal locomotion and a left-hand preference when descending, although there was no significant preference in climbing locomotion and most individuals did not show significant individual preferences. Hopkins (2008) found similar results in captive chimpanzees regarding a left-hand preference when descending and suggested that this could indicate a specialization of the left hand in supporting the body, freeing the right hand to initiate movement. Regaiolli et al. (2016) suggest a link between locomotion preferences and other lateralised behaviours, as the left-hand specialization that they find when descending in captive great apes can be explained by the left-hand specialization in supporting the body, which, according to the Postural Origins Theory (MacNeilage et al., 1987) would have freed the right hand to specialise in manipulating objects. In contrast with studies in captivity, wild chimpanzees do not show evidence of individual or population level lateralization (Marchant & McGrew, 1996), which might be due to captive studies having a higher level of terrain uniformity and being able to obtain more detailed observations.

Previous research in motor and social laterality in chimpanzees has focused on leading arm during locomotion (Hopkins, 2008; Morcillo et al., 2006; Regaiolli et al., 2016) and on the influence of social stimuli on hand laterality (Quaresmini et al., 2014). However, little is known about how social stimuli might affect the way chimpanzees freely move around each other. From previous research, chimpanzees would be expected to keep conspecifics on their left side, particularly if they can be potential threats, and show a right arm preference to initiate quadrupedal locomotion. This study will investigate lateralization in movement in a social environment, henceforth referred to as sidedness, as well as arm preference when walking and climbing and whether there are individual or population level preferences. Similarly, this study will investigate if sidedness is influenced by potential threats from conspecifics. Observations of agonistic interactions between chimpanzees were used in order to study those potential threats while passing close to other group members. The hypotheses of this study are: 1) chimpanzees will show a left bias in sidedness, that is, they will tend to use their left side more often when walking around chimpanzees that can potentially initiate conflict with them; and 2) walking and climbing preferences will be correlated with sidedness.

Method

Sample

The sample consisted of a group of 19 chimpanzees housed at the chimpanzee colony of Chester Zoo. For more details on the individual chimpanzees, the group structure and the enclosure see Chapter 2.

Procedure

This study used ten-minute continuous focal samples to assess locomotion laterality and passing sidedness, choosing focal subjects opportunistically while attempting to collect a similar amount of data for each animal. Data collection for locomotion was conducted in two periods: from January to April 2017 and from June to August 2019. Locomotion was assessed using two measures: quadrupedal and climbing locomotion. When starting quadrupedal locomotion from a sitting posture, chimpanzees use one hand first to support their body and then extend the opposite limb to initiate movement. Leading limb was assessed by recording the extended limb used to start moving from a sitting posture into quadrupedal movement (Morcillo et al., 2006; Regaiolli et al., 2016). Leading limb in climbing was assessed by registering the first hand used to initiate climbing.

Data collection for Sidedness was conducted from June to August 2019. Passing sidedness was recorded when the focal chimpanzee passed within two arms' length of another animal/s. The name of the animal/s passed were recorded and three codes were used to record information regarding positioning (Table 1): 1) the lateral position of the focal animal toward one or more conspecifics, recording the focal animal's shoulder closest to the conspecific as left or right; 2) the position that the conspecifics were facing while being passed , recorded as "front", when they were facing the focal animal or as "back" when conspecific had their backs towards the focal animal; and 3) whether only the focal was moving or both were in motion. Any passes that were made where forced sidedness occurred (i.e. the other chimpanzee is at the right side of a door, leaving the passing chimpanzee no option but to pass them on their right when going through the door) were not recorded (Dadda et al., 2003). This sidedness measure is comparable to previous motor bias in relation to passing close to obstacles (Barnard et al., 2016; Versace et al., 2007), although the present study codes the lateral position of the social stimuli, rather than the path of the focal animal (i.e. in the present stimuli, a "left pass" is when a chimpanzee keeps a conspecific on their left side when passing them). Sidedness was recorded both in the outdoor and indoor parts of the enclosure, although the outdoor area presented more opportunities for observing sidedness. Inter-rater reliability was calculated using Cohen's Kappa based on four 10-minute focal observations, obtaining a coefficient of .8 for the type of sidedness (i.e. front pass or back pass), with an agreement of 100% for the side of the pass in any case.

Table 1
Sidedness categories

	Focal moving		Both moving	
Front	Left	Right	Moving Left	Moving Right
Back	Back Left	Back Right	Back Moving Left	Back Moving Right

Agonistic Interactions

Data for agonistic interactions were collected from January to December 2017, recording agonistic behaviours described using Clark's (2011) ethogram *ad libitum* (Altmann, 1974). Half-weighted ratio indices ($E_{AB} = \frac{x}{x+yAB+\frac{1}{2}(yA+yB)}$) were calculated in order to define the edges of the network estimating the proportion of interactions between 0 and 1, where 0 indicates that they never displayed agonistic interactions and 1 that they displayed them in every observation (Farine & Whitehead, 2015). Half-weighted ratios are used as a more conservative estimation of association than weighted ratios, less biased when there is a chance of missing observations of individuals (Farine & Whitehead, 2015). The ratios were used to create a directed (asymmetrical) social network matrix (see Table 2 for an example showing how Carlos displays more agonistic behaviours to Dylan than Dylan does to Carlos, values in the diagonal are excluded from matrices as they do not reflect interactions between individuals) (Whitehead & James, 2015).

Table 2
Example of an agonistic matrix

	Carlos	Dylan
Carlos		0.609
Dylan	0.087	

Data Analysis

Sidedness observations were recorded in matrices detailing left and right passes of each individual to each other individual in the group (see Table 3 for an example, where Carlos does 3 passes on the left and 2 on the right to Dylan, while Dylan passes Carlos twice on the left). Total z-scores for sidedness were calculated by combining all the observations for a focal, obtaining a total score for each individual in each sidedness category. Laterality indices (LI) were calculated for the total sidedness for each individual following the formula LI = (R – L) / (R + L) (Hopkins, 1995), where R was the frequency of right passes and L was the frequency of left passes. The LI range from -1, indicating a left-hand preference to +1 indicating a right-hand preference, with values close to 0 indicating no preference. Similarly, LI were calculated for leading arm and leading arm when climbing for each individual. Following Fletcher and Weghorst's (2005) criteria, individuals with fewer than eight observations per behaviour were excluded from the analysis. One sample t-tests were used to investigate group-level preferences by testing whether the mean laterality indices were significantly different from 0, using Bonferroni's correction to avoid increasing the type-1 error. Mann-Whitney U tests were used to examine differences between hand-reared and mother-reared chimpanzees in sidedness and locomotion laterality, using Bonferroni's correction to avoid increasing the type-1 error. Alpha level was p = .05 for all tests. Data analysis was carried out in SPSS v. 26.

Table 3
Example of a matrix of observed passes

	Carlos		Dylan	
	Left	Right	Left	Right
Carlos			3	2
Dylan	2	0		

In order to create a matrix that reflected sidedness for each dyad, dyadic sidedness (DS) indices were calculated for each dyad, using the formula DI = ([R – L] / [R + L]) + 2. This formula is adapted from Hopkins' (1995) formula so that a score of 1 indicates a left-side preference, a score of 3 indicates a right-side preference and a score of 2 indicates no preference (see Table 4 for an example, reflecting the dyadic sidedness of Carlos passing Dylan as -.2, which indicates a small tendency to pass on the left, and the dyadid sidedness of Dylan passing Carlos as -1, which indicates that Dylan always passed Carlos on the left). This adaptation is required, as matrix analysis would treat scores of 0 as absence of passes in a dyad, and it is necessary to discriminate between dyads with ambiguous preferences and dyads with no observations. Dyads with only 1 observation were excluded, as they would result in a score of -1 or 1 and could bias the results. Quadratic Assignment Procedure (QAP) correlations were calculated in R v. 3.6.1 using the package "sna" (Butts, 2019) to test the consistency of grooming, affiliative and agonistic behaviours across the three time periods. This procedure correlates two matrices by modifying them into two columns and calculating Pearson's *r* between them. It creates a set number of random permutations with the rows and columns of the matrices to create a distribution to compare with the correlation obtained to calculate the significance of the correlation. The *p*-value is calculated by determining the proportion of times that the random correlations are larger than the observed correlation. All analyses used 5000 permutations.

Back sidedness, moving sidedness and moving back sidedness were excluded from these analyses due to the high number of dyads (57% in back sidedness, 81.9% in moving sidedness and 79.7% in moving back sidedness) with only one observation. Spearman's rho was used to test for correlations between laterality indices of locomotion and sidedness. Alpha level was p = .05 for all tests.

Table 4
Example of a matrix displaying laterality indices

	Carlos	Dylan
Carlos		-.2
Dylan	-1	

Results

Sidedness

Table 5 shows the laterality indices for front pass, back pass, moving pass, moving back pass and total pass for all individuals that performed 8 or more passes per category. Only one individual (Mandy) is significantly lateralised in front passing, preferring to pass others on her left side, and no individual was lateralised for any of the other types of passing. Table 6 shows the means and standard deviations of all sidedness variables.

Table 5

Laterality indices for sidedness measures

	Front pass	Back pass	Moving pass	Moving back pass	Total pass
Carlos	.20	.00	.23	-.33	.06
Eric	-.08	.03			-.03
Dylan	-.25	-.22	.54		-.07
Friday	-.09	-.29			-.26
Nicky	-.14		.20		-.13
Wilson	-.11	-.40	-.40		-.21
Boris	.04				.16
Tina	0	.07	.20	.24	.08
Patti	0	.10		-.14	.03
Chrissie	0	.00			.00
Vila	-.14	.11	.25		.04
ZeeZee	-.08	.20			.08
Layla	-.09	-.10	.50		.01
Sally	-.16	-.43			-.05
Alice	.29	-.20			-.17
Sarah	-.08				-.05
Mandy	-.65*	.20			-.20
Farthing	.05	-.14			.00
Rosie	.07	.00			.04

* Indicates a significant z-score.

Table 6

Means and standard deviations for front pass, back pass, moving pass, moving back pass and total pass.

	Mean (SD)
Front pass	-.07 (.19)
Back pass	-.07 (.2)
Moving pass	.22 (.31)
Moving back pass	-.8 (.29)
Total pass	-.04 (.11)

The one sample t-tests did not find significant group lateralization for front pass (*t*(18)= -1.58, *p*= .131), back pass (*t*(15)= -1.36, *p*= .195), moving pass (*t*(6)= 1.87, *p*= .111), moving back pass (*t*(2)=-.458, *p*= .692) or total pass (*t*(18)= -1.36, *p*= .191). Mann-Whitney U tests did not find significant differences between mother-reared and hand-reared chimpanzees in front pass (*U*(N=19)= 48, *p*= .467), back pass (*U*(N=16)= 28.5, *p*=.599), moving pass (*U*(N=7)= 9.5, *p*= .095) or total pass (*U*(N=19)= 54.5, *p*= .179).

Motor Laterality

Table 7 shows the laterality indices for leading arm and leading arm when climbing for individuals with more than eight observed behaviours. Three chimpanzees show significant leading arm preference in quadrupedal position, one preferring the right hand (Carlos) and two preferring the left hand (Friday and Vila). Only one individual showed a significant leading arm preference when climbing, using the right hand more often than the left (Wilson). However, some individuals show moderate laterality indices of .3 or higher in absolute value, in quadrupedal leading arm (Dylan, Boris, Sarah) and in leading arm when climbing (Eric, Boris, Vila, Zee Zee, Layla, Fathing, Rosie). Table 8 shows the means and standard deviations of leading arm and leading arm when climbing.

Table 7
Laterality indices for Leading Arm and Leading Arm when Climbing.

	Leading Arm Index	Leading Arm Climbing Index
Carlos	.40	
Eric	-.05	.33
Dylan	-.41	.00
Friday	-.50	
Nicky	.04	-.17
Wilson	.26	.85
Boris	-.33	.33
Tina	.24	.20
Patti	.12	.18
Chrissie	-.08	.00
Vila	-.60	.45
ZeeZee	.20	-.50
Layla	.00	-.60
Sally	.25	.20
Alice	.22	.07
Sarah	.30	.11
Mandy	.17	.14
Farthing	.10	.43
Rosie	.14	-.43

Table 8
Means and standard deviations for leading arm and leading arm when climbing.

	Mean (SD)
Leading arm	.03 (.29)
Leading arm when climbing	.09 (.37)

The one sample t-tests using laterality indices did not find group-level lateralization for leading arm (*t*(18)= .38, *p*= .709) or for leading arm when climbing (*t*(16)= 1.05, *p*= .309). Mann-Whitney U tests did not find significant differences between mother-reared and hand-reared chimpanzees in quadrupedal leading arm (*U*(N=19)= 45, *p*= .639) or climbing leading arm (*U*(N=17)= 28.5, *p*= .879).

Sidedness Bias and Agonistic Interactions

The QAP tests found no significant correlations between agonistic interactions and either front sidedness (*r*= -.03, *p*= .67) or total sidedness (*r*= -.002, *p*= .504).

Motor Preferences and Sidedness

Spearman tests found no significant correlation between leading arm and front pass, back pass or total pass, or between leading arm when climbing and front pass, back pass or total pass. Correlation coefficients can be seen in Table 9.

Table 9
Spearman correlations (p values) between locomotion laterality and sidedness

	Front pass	Back pass	Total pass
Leading arm	.242 (.318)	-.102 (.707)	.000 (1)
Leading arm when climbing	-.063 (.809)	-.136 (.644)	-.054 (.838)

Discussion

Most individuals showed weak lateralization in sidedness measures and, contrary to what was predicted based on previous studies (Quaresmini et al., 2014), there was no group-level bias towards passing individuals on the left side. Similarly, most individuals were not significantly lateralised in leading arm and the findings of the one sample t-test diverge from past research (Hopkins, 2008; Morcillo et al., 2006; Regaiolli et al., 2016), showing no significant group-level preference. The data shows that hand-reared and mother-reared chimpanzees did not significantly differ in their laterality for any of the measures. The first hypothesis predicted, based on previous research (Casperd & Dunbar, 1996), that chimpanzees would tend to pass other individuals more on the left side when they often interact agonistically with those individual; however, the findings do not support this prediction, as the QAP tests show no significant correlations between agonistic interactions and sidedness. The second hypothesis predicted that sidedness would show a relationship to leading arm when walking or climbing; however, the data do not support this hypothesis, as leading arm was not correlated with sidedness laterality, indicating that sidedness might not be affected by motor preferences.

Regarding sidedness lateralization, the results indicate that most chimpanzees do not have an individual preference towards passing conspecifics on any particular side. Additionally, the findings do not support the prediction that chimpanzees would show a group bias towards passing conspecifics on their left side, as there was no significant group bias towards either side. These findings seem to contradict previous research in mammals that report biases towards keeping conspecifics on the left (Hill et al., 2017; Karenina, Giljov, Glazov, & Malashichev, 2013; Karenina, Giljov, Ivkovich, et al., 2013). However, while previous literature in mammals has focused mostly on mother-infant dyads (Karenina et al., 2017), the present study investigates a more general sidedness involving any possible dyad in a group of chimpanzees. A possible interpretation for the contradictory results is that the right hemisphere of the brain is particularly involved in infant vigilance, but it does not have a strong dominance over attention toward other conspecifics. Similarly, the present study also does not support the findings of Quaresmini et al., (2014) that suggest that chimpanzees have a trend towards keeping conspecifics on the left side, although it is important to keep in mind that Quaresmini et al., (2014) studied positioning only during foraging and that their results were just above the critical level to consider the trend statistically significant. While more research is needed to clarify if foraging does have an effect on sidedness, it is possible that chimpanzees are more vigilant, and thus, engage their right hemisphere, when eating in order to avoid food competition than when approaching and passing conspecifics.

Furthermore, the results did not find any significant correlation between sidedness and agonistic interactions. The findings indicate that chimpanzees do not have a tendency to use one side preferentially when moving around conspecifics that have often displayed agonistic behaviours at them. This does not support the predictions based on previous studies (Casperd & Dunbar, 1996) that primates tend to use their left side to pass conspecifics with which they often have agonistic interactions. The right hemisphere and left side dominance of agonistic interactions is well known in vertebrates (Salva et al., 2002), including primates (Casperd & Dunbar, 1996). However, Casperd and Dunbar (1996) reported that the retreating animal in an agonistic interaction, in their case it was usually the dominant walking away, did not show a significant left-side preference. This is interesting, as it suggests that the presence of a possible threat is not enough to elicit this left-side bias and it is, instead, the actual interaction which can potentially cause primates to use their left side to focus their attention on their rival. The results of the current study, however, are difficult to compare with Casperd and Dunbar's (1996) findings, as sidedness was not recorded during agonistic interactions but, rather, during free movement of the chimpanzees on their enclosure. This suggests that studying sidedness during specific behaviours, such as foraging and social interactions might result in stronger lateral biases at the individual and population level.

Regarding leading arm preference during locomotion, the results indicate that most chimpanzees showed weak preferences when initiating quadrupedal or climbing movement. There was no population level laterality in leading arms, regardless of the posture. These findings support Marchant and McGrew's (1996) study that showed no population level laterality in locomotion in the wild. Moreover, although these results seem to contrast with the findings of Morcillo et al., (2006) that report a significant population level right-hand preference in quadrupedal posture, the average percentage of overall right-hand use was only 57% which, although significant, is a small lateral effect. Additionally, Morcillo et al.'s (2006) study uses a sample of ten chimpanzees and, although seven of them are not significantly lateralised, three are strongly lateralised towards their right hand. These three individuals might be disproportionally affecting the group average in such a small sample. While the sample of the current study is bigger than Morcillo et al.'s (2006) sample, including 19 chimpanzees, and a similar lack of individual lateralization is found, more research is needed in order to better understand quadrupedal locomotion preferences in chimpanzees.

Lastly, locomotion preferences were not correlated with sidedness, which is an expected result given how neither locomotion nor sidedness elicited significant individual preferences in most chimpanzees. Although this is the first study to investigate sidedness and its relationship with locomotion, Hopkins (2008) and Regaiolli et al., (2016) have suggested a link between locomotion preferences and other lateralised behaviours. According to the Postural Origins Theory (MacNeilage et al., 1987), a left-hand specialization in supporting the body would have freed the right hand, which would have consequently specialised in manipulating objects. The findings of this study do not indicate that lateralisation in locomotion, whether quadrupedal or climbing, is common or that it has a link with sidedness. However, this question is still worth considering in future research when investigating sidedness in more specific behaviours. For example, research in sidedness during agonistic interactions would benefit from considering laterality in hand use during physical attacks and threats, as it might influence the positioning of the whole body.

Although this study offers a new perspective to the study of laterality, investigating both sidedness and motor laterality, there are a number of limitations in this research that need to be kept in mind when interpreting the findings. First, it is important to carefully consider space availability when investigating sidedness. The methodology used considered the potential constraint of small spaces, opting to not record passes when the path of the passing chimpanzee is restricted, but there are other, less obvious features of the terrain such as paths, slopes or stones that might influence sidedness. For example, chimpanzees might prefer to remain on the most-walked path rather than to step into the grass, and this might influence the side they pass others on. The influence of the terrain during free movement is difficult to control and account for in naturalistic observation, even in captivity, meaning that the study of sidedness might be better suited for experiments in more controlled environments. Another potential limitation has to do with the social environment of the group, since the group was undergoing the introduction of a new female and a period of dominance instability where two young male chimpanzees were challenging the dominant male. Dominance instability is known to have an effect on the way chimpanzees interact with each other (Koyama, Ronkainen & Aureli, 2017) and could make agonistic interactions less stable, as the group structure could be undergoing changes even during the period of data collection.

The aim of this study was to explore a possible bias in social positioning. This objective rests on a rationale based on studies that have found a tendency in primates to keep conspecifics to their left, either while picking up pieces of food (Quaresmini et al., 2014) or during agonistic interactions (Casperd & Dunbar, 1996). While both studies seem to point towards a left visual preference towards observing conspecifics and, in addition to the points previously discussed for each of those studies, it is important to reconsider some of the interpretations of these studies. Visual lateralization has not been studied as often as other forms of lateralization in primates and it is usually studied in the form of eye preference in experimental tasks that require the animals to look through a hole with a single eye (Fitch & Braccini, 2013). Using this experimental task, chimpanzees show a bias towards using the left eye when viewing a realistic model of a snake, and towards the right eye when viewing food (Braccini et al., 2012), which is similar to the biases shown in other primate species (Fitch & Braccini, 2013). However, it is important to draw a distinction between eye preference in an experimental task that forces the animal to look with one eye and visual preference. Other animals such as sheep (Pierce et al., 2000) and birds (Vallortigara, 1992; Vallortigara & Andrew, 1994) have lateral eyes that clearly separate each visual hemifield, primates have overlapping visual hemiphields. Investigating visual preference in animals that have frontally placed eyes is difficult because they have overlapping visual hemiphields, unlike animals with laterally placed eyes.

A second source from which this study drew to construct its rationale is the tendency that some primates, including humans and rhesus macaques, show to inspect the right side of conspecific faces (Guo et al., 2009). This tendency has, in the past, been interpreted as a bias towards using the left visual field to observe conspecifics (Guo et al., 2009). However, a different interpretation of their results is that the bias is not caused by a visual preference, but rather by the right-side bias of facial emotional expression present in primates (Fernández-Carriba et al., 2002). This would explain why this bias is only present when inspecting upright faces but not inverted faces and why dogs only show this tendency when inspecting human faces, but not faces of other animals (Guo et al., 2009). Overall, it is important to acknowledge that primates are not prime candidates to explore facets of visual lateralization such as sidedness.

In conclusion, no individual or population level preference in sidedness was found and, contrary to what was predicted based on previous literature (Casperd & Dunbar, 1996), sidedness did not show a relationship with agonistic interactions, meaning chimpanzees did not prefer to use their left side when passing potential threats. Similarly, the study did not find individual or population level preferences in motor laterality, failing to replicate previous findings (Morcillo et al., 2006) that show an overall population level tendency to use the right hand to initiate movement from a quadrupedal posture. Lastly, the results did not find a relationship between motor laterality and sidedness. Overall, these findings could indicate that the terrain might have an influence in the way chimpanzees move around each other. Although more research is needed to further understand the role of a possible left-side bias for agonistic behaviours, the findings of this study might indicate that, when enough space is available, chimpanzees do not show a particular preference towards passing conspecifics on any particular side. This draws attention to the importance of enclosures that allow chimpanzees to avoid possible agonistic interactions when walking in close proximity to their conspecifics. Instead, it is possible that sidedness might be more informative when studied during particular interactions (i.e. during fights or during foraging), rather than during free movement.

References

Altmann, J. (1974). observational study of behavior: Sampling methods. *Behaviour, 49*(3), 39.

Ariyomo, T. O., & Watt, P. J. (2013). Aggression and sex differences in lateralization in the zebrafish. *Animal Behaviour*, *86*(3), 617–622. https://doi.org/10.1016/j.anbehav.2013.06.019

Austin, N. P., & Rogers, L. J. (2007). Asymmetry of flight and escape turning responses in horses. *Laterality*, *12*(5), 464–474. https://doi.org/10.1080/13576500701495307

Barnard, S., Matthews, L., Messori, S., Podaliri-Vulpiani, M., & Ferri, N. (2016). Laterality as an indicator of emotional stress in ewes and lambs during a separation test. *Animal Cognition*, *19*(1), 207–214. https://doi.org/10.1007/s10071-015-0928-3

Bisazza, A., Cantalupo, C., Capocchiano, M., & Vallortigara, G. (2000). Population lateralisation and social behaviour: A study with 16 species of fish. *Laterality: Asymmetries of Body, Brain and Cognition*, *5*(3), 269–284. https://doi.org/10.1080/713754381

Bisazza, A., & De Santi, A. (2003). Lateralization of aggression in fish. *Behavioural Brain Research*, *141*(2), 131–136. https://doi.org/10.1016/S0166-4328(02)00344-3

Butts, C.T. (2019). Sna: Tools for social network analysis. R package version 2.5 https://CRAN.R-project.org/package=sna

Casperd, J. M., & Dunbar, R. I. M. (1996). Asymmetries in the visual processing of emotional cues during agonistic interactions by gelada baboons. *Behavioural Processes*, *37*(1), 57–65. https://doi.org/10.1016/0376-6357(95)00075-5

Chivers, D. P., McCormick, M. I., Allan, B. J. M., Mitchell, M. D., Gonçalves, E. J., Bryshun, R., & Ferrari, M. C. O. (2016). At odds with the group: Changes in lateralization and escape performance reveal conformity and conflict in fish schools. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1841), 20161127. https://doi.org/10.1098/rspb.2016.1127

Clark, F. E. (2011). Space to choose: Network analysis of social preferences in a captive chimpanzee community, and implications for management. *American Journal of Primatology, 73*(8), 748–757. https://doi.org/10.1002/ajp.20903

Corballis, M. C. (2009). The evolution and genetics of cerebral asymmetry. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *364*(1519), 867–79. https://doi.org/10.1098/rstb.2008.0232

Corballis, M. C. (2014). Left brain, right brain: Facts and fantasies. *PLoS Biology, 12*(1), e1001767. https://doi.org/10.1371/journal.pbio.1001767

Dadda, M., Sovrano, V. A., & Bisazza, A. (2003). Temporal pattern of social aggregation in tadpoles and its influence on the measurement of lateralised response to social stimuli. *Physiology and Behavior*, *78*(2), 337–341. https://doi.org/10.1016/S0031-9384(02)01001-6

Farine, D. R., & Whitehead, H. (2015). Constructing, conducting and interpreting animal social network analysis. *Journal of Animal Ecology*, *84*(5), 1144–1163. https://doi.org/10.1111/1365-2656.12418

Fernández-Carriba, S., Loeches, Á., Morcillo, A., & Hopkins, W. D. (2002). Asymmetry in facial expression of emotions by chimpanzees. *Neuropsychologia*, *40*, 1523–1533. https://doi.org/10.1016/S0028-3932(02)00028-3

Fitch, W. T., & Braccini, S. N. (2013). Primate laterality and the biology and evolution of human handedness: A review and synthesis. *Annals of the New York Academy of Sciences*, *1288*(1), 70–85. https://doi.org/10.1111/nyas.12071

Fletcher, A., & Weghorst, J. (2005). Laterality of hand function in naturalistically housed chimpanzees (*Pan troglodytes*). *Laterality: Asymmetries of Body, Brain and Cognition*, *10*(3), 219–242. https://doi.org/10.1080/13576500442000049

Ghirlanda, S., Frasnelli, E., & Vallortigara, G. (2009). Intraspecific competition and coordination in the evolution of lateralization. *Philosophical Transactions of the Royal Society*, *364*, 861–866. https://doi.org/10.1098/rstb.2008.0227

Ghirlanda, S., & Vallortigara, G. (2004). The evolution of brain lateralization: A game- theoretical analysis of population structure. *The Royal Society*, *271*, 853–857. https://doi.org/10.1098/rspb.2003.2669

Giljov, A., Karenina, K., & Malashichev, Y. (2018). Facing each other: Mammal mothers and infants prefer the position favouring right hemisphere processing. *Biology Letters*, *14*(1), 20170707. https://doi.org/10.1098/rsbl.2017.0707

Guo, K., Meints, K., Hall, C., Hall, S., & Mills, D. (2009). Left gaze bias in humans, rhesus monkeys and domestic dogs. *Animal Cognition*, *12*(3), 409–418. https://doi.org/10.1007/s10071-008-0199-3

Hill, H. M., Guarino, S., Calvillo, A., Gonzalez, A., Zuniga, K., Bellows, C., Polasek, L., & Sims, C. (2017). Lateralized swim positions are conserved across environments for beluga (*Delphinapterus leucas*) mother–calf pairs. *Behavioural Processes*, *138*, 22–28. https://doi.org/10.1016/j.beproc.2017.01.018

Hook, M. A., & Rogers, L. J. (2008). Visuospatial reaching preferences of common marmosets (*Callithrix jacchus*): An assessment of individual biases across a variety of tasks. *Journal of Comparative Psychology*, *122*(1), 41–51. https://doi.org/10.1037/0735-7036.122.1.41

Hopkins, W. D. (1995). Hand preferences for simple reaching in juvenile chimpanzees (*Pan troglodytes*): Continuity in development. *Developmental Psychology*, *31*(4), 619–625.

Hopkins, W. D. (2004). Laterality in maternal cradling and infant positional biases: Implications for the development and evolution of hand preferences in nonhuman primates. *International Journal of Primatology*, *25*(6), 1243-1265. https://doi.org/10.1023/B:IJOP.0000043961.89133.3d

Hopkins, W. D. (2008). Locomotor limb preferences in captive chimpanzees (*Pan troglodytes*): Implications for morphological asymmetries in limb bones. *American Journal of Physical Anthropology*, *137*(1), 113–118. https://doi.org/10.1002/ajpa.20834

Hopkins, W. D., Bard, K. A., Jones, A., & Bales, S. L. (1993). Chimpanzee hand preference in throwing and infant cradling: Implications for the origin of human handedness. *Current Anthropology*, *34*(5), 786–790. Retrieved from http://www.jstor.org/stable/2744291

Hopkins, W. D., Cantalupo, C., Wesley, M. J., Hostetter, A. B., & Pilcher, D. L. (2002). Grip morphology and hand use in chimpanzees (*Pan troglodytes*): Evidence of a left hemisphere specialization in motor skill. *Journal of Experimental Psychology: General*, *131*(3), 412–423. https://doi.org/10.1037//0096-3445.131.3.412

Hopkins, W. D., Gardner, M., Mingle, M., Reamer, L., & Schapiro, S. J. (2013). Within- and between-task consistency in hand use as a means of characterizing hand preferences in captive chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, *127*(4), 380–391. https://doi.org/10.1037/a0031071

Karenina, K., Giljov, A., Glazov, D., & Malashichev, Y. (2013). Social laterality in wild beluga whale infants: Comparisons between locations, escort conditions, and ages. *Behavioral Ecology and Sociobiology*, *67*(7), 1195–1204. https://doi.org/10.1007/s00265-013-1545-2

Karenina, K., Giljov, A., Ingram, J., Rowntree, V. J., & Malashichev, Y. (2017). Lateralization of mother-infant interactions in a diverse range of mammal species. *Nature Ecology and Evolution*, *1*(2), 30. https://doi.org/10.1038/s41559-016-0030

Karenina, K., Giljov, A., Ivkovich, T., Burdin, A., & Malashichev, Y. (2013). Lateralization of spatial relationships between wild mother and infant orcas, Orcinus orca. *Animal Behaviour*, *86*(6), 1225–1231. https://doi.org/10.1016/j.anbehav.2013.09.025

Karenina, K., Giljov, A., de Silva, S., & Malashichev, Y. (2018). Social lateralization in wild Asian elephants: visual preferences of mothers and offspring. *Behavioral Ecology and Sociobiology*, *72*(2), 21. https://doi.org/10.1007/s00265-018-2440-7

Koyama, N. F., Ronkainen, K., & Aureli, F. (2017). Durability and flexibility of chimpanzee grooming patterns during a period of dominance instability. *American Journal of Primatology*, *79*(11), e22713. https://doi.org/10.1002/ajp.22713

Lindell, A. K. (2013). Continuities in emotion lateralization in human and non-human primates. *Frontiers in Human Neuroscience*, *7*, 1–9. https://doi.org/10.3389/fnhum.2013.00464

Lippolis, G., Westman, W., McAllan, B. M., & Rogers, L. J. (2005). Lateralisation of escape responses in the stripe-faced dunnart, *Sminthopsis macroura* (Dasyuridae: Marsupialia). *Laterality*, *10*(5), 457–470. https://doi.org/10.1080/13576500442000210

Llorente, M., Mosquera, M., & Fabré, M. (2009). Manual laterality for simple reaching and bimanual coordinated task in naturalistic housed *Pan troglodytes*. *International Journal of Primatology*, *30*, 183–197. https://doi.org/10.1007/s10764-009-9338-1

Lonsdorf, E. V, & Hopkins, W. D. (2005). Wild chimpanzees show population level handedness for tool use. *Proceedings of the National Academy of Sciences of the United States of America*, *102*(35), 12634–12638. https://doi.org/10.1073/pnas.0505806102

MacNeilage, P. F., Studdert-Kennedy, M. G., & Lindblom, B. (1987). Primate handedness reconsidered. *Behavioural and Brain Sciences*, *10*(2), 247–303. Retrieved from http://journals.cambridge.org

Marchant, L. F., & Mcgrew, W. C. (1996). Laterality of limb function in wild chimpanzees of Gombe National Park: Comprehensive study of spontaneous activities. *Academic Press Limited Journal of Human Evolution*, *30*(5), 427–443.

Marchant, L. F., & McGrew, W. C. (2013). Handedness is more than laterality: Lessons from chimpanzees. *Annals of the New York Academy of Sciences*, *1288*(1), 1–8. https://doi.org/10.1111/nyas.12062

McGrew, W. C., & Marchant, L. F. (1992). Chimpanzees, tools and termites: Hand preference or handedness? *Current Anthropology*, *33*(1), 114–119.

Meguerditchian, A., Vauclair, J., & Hopkins, W. D. (2013). On the origins of human handedness and language: A comparative review of hand preferences for bimanual coordinated actions and gestural communication in nonhuman primates. *Developmental Psychobiology*, *55*(6), 637–650. https://doi.org/10.1002/dev.21150

Morcillo, A., Fernandez-Carriba, S., & Loeches, A. (2006). Asymmetries in postural control and locomotion in chimpanzees (*Pan troglodytes*). *American Journal of Primatology*, *68*(8), 802–811. https://doi.org/10.1002/ajp.20280

Mosquera, M., Llorente, M., Riba, D., Estebaranz, F., González-Brao, M., Lorenzo, C., Sanmartí, N., Toll, M., Carbonell, E., & Feliu, O. (2006). Ethological study of manual laterality in naturalistic housed chimpanzees (*Pan troglodytes*) from the Mona Foundation Sanctuary (Girona, Spain). *Laterality*, *12*(1), 19–30. https://doi.org/10.1080/13576500600886754

Quaresmini, C., Forrester, G. S., Spiezio, C., & Vallortigara, G. (2014). Social environment elicits lateralized behaviors in gorillas (*Gorilla gorilla gorilla*) and chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, *128*(3), 276–284. https://doi.org/10.1037/a0036355

R Core Team (2019). R: A language and environment for statistical computing. *R Foundation for Statistical Computing*, Vienna, Austria. https://www.R-project.org/

Regaiolli, B., Spiezio, C., & Hopkins, W. D. (2016). Three Actions, two groups: Looking for the origin of primate manual lateralization. *Journal of Comparative Psychology*, *130*(3), 259–268. https://doi.org/10.1037/com0000031

Reynolds Losin, E. A., Russell, J. L., Freeman, H., Meguerditchian, A., & Hopkins, W. D. (2008). Left hemisphere specialization for oro-facial movements of learned vocal signals by captive chimpanzees. *PLoS ONE*, *3*(6), e2529. https://doi.org/10.1371/journal.pone.0002529

Rogers, L. J. (1989). Laterality in animals. *International Journal of Comparative Psychology*, *3*(1).

Rogers, L. J. (2009). Hand and paw preferences in relation to the lateralized brain. *Philosophical Transactions of the Royal Society*, *364*, 943–954. https://doi.org/10.1098/rstb.2008.0225

Rogers, L. J. (2017). A matter of degree: Strength of brain asymmetry and behaviour. *Symmetry*, *9*(12), 57. https://doi.org/10.3390/sym9040057

Rogers, L., & Vallortigara, G. (2015). When and why did brains break symmetry? *Symmetry*, *7*(4), 2181–2194. https://doi.org/10.3390/sym7042181

Salva, O. R, Regolin, L., Mascalzoni, E., & Vallortigara, G. (2012). Cerebral and behavioural asymmetries in animal social recognition. *Comparative Cognition & Behaviour Reviews*, *7*, 110–138. https://doi.org/10.3819/ccbr.2012.70006

Sieratzki, J. S., & Woll, B. (1996). Why do mothers cradle babies on their left? *Lancet*, *347*(9017), 1746–1748.

Sobel, N., Supin, A. Y., & Myslobodsky, M. S. (1994). Rotational swimming tendencies in the dolphin (*Tursiops truncatus*). *Behavioural Brain Research*, *65*(1), 41–45. https://doi.org/10.1016/0166-4328(94)90071-X

Peirce, J. W., Leigh, A. E., & Kendrick, K. M. (2000). Configurational coding, familiarity and the right hemisphere advantage for face recognition in sheep. *Neuropsychologia*, *38*(4), 475–483. https://doi.org/10.1016/S0028-3932(99)00088-3

Vallortigara, G. (1992). Right hemisphere advantage for social recognition in the chick. *Neuropsychologia*, *30*(9), 761–768. https://doi.org/10.1016/0028-3932(92)90080-6

Vallortigara, G. (2000). Comparative neuropsychology of the dual brain: A Stroll through animals' left and right perceptual worlds. *Brain and Language*, *73*(2), 189–219. https://doi.org/10.1006/brln.2000.2303

Vallortigara, G., & Andrew, R. J. (1994). Differential involvement of right and left hemisphere in individual recognition in the domestic chick. *Behavioural Processes*, *33*(1), 41–57. https://doi.org/10.1016/0376-6357(94)90059-0

Vallortigara, G., & Rogers, L. J. (2005). Survival with an asymmetrical brain: Advantages and disadvantages of cerebral lateralization. *Behavioral and Brain Sciences*, *28*, 575–633.

Versace, E., Morgante, M., Pulina, G., & Vallortigara, G. (2007). Behavioural lateralization in sheep (*Ovis aries*). *Behavioural Brain Research, 184*(1), 72–80.

Wallez, C., Schaeffer, J., Meguerditchian, A., Vauclair, J., Schapiro, S. J., & Hopkins, W. D. (2012). Contrast of hemispheric lateralization for oro-facial movements between learned attention-getting sounds and species-typical vocalizations in chimpanzees: Extension in a second colony. *Brain and Language*, *123*(1), 75–79. https://doi.org/10.1016/J.BANDL.2012.07.002

Whitehead, H., & James, R. (2015). Generalized affiliation indices extract affiliations from social network data. *Methods in Ecology and Evolution,* *6*(7), 836–844. https://doi.org/10.1111/2041-210X.12383

Chapter 4. Laterality and Behavioural Style in Chimpanzees

Summary

Previous chapters have introduced different measures of laterality as well as its links with general aspects of behaviour. Chapter 4 builds from previous chapters by using data on laterality in order to tackle one of the central topics of the thesis: if lateralization is rooted in emotional processing and hemispheric lateralization, there could be a link between laterality and individual differences in behaviour. In order to address this question, this study utilises behavioural data to assess individual differences in behaviour in the chimpanzee group and studies the link between behavioural style and laterality.

Introduction

The evolution of laterality is a topic that has been of interest for decades (Corballis, 1989; MacNeilage et al., 1987). One proposed explanation for the appearance of population level laterality is that current behaviours are lateralised in a way that reflects early asymmetries in vertebrate evolution (Fitch & Braccinni, 2013). In particular, sensory asymmetries likely existed early in evolution and could be at the base of how limb and hand preferences are lateralised (Rogers, 2009). This early sensory lateralization has its roots in how each hemisphere processes stimuli in different ways: the left hemisphere processes expected stimuli while the right processes unexpected stimuli (Rogers & Vallortigara, 2015). The right hemisphere specialization in processing unexpected stimuli has been linked to vigilance, escape responses and aggression (Rogers & Vallortigara, 2015) and, similarly, to a higher control of emotional expressions (Salva et al., 2012). Individual differences of behaviour are deeply connected with emotional processing and expression (Carver et al., 2000), which has led recent research to begin exploring a possible link between laterality and personality.

There are multiple definitions of personality, some of them emphasising a particular aspect such as traits, moods or emotions (Gosling, 2001). A broad definition often used in animal research is "any individual differences in behaviour that are or are thought to be stable across time and situations" (p. 654) (Freeman & Gosling, 2010). Research in animal personality has grown in the past two decades (Gosling, 2001; 2008), particularly in primates (Freeman & Gosling, 2010; Weiss et al., 2011). Most studies in chimpanzees have focused on measuring personality through trait ratings questionnaires (Murray, 1998, 2002; King & Landau, 2003; King et al., 2005; Freeman et al., 2013; Úbeda & Llorente, 2015) or behavioural codings (Koski, 2011; Uher, 2008, Uher et al., 2008) as well as studying the underlying structure of personality (Koski, 2014; Weiss et al., 2011). Recently, research has started exploring further questions such as its evolutionary drivers and consequences (Wolf & Weissing, 2012) and the interaction between personality and laterality (Rogers, 2009, 2017) as well as the practical implications of both personality and laterality research for animal welfare (Fernández-

Lázaro et al., 2019; Gartner & Weiss, 2018; Robinson et al., 2017; Rogers, 2011). This study focuses on the study of behavioural styles, which is a concept that, although often included in the broader definition of personality (Freeman & Gosling, 2013) is also used to refer to individual differences in behaviour when temporal stability is not directly assessed (Anestis, 2005; 2006).

Hemispheric laterality refers to an asymmetry in structure, process, or function (Bisazza, Rogers, & Vallortigara, 1998). This asymmetry is present in a large number of vertebrates (see Wiper, 2017 for a review) with each hemisphere specializing in processing information in different ways (Rogers & Vallortigara, 2015). This is relevant when processing emotions (Leliveld et al., 2013), stress and fear responses (Ocklenburg et al., 2016) and social behaviours (Salva, et al., 2012). The specialization of the right hemisphere in vigilance and avoidance behaviours (Rogers, 2009) can manifest in a clear lateralization of approach and withdrawal behaviours in primates (Fernández-Lázaro et al., 2019; Rogers, 2018), including humans (Davidson et al., 1990). Avoidance and withdrawal is a central element of some conceptualizations of personality, such as “coping styles” (Carver et al., 2000; Koolhaas et al., 1999; Koolhaas et al., 2010) and thus, better understanding of lateralization can greatly contribute to the study of personality. Similarly, understanding lateralization in the processing of social stimuli and behaviours is important, as the social environment in particular plays a role in shaping individual behaviour (Krause et al., 2010) and has to be carefully considered when investigating laterality, as primate research highlights the importance of social factors of personality such as sociability and positive affect (Morton et al., 2013; Koski, 2011).

Several studies have found a relationship between lateralised behaviour and personality, often showing that a dominance of the right hemisphere, manifested in behavioural biases to the left, is linked to stress-related behaviours. For example, Rainbowfish (*Melanotaenia nigrans*) that are lateralised are bolder than non-lateralised, and left-lateralised are bolder than right-lateralised (Brown & Bibost, 2014). Left-pawed dogs (*Canis lupus familiaris*) display more stress-related behaviours (Barnard et al., 2018) and pigs (*Sus scofra*) that are lateralised to the left when manipulating objects with their snout are less bold than those lateralised to the right (Goursot et al., 2019). However, there is also contradictory evidence showing that right-pawed dogs scored higher in stranger-directed fear (Wells et al., 2019) and that non-lateralised dogs score higher in aggressiveness than either left- or right-lateralised dogs (Barnard et al., 2017). This apparent contradiction might be explained by differences in the aspects of personality measured and indicates a complex relationship between laterality and personality.

Similarly, the link between laterality and personality in primates is not yet clear. For example, although sex differences in laterality are not typical in primates (Papademetriou et al., 2005), the relationship between laterality and personality might manifest differently in males and females. In male rhesus macaque, left-handed individuals react more submissively to conspecifics (Westergaard et al., 2003), while the opposite trend was found in females, where left-handed macaques were less likely to act submissively (Westergaard et al., 2004). These sex differences are uncommon in primates and authors acknowledge that they are difficult to interpret, although they suggest that such differences might be partially explained by sex divergences in aggression and rank in macaques (Westergaard et al., 2004). Most studies, however, do not report sex differences in the association between personality and laterality. In common marmosets, personality is associated with strength of hand preference, but with direction (Tomassetti et al., 2019). However, studies have found that left-handed marmosets take longer to explore new places (Cameron & Rogers, 1999 in *Callithrix jacchus*; Braccini & Caine, 2009 in *Callithrix geoffroyi*) and receive more aggression from their group (Gordon & Rogers, 2015). Interestingly, this tendency of left-handed primates to take longer to begin exploring new areas and objects has been observed in several species of primates (Fernández-Lázaro et al., 2019), including chimpanzees (Hopkins & Bennett, 1994). Overall, existing evidence points to a relationship between laterality in hand use and exploration style, or boldness, in primates, but more research is needed to investigate if there is a link between laterality and other aspects of personality.

An important point to consider when interpreting this area of research is the type of measure used in order to assess laterality. While hand or paw preference are common measures of laterality in animals (Rogers, 2009), the type of task can potentially require a preferential use of a process lateralised in one hemisphere. For example, bimanual coordinated tasks, such as the tube task, elicit population level preferences in chimpanzees while other tasks do not (Hopkins, 1995; Hopkins et al., 2004; Hopkins et al., 2005; Llorente et al., 2009; Llorente et al., 2011). Bimanual coordinated tasks require two independent and simultaneous actions, holding the tube and reaching for the food inside, which strengthens the overall bias in laterality (Hopkins, 1995; Hopkins et al., 2015) and might result in a preferential use of the right hand and left hemisphere for fine manipulation when reaching for the food. Measures that require the specialised use of the left or right hemisphere are likely the same in all individuals and may not be as useful when the objective is to assess lateral dominance of each individual (Gordon & Rogers, 2015). Instead, simple reaching tasks that do not require specialised processes are likely better indications of a predisposition to use, or "dominance" of, one hemisphere (Rogers, 2009; Gordon & Rogers, 2015). Studies have found that hand preference as measured by simple reach is linked to exploration style in chimpanzees, with right-handed lateralisation being associated with a bolder exploration style (Hopkins & Bennett, 1994). However, while simple reach appears to be a more appropriate measure to study the link of personality, as it might be a better indicator of hemispheric dominance, using simple reach measures might come at the cost of a reduced temporal consistency. While hand preference in simple reach has proven to be consistent in the short term, between two (see Chapter 2) and 10 years (Padrell et al., 2019), bimanual tasks appear to be more consistent in periods longer than 10 years (Padrell et al., 2019). Another complementary approach to using simple reach as a measure for laterality is to study congruency in more than one lateralised behaviour. Research has shown that evaluating congruent laterality by using two measures of laterality, such as ear and hand preference in humans (Wright et al., 2013) or tail and snout laterality in pigs (Goursot et al., 2019), can be a more informative approach to studying laterality as a predictor of personality.

Research has shown the importance of hemispheric dominance in emotional processing (Salva et al., 2012). In particular, a dominance of the right hemisphere might be associated with an enhanced stress reaction, which can lead to a more reactive or cautious approach to novel or social situations. Right hemispheric dominance is associated with less exploration in chimpanzees (Hopkins & Bennet, 1994) and could potentially influence overall personality. Additionally, previous studies have shown the importance of investigating strength of lateralization (Tomassetti et al., 2019) as well as congruent laterality (Goursot et al., 2019) when investigating the association between personality and laterality in animals.

The objective of this study is to further explore the relationship between behavioural style and laterality in chimpanzees. This study will expand current knowledge by investigating broader aspects of behavioural differences in chimpanzees, using behavioural measures (Koski, 2011), and by utilising multiple measures of laterality in order to determine if congruent laterality is a better predictor of personality than hand preference in simple reach. Based on previous findings, the hypotheses of this study are: 1) behavioural style will be related to direction of laterality, such that left-lateralized chimpanzees are less social, 2) behavioural style will be related to strength of laterality, so that non-lateralised are less social, and 3) chimpanzees with a congruent right preference will be more social than those with a congruent left preference or mixed preference.

Methods

Sample

The sample consisted of a group of 19 chimpanzees housed at the chimpanzee colony of Chester Zoo. For more details on the individual chimpanzees, the group structure and the enclosure see Chapter 2.

Procedure

Behavioural Style Observations

Data collection for behavioural style took place between January 2017 and December 2017 and consisted of 20-minute focal sessions, using 1-minute instantaneous sampling to record state behaviour and proximity of individuals within arm's reach of the focal animal (see Chapter 5 for more detail regarding the method of observation). Social interactions of all individuals were recorded *ad libitum* (Altmann, 1974; Clark, 2011, also see Chapter 5 for more details). Focal subjects were chosen opportunistically from those that were clearly visible, balancing the focal subject to observe all individuals for a similar amount of time. Each chimpanzee was observed for an average of 950 minutes, ranging from 900 to 1020 minutes.

Initially, 18 behaviours were recorded based on previous works (Koski, 2011; Massen & Koski, 2014), including behaviours that had to be excluded (scratch) and variables that were later pooled into a broader category for affiliative (beg, share food and sexual) and aggressive (dominance mount, displace, noncontact threat, attack) behaviour due to a lack of sufficient data. A total of 12 variables were used in the final analyses (Table 1). Most variables were calculated either as frequency per hour or minute per hour. Grooming density was calculated as the total number of individuals that were seen engaged in grooming with the focal at any point during the observation period, divided by all possible grooming partners. Grooming diversity was calculated using the Shannon-Wiener diversity index (di Bitetti, 2000; Koski, 2011), as:

Grooming diversity = $H/H_{\max}$

$H = -\sum p_i \ln(p_i)$

In which p_i is the proportion of individual's grooming effort given to the ith individual

$H_{\max} = \ln(N - 1)$

In which N is the number of individuals in the group. Grooming diversity is represented in an index with values between 0, which indicates a perfect skew in which the focal only grooms one individual, and 1, which indicates that the focal grooms all members of the group equally.

Table 1

Behavioural variables

Variable	Definition
Grooming given	Minutes that the focal spent grooming / hour observed
Grooming received	Minutes that the focal was groomed / hour observed
Grooming diversity	Shannon-Wiener diversity index adjusted for group size
Grooming density	Total number of individuals the focal subject groomed divided by all available grooming partners
Self-groom	Minutes spent self-grooming / hour observed
Number of neighbours	Average number of individuals within two arm's reach measured once per minute observed
Times approached	Frequency of times other individuals approached the focal / hour observed
Approach others	Frequency of times the focal approached others / hour observed
Play	Frequency of times the individual was observed playing / hour observed
Affiliative behaviours	Frequency of affiliative behaviours by the focal / hour
Aggression	Frequency of aggressive behaviours by the focal / hour
Activity	Minutes that the focal spent not resting or self-grooming / hour observed.

Behavioural Style Structure

In order to obtain the overall behavioural style scores, Principal Component Analysis was conducted on the variables to identify the underlying dimensions using a varimax rotation (Freeman et al., 2013; King & Figueredo, 1997). Additionally, Regularised Exploratory Factor Analysis (REFA, Jung & Lee, 2011), a specialised technique designed to identify factors when the sample size is very small was used in order to further understand the underlying dimensions (Úbeda & Llorente, 2015). The final factor scores were calculated using the regression method based on the final REFA solution

(Koski, 2011). Using a conservative criterion (Weiss et al., 2011; Úbeda & Llorente, 2015), variables with loadings ≥ 5 in a factor were considered salient. These analyses were run using SPSS v26.

Laterality Measures

Laterality was assessed on two different actions: hand preference in quadrupedal simple reach, as it is the most common unimanual presition tasks done spontaneously by chimpanzees, and quadrupedal locomotion laterality in order to have a second laterality measure independent from hand preference. Data collection for hand preference was conducted in two periods: from January to April 2017 and from June to August 2019 using continuous focal samples of ten minutes, switching focal subject when appropriate to maximize data collection (for temporal consistency, see Chapter 2). For more information regarding the calculation of the scores, reliability, temporal stability and other methodological aspects, see Chapter 3. For quadrupedal locomotion laterality, data collection was conducted from June to August 2019, using continuous focal samples of ten minutes and switching focal subject when appropriate to maximize data collection. For more information see Chapter 3. All observations were collected from approximately 10am until 3pm, during standard zoo opening hours.

Additionally, congruent laterality was assessed by looking at the laterality index (explained below) score for simple reach and locomotion for each chimpanzee. If both indices showed a left bias the chimpanzee was classified as “left-congruent”, if both indices showed a right bias it was classified as “right-congruent”, if the indices showed different biases it was classified as “mixed”. The cut-off point for considering a chimpanzee as lateralised was a laterality index of -.20 for left-biased and .20 for right biased (Padrell et al., 2019).

Data Analysis

Laterality indices for hand preference and locomotion were calculated using the formula HI = (R – L) / (R + L) (Hopkins, 1995), where R was the frequency of right-hand use and L was the frequency of left-hand use. HI ranges from -1, indicating a left-hand preference and 1 indicates a right-hand preference, with values close to 0 indicating no preference. Strength of hand preference and strength of locomotion laterality were assessed using the absolute measure for HI (Wiper, 2017), independent of the direction of the preference.

Hypotheses one (behavioural style will show a relationship with laterality, so that left-lateralised chimpanzees are less social) and two (behavioural style will show a relationship with strength of laterality, so that non-lateralised are less social) of the study were tested using multiple lineal regression (Tomassetti et al., 2019). The regression models used the factors obtained in the factor analysis as outcome variables and hand preference, locomotion, as well as strength of hand preference and strength of locomotion as predictor variables. Sex and age were also included as predictor variables in the models. Additionally, in order to see if relatedness could predict similarity in behavioural style, QAP correlations were run inputting similarity matrices for the factors of behavioural style as outcome variables and estimated relatedness as predictor variables using 5000 permutations in UCINET v6.708. For more information regarding QAP analysis see methods of Chapter 3. Each factor of behavioural style was converted into a similarity matrix using UCINET 6.708. Similarity matrices display the difference between nodes on certain attributes, so that a lower score indicates that both individuals have similar values in that variable. The difference between nodes was calculated as the absolute difference between individuals' score on a factor of behavioural style. Relatedness was estimated from the data on parent-offsping information offered by the zoo (see Appendix I). As not all father-offspring relationships were known, chimpanzees that shared a mother but had no information on father were assumed to be half-siblings. Individuals not known to be related were assumed to have have a relatedness of 0.

Hypothesis three of the study (chimpanzees with a congruent right preference will be more social than those with a congruent left preference or mixed preference) was examined using Kruskal-Wallis tests to investigate if left-congruent, right-congruent and mixed lateralised chimpanzees differed in their sociability, positive affect and influence scores. Post-hoc Mann-Whitney tests were used with a Bonferroni correction to further investigate group differences if a test was significant. Alpha level was 0.05 for all tests. All analyses were done using SPSS v26.

Results

Descriptive Statistics

Descriptive statistics for all behavioural measures can be seen in Table 2. Descriptive statistics for laterality measures are displayed in Table 3.

Table 2
Mean and standard deviation for behavioural measures (N=19).

	Mean	Standard deviation
Grooming given	14.49	6.01
Grooming received	14.54	5.18
Grooming diversity	43.07	21.54
Grooming density	0.78	0.11
Self grooming	0.85	0.73
Number of neighbours	1.55	0.27
Times approached	4.07	1.20
Approach others	3.83	1.25
Play	0.25	0.46
Affiliative behaviour	1.24	0.98
Aggression	0.90	1.42

Activity	23.89	6.58

Note: Variables are measured in minutes per hour (grooming given and received, self-groom and activity) or frequency per hour (times approced, approach others, play, affiliative behaviours and aggression). Grooming density indicates the total number of grooming partners divided by the the available amount. Number of neighbours indicates the total amount of neighbours within two arm's reach.

Table 3
Mean and standard deviation for laterality indices (HI) for different measures (N=19)

	Mean	Standard deviations
Simple reach	0.03	0.53
Strength of simple reach	0.44	0.28
Leading arm	0.25	0.29
Strength of leading arm	0.23	0.16

Behavioural Style Structure

The findings of the factor analysis showed a significant Bartlett's test of sphericity (*X*2(66)= 170.42, *p*< .001), indicating that the data is appropriate for factor analysis. However, the Kaiser-Meyer-Olkin measure of sampling adequacy was .491, which is below the cut-off for acceptable data structure (.5). This indicates that some factors would have few variables that do not correlate highly with others in the analyses. Upon further inspection, one of the factors extracted, using both PCA and REFA, only contained the variable self-grooming, contributing to a low KMO measure. The analyses were repeated excluding self-grooming, finding a significant Bartlett's test of sphericity (*X*2(55)= 145.99, p < .001) and an adequate KMO this time (.559).

After inspection of the scree plot and consideration of factors with an eigenvalue greater than 1, three factors were extracted, explaining 75.88% of the variance in the data. Factor loadings for both the Principal Component Analysis and Regularised Exploratory Factor Analysis are shown in Table 4. Factor 1 positively loaded “grooming given”, “grooming received”, “grooming diversity”, “grooming density” and “activity” in the PCA; this factor also positively loaded “number of neighbours” in the REFA. This factor was named “popularity”. Factor 2 positively loaded “approach others”, “play” and “affiliative behaviours” in both analyses. This factor was named “sociability”. Factor 3 positively loaded “times approached”, “aggression” and “number of neighbours” in the PCA, but it only loaded “times approached” and “aggression” in the REFA. This factor was named “influence”.

Table 4

Factor loadings obtained using Principal Component Analysis and Regularised Exploratory Factor Analysis

	Principal Component Analysis			Regularised Exploratory Factor Analysis		
	Popularity	Sociability	Influence	Popularity	Sociability	Influence
Grooming given	**0.970**	-0.077	0.050	**0.988**	-0.081	-0.034
Grooming received	**0.826**	0.079	0.300	**0.806**	0.083	0.253
Grooming diversity	**0.956**	-0.163	0.006	**0.963**	-0.170	-0.073
Grooming density	**0.640**	-0.040	0.184	**0.562**	-0.032	0.127
Number of neighbours*	**0.500**	-0.160	**0.590**	**0.510**	-0.125	0.470
Times approached	0.086	-0.130	**0.886**	0.168	-0.122	**0.902**
Approach others	0.156	**0.797**	0.128	0.155	**0.678**	0.084
Play	-0.144	**0.776**	-0.181	-0.154	**0.650**	-0.113
Affiliative behaviours	-0.036	**0.930**	0.077	-0.034	**0.982**	0.082
Aggression	0.080	0.285	**0.769**	0.173	0.241	**0.540**
Activity	**0.869**	0.404	0.034	**0.869**	0.410	-0.035

Note: Values in **bold** indicate an adequate (>.500) loading. The variable marked with * indicates that the highest loading is in a different factor when comparing PCA and REFA.

First and Second Hypotheses

The regression analyses showed that laterality measures do not significantly predict popularity (*F*(6,12)= 1.123, *p*= .700, R^2= .450), coefficients can be seen in Table 5. Laterality measures could not predict sociability (*F*(6,12)= .444, *p*= .836, R^2= .182), coefficients can be seen in Table 6. Lastly, laterality measures could not predict influence (*F*(6,12)= 2.082, *p*= .132, R^2= .510), coefficients can be seen in Table 7. The models did not show indications of collinearity problems (hand preference VIF = 2.78; strength of hand preference VIF = 2.44; locomotion VIF =2.03; strength of locomotion VIF = 1.46; sex VIF = 2.42; age VIF = 1.47).

Table 5
Coefficients for the regression models predicting popularity

Predictors	B	SE B	B	*t*	*P*
Intercept	0.475	0.768		0.619	0.547
Hand preference	-1.447	0.720	-0.774	-2.009	0.068
Strength of hand preference	1.040	1.143	0.300	0.910	0.381
Locomotion	1.234	1.286	0.346	0.960	0.356
Strength of locomotion	1.898	1.714	0.309	1.107	0.290
Sex	-1.038	0.723	-0.516	-1.435	0.177
Age	-0.035	0.021	-0.460	-1.642	0.127

Table 6
Coefficients for the regression models predicting sociability

Predictors	B	SE B	B	*t*	*p*
Intercept	-0.346	0.946		-0.366	0.721

Hand preference	-0.068	0.888	-0.033	-0.077	0.940
Strength of hand preference	1.049	1.409	0.277	0.745	0.471
Locomotion	1.549	1.585	0.399	0.977	0.348
Strength of locomotion	1.818	2.114	0.271	0.860	0.406
Sex	-0.181	0.892	-0.083	-0.203	0.842
Age	-0.024	0.026	-0.286	-0.901	0.385

Table 7

Coefficients for the regression models predicting influence

Predictors	B	SE B	β	*t*	*p*
Intercept	-0.862	0.641		-1.344	0.204
Hand preference	0.973	0.601	0.545	1.618	0.132
Strength of hand preference	0.046	0.954	0.014	0.048	0.963
Locomotion	-0.970	1.074	-0.285	-0.903	0.384
Strength of locomotion	0.646	1.432	0.110	0.451	0.660
Sex	1.774	0.604	0.924	2.936	0.012
Age	0.015	0.018	0.208	0.847	0.414

The QAP correlations showed that relatedness could not predict influence (*r*= 0, *p*= .09), popularity (*r*= 0, *p*= .22), or sociability (*r*= 0, *p*= .475).

Third Hypothesis

Descriptive analysis for the behavioural style variables when dividing the group using congruent laterality can be seen in Table 8.

Table 8

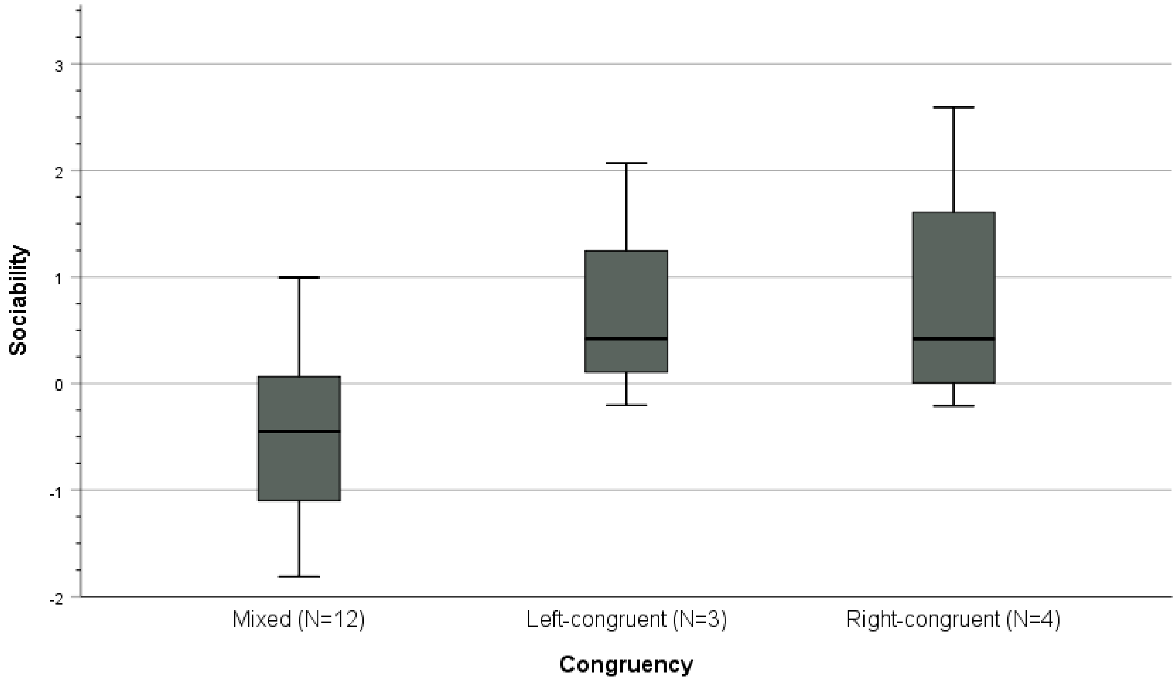
Mean and standard deviation for popularity, sociability and influence based on congruent laterality

Behavioural factor	Laterality	Mean	Standard deviation
Popularity	Mixed (N=12)	-0.10	0.57
	Left-congruent (N=3)	0.34	1.75
	Right-congruent (N=4)	0.05	1.60
Sociability	Mixed (N=12)	-0.46	0.80
	Left-congruent (N=3)	0.76	1.17
	Right-congruent (N=4)	0.81	1.24
Influence	Mixed (N=12)	-0.29	0.87
	Left-congruent (N=3)	0.70	1.31
	Right-congruent (N=4)	0.33	0.75

The results for the Kruskal-Wallis tests show that there are no significant effects for left-congruent, right-congruent and mixed lateralised chimpanzees in popularity (*H*(2)= .368, *p*= .832) or influence (*F*(2)= 2.074, *p*= .355). There is a significant effect for sociability (*F*(2)= 6.429, *p*= .040). However, further inspection of post hoc tests did not find any significant effect between left-congruent and right-congruent (*p*= 1) or between left-congruent and mixed (*p*=.180), although there was a tendency close to significance (*p*=.113) for the mixed laterality group to show less sociability than the right-congruent group, as displayed in Figure 4.

Figure 4

Box plot showing medians (black line), the middle quartiles (box) and the upper and lower quartiles (whiskers) for sociability scores for mixed, left-congruent and right-congruent



Discussion

Overall, the data show three clear behavioural style factors arising from the behavioural variables: popularity, sociability and influence. These factors were obtained through two different methods of dimension reduction: Principal Component Analysis and Regularised Exploratory Factor Analysis. However, the results do not support the hypotheses of this study. Hypothesis one proposed that laterality would show a relationship with behavioural style and hypothesis two proposed that strength of laterality would show a relationship with behavioural style. Regression analyses did not find that laterality, measured as hand preference in simple reach and as locomotion preference, or strength of laterality could predict behavioural style. The third hypothesis of the study stated that chimpanzees with a congruent right preference (those that are lateralised to the right in both hand and locomotion preference) would be more social than chimpanzees with either congruent left or mixed preference. The findings of the study do not support this hypothesis there was a non-significant tendency for right-congruent chimpanzees to show higher scores in sociability than those with mixed laterality.

The findings regarding the underlying dimensions of behavioural style show three clear factors. Popularity clusters most grooming behaviours together, as well as number of neighbours and activity, resulting in a factor that indicates grooming-oriented social interactions. Sociability loads positive social interactions between chimpanzees that do not involve grooming, resulting in a factor that loads other affiliative interactions. Influence loads aggressive behaviours and times being approached. These results are analogous to Koski's (2011) findings, reflecting clear social factors of personality, with some differences. One particular difference is that Koski (2011) found a factor named anxiety that did not load any social interaction but, instead, loaded anxiety-related behaviours. A particularly interesting finding is the fact that aggressive behaviour loads on the same factor as times being approached by others. This could be interpreted as a factor reflecting dominance, as the two chimpanzees with the higher score in influence were the dominant male, Dylan (Koyama et al., 2017) as well as a young male that could contest the dominance of the group, Carlos. Interestingly, Freeman et al. (2013) found that dominance correlates with aggressive behaviours but also with social grooming while, in the current data, grooming variables correlate highly together but do not correlate with aggressive behaviours (see chapter 5 for more information on grooming). This highlights the multidimensional nature of dominance, as it encompasses many different aspects of chimpanzee social life, not only aggression and conflict (Funkhouser et al., 2018). However, there are clear individual differences in dominance style (Foster et al., 2009), and these can be accurately rated for each individual chimpanzee (Freeman et al., 2013; King & Figueredo, 1997). Thus, it is important to consider behavioural styles, such as influence, independently of individual dominance, as they might offer a complementary picture, showing how each individual behavioural style translates into social interactions (Funkhouser et al., 2018; Koski, 2011).

The data do not support hypotheses one and two, as neither laterality nor strength of laterality were predictors of behavioural style. The findings of this study contrast with previous research that show personality differences between right- and left-handed primates. Previous research has shown that left-handed primates show a less proactive exploration style in novel environments and towards novel objects (Braccini & Caine, 2009; Cameron & Rogers, 1999; Fernández-Lazaro et al., 2019; Hopkins & Bennet, 1994). However, the current study focused on general differences of behaviour rather than exploration style and the divergence in results with respect to past research seems to indicate that laterality is only related to differences in personality in novel tasks and environments. Similarly, this study did not find a relationship between influence and laterality, although past research has found links between aggressive behaviour and laterality in macaques (Westergaard et al., 2003; 2004) and marmosets (Gordon & Rogers, 2015). However, this is not the first study showing conflicting results. When measuring personality through behavioural tests, Tomassetti et al. (2019) did not find that laterality could predict personality, although strength of laterality predicted the single factor that arose from the behavioural measures. Previous findings can be interpreted as a result of the influence of hemispheric dominance in emotional processing (Leliveld et al., 2013; Salva et al., 2012). For example, individuals with a right hemispheric dominance might have an enhanced stress reaction, which can lead them to take longer to explore new areas or to be less aggressive in fights. However, the multifaceted and complex nature of chimpanzee social structure might mediate in the relationship between hemispheric dominance and behavioural style. Chimpanzees display aggression not only as a response to an immediate stimulus but also as a "strategy" to defend their position in the agonistic hierarchy (Noë et al., 1980).

The data does not fully support hypothesis three of the study, as there was no significant effect of laterality in behavioural style. However, the data shows a tendency for right-congruent chimpanzees to have a higher score in sociability than mixed lateralised. Research has shown that congruent laterality is a better predictor of personality than a single laterality measure (Goursot et al., 2019; Wright et al., 2013), which can explain why this tendency appears when studying convergent laterality, but not when investigating separate lateralised measures. However, as the difference is between right-congruent and mixed lateralised, but not between right- and left-congruent, it is difficult to conclude whether this is reflecting an effect of the direction of laterality or of its strength. Likewise, sample size was particularly small, as only three chimpanzees were categorised as left-congruent and four were right-congruent. Higher sociability in right-congruent chimpanzees can be explained by the role of the left hemisphere of the brain in dealing with expected stimuli (Wiper, 2017). It is interesting that grooming, a well-known social behaviour, does not show a similar tendency. However, popularity, the factor upon which all grooming behaviours load, also includes non-social variables such as activity and, at the same time, it might be more affected by group dynamics as grooming is often used to create and maintain alliances (Lehmann et al., 2007; Kudo & Dunbar, 2001; Dunbar, 2010). This role of grooming as a facilitator of alliances might require different processing to other affiliative behaviours and be lateralised in a different way.

While the present findings show only a tendency, and not statistically significant results, they could be pointing towards a specialization of the left hemisphere to control affiliative behaviours with short durations, such as hug, kiss and play, while not being involved in grooming. Regarding early sensory lateralization, this could be interpreted as a manifestation of the left hemisphere to deal with expected stimuli; in this case, short affiliative interactions with known group members. Although it would be reasonable to expect to find a higher level of aggression in left-congruent chimpanzees, as the right hemisphere processes aggression and unexpected stimuli (Rogers & Vallortigara, 2015), it is important to note that many aggressive behaviours in chimpanzees are displays of dominance or non-contact threats that are not unexpected by other group members. More research is needed to further investigate this tendency of right-congruent laterality to be associated with sociability, and to better understand the possible relationship between social structure and laterality.

While this study presents new findings that expand the understanding of the way laterality is, or is not, related to behavioural style, there are a number of limitations that are worth considering when interpreting the present results. First, the current study only investigates social factors of behavioural style, while past research has mainly shown links between laterality and non-social personality (Braccini & Caine, 2009; Cameron & Rogers, 1999; Fernández-Lazaro et al., 2019; Hopkins & Bennet, 1994). The data initially included scratching and self-grooming as stress-related behaviours, but the first had to be excluded due to insufficient data and the latter loaded on a factor without any additional variables. Given the predominant role of the right hemisphere in processing stress, further research investigating if laterality predicts stress and anxiety in chimpanzees would help interpreting the findings of this study. Second, while the application of congruent laterality is a useful addition that allows for an interesting approach to the study of lateral dominance, the sample of the present study contained a number of chimpanzees that were not lateralised in locomotion laterality. This resulted in a large number of chimpanzees, 12 out of the 19, having mixed laterality. Laterality in locomotion might not be an appropriate measure to assess congruent laterality due to the overall low levels of individual lateralization. Visual laterality might be a better alternative, as it is already used in humans to assess congruent laterality (Wright et al., 2013) and chimpanzees are known to display eye preferences (Braccini et al., 2012; Hopkins, 1997) that correlate with hand preference (Braccini et al., 2012).

Additionally, it would be interesting to further investigate laterality and individual differences of behaviour using other methods of assessing personality. For example, trait ratings might be particularly appropriate as they are based on raters' experiences over long periods of time and different contexts (Freeman et al., 2013). This suggests that traits might be less affected by the dynamics of the social network that can heavily influence some behavioural measures, particularly grooming. Further, taking the group structure into account could help to better understand how the social network might be mediating in the expression of sociality and thus offer a clearer picture of how laterality is related to personality. Research has shown that chimpanzees with similar personalities tend to spend more time together (Massen & Koski, 2014) but further research would help explore the role of laterality in the manifestation of sociability through affiliative behaviours even further.

In conclusion, the results of this study found that neither laterality nor strength of laterality were significant predictors of behavioural style. Congruent laterality did not show any significant difference between left-congruent and right-congruent chimpanzees, although right-congruent chimpanzees showed a non-significant tendency to score higher in sociability. Overall, this study presents new findings regarding the possible role of the left hemisphere in chimpanzee behavioural style, although more research is needed in order to further explore this relationship. In particular, future research should consider studying the social structure and how it might affect the expression of social factors of behavioural style.

References

Altmann, J. (1974). Observational study of behavior: Sampling methods. *Behaviour, 49*(3), 227–267.

Anestis, S. F. (2005). Behavioral style, dominance rank, and urinary cortisol in young chimpanzees (*Pan troglodytes*). *Behaviour, 142*(9–10), 1245–1268. https://doi.org/10.1163/156853905774539418

Anestis, S. F. (2006). Testosterone in juvenile and adolescent male chimpanzees (*Pan troglodytes*): Effects of dominance rank, aggression, and behavioral style. *American Journal of Physical Anthropology, 130*(4), 536–545. https://doi.org/10.1002/ajpa.20387

Barnard, S., Wells, D. L., & Hepper, P. G. (2018). Laterality as a predictor of coping strategies in dogs entering a rescue shelter. *Symmetry*, *10*(11), 538. https://doi.org/10.3390/sym10110538

Barnard, S., Wells, D. L., Hepper, P. G., & Milligan, A. D. S. (2017). Association between lateral bias and personality traits in the domestic dog (*Canis familiaris*). *Journal of Comparative Psychology*, *131*(3), 246–256. https://doi.org/10.1037/com0000074

Bisazza, A., J. Rogers, L., & Vallortigara, G. (1998). The origins of cerebral asymmetry: A review of evidence of behavioural and brain lateralization in fishes, reptiles and amphibians. *Neuroscience & Biobehavioral Reviews*, *22*(3), 411–426. https://doi.org/10.1016/S0149-7634(97)00050-X

Braccini, S. N., & Caine, N. G. (2009). Hand preference predicts reactions to novel foods and predators in marmosets (*Callithrix geoffroyi*). *Journal of Comparative Psychology*, *123*(1), 18–25. https://doi.org/10.1037/a0013089

Brown, C., & Bibost, A. L. (2014). Laterality is linked to personality in the black-lined rainbowfish, Melanotaenia nigrans. *Behavioral Ecology and Sociobiology*, *68*, 999–1005. https://doi.org/10.1007/s00265-014-1712-0

Cameron, R., & Rogers, L. J. (1999). Hand preference of the common marmoset (*Callithrix jacchus*). Problem solving and responses in a novel setting. *Journal of Comparative Psychology*, *113*(2), 149–157.

Carver, C. S., Sutton, S. K., & Scheier, M. F. (2000). Action, emotion and personality: emerging conceptual integration. *Personality and Social Psychology Bulletin*, *26*, 741–751.

Clark, F. E. (2011). Space to choose: Network analysis of social preferences in a captive chimpanzee community, and implications for management. *American Journal of Primatology*, *73*(8), 748–757. https://doi.org/10.1002/ajp.20903

Corballis, M. C. (1989). Laterality and human evolution. *Psychological Review*, *96*(3), 492–505. https://doi.org/10.1037/0033-295X.96.3.492

Di Bitetti, M. S. (2000). Does brain lateralization have practical implications for improving animal welfare. *Behaviour*, *137*(11), 1517–1540. https://doi.org/10.1163/156853900502709

Davidson, R. J., Ekman, P., Saron, C. D., Senulis, J. A., & Friesen, W. V. (1990). Approach-withdrawal and cerebral asymmetry: Emotional expression and brain physiology: I. *Journal of Personality and Social Psychology*, *58*(2), 330–341. https://doi.org/10.1037/0022-3514.58.2.330

Dunbar, R. I. M. (2010). The social role of touch in humans and primates: Behavioural function and neurobiological mechanisms. *Neuroscience & Biobehavioral Reviews*, *34*(2), 260–268. https://doi.org/10.1016/J.NEUBIOREV.2008.07.001

Fernández-Lázaro, G., Latorre, R., Alonso-García, E., & Barja Núñez, I. (2019). Nonhuman primate welfare: Can there be a relationship between personality, lateralization and physiological indicators? *Behavioural Processes*, *166*, 103897. https://doi.org/10.1016/j.beproc.2019.103897

Fitch, W. T., & Braccini, S. N. (2013). Primate laterality and the biology and evolution of human handedness: A review and synthesis. *Annals of the New York Academy of Sciences*, *1288*(1), 70–85.

Freeman, H. D., Brosnan, S. F., Hopper, L. M., Lambeth, S. P., Schapiro, S. J., & Gosling, S. D. (2013). Developing a comprehensive and comparative questionnaire for measuring personality in chimpanzees using a simultaneous top-down/bottom-up design. *American Journal of Primatology*, *75*(10), 1042–1053. https://doi.org/10.1002/ajp.22168

Freeman, H. D., & Gosling, S. D. (2010). Personality in nonhuman primates: A review and evaluation of past research. *American Journal of Primatology*, *72*(8), 653–671. https://doi.org/10.1002/ajp.20833

Gartner, M. C., & Weiss, A. (2018). Studying primate personality in zoos: Implications for the management, welfare and conservation of great apes. *International Zoo Yearbook*, *52*(1), 79–91. https://doi.org/10.1111/izy.12187

Gordon, D. J., & Rogers, L. J. (2015). Cognitive bias, hand preference and welfare of common marmosets. *Behavioural Brain Research*, *287*, 100–108. https://doi.org/10.1016/j.bbr.2015.03.037

Gosling, S. D. (2001). From mice to men: What can we learn about personality from animal research? *Psychological Bulletin*, *127*(1), 45–86. https://doi.org/10.1037//0033-2909.127.1.45

Gosling, S. D. (2008). Personality in non-human animals. *Social and Personality Psychology Compass*, *2*(2), 985–1001. https://doi.org/10.1111/j.1751-9004.2008.00087.x

Goursot, C., Düpjan, S., Kanitz, E., Tuchscherer, A., Puppe, B., & Leliveld, L. M. C. (2019). Assessing animal individuality: Links between personality and laterality in pigs. *Current Zoology*, *65*(5), 541–551. https://doi.org/10.1093/cz/zoy071

Hopkins, W. D. (1995). Hand preferences for a coordinated bimanual task in 110 chimpanzees (*Pan troglodytes*): Cross-sectional analysis. *Journal of Comparative Psychology*, *109*(3), 291–297.

Hopkins, W. D., & Bennett, A. J. (1994). Handedness and approach-avoidance behavior in chipanzees (*Pan*). *Journal of Experimental Psychology: Animal Behavior Processes*, *20*(4), 413–418. https://doi.org/10.1037/0097-7403.20.4.413

Hopkins, W. D., Cantalupo, C., Freeman, H., Russel, J., Kachin, M., & Nelson, E. (2005). Chimpanzees are right-handed when recording bouts of hand use. *Laterality*, *10*(2), 121–130.

Hopkins, W. D., Misiura, M., Pope, S. M., & Latash, E. M. (2015). Behavioral and brain asymmetries in primates: A preliminary evaluation of two evolutionary hypotheses. *Annals of the New York Academy of Sciences*. *1359*(1), 65-83 https://doi.org/10.1111/nyas.12936

Hopkins, W. D., Wesley, M. J., Kay Izard, M., Hook, M., & Schapiro, S. J. (2004). Chimpanzees (*Pan troglodytes*) are predominantly right-handed: replication in three populations of apes. *Behavioural Neuroscience*, *118*(3), 659–663. https://doi.org/10.1037/0735-7044.118.3.659

Jung, S., & Lee, S. (2011). Exploratory factor analysis for small samples. *Behavior Research Methods*, *43*(3), 701–709. https://doi.org/10.3758/s13428-011-0077-9

King, J. E., & Landau, V. I. (2003). Can chimpanzee (*Pan troglodytes*) happiness be estimated by human raters? *Journal of Research in Personality*, *37*(1), 1–15. https://doi.org/10.1016/S0092-6566(02)00527-5

King, J. E., Weiss, A., & Farmer, K. H. (2005). A chimpanzee (*Pan troglodytes*) analogue of cross-national generalization of personality structure: Zoological parks and an African sanctuary. *Journal of Personality*, *73*(2), 389–410. https://doi.org/10.1111/j.1467-6494.2005.00313.x

Koyama, N. F., Ronkainen, K., & Aureli, F. (2017). Durability and flexibility of chimpanzee grooming patterns during a period of dominance instability. *American Journal of Primatology*, *79*(11), e22713. https://doi.org/10.1002/ajp.22713

Koolhaas, J. M., de Boer, S. F., Coppens, C. M., & Buwalda, B. (2010). Neuroendocrinology of coping styles: Towards understanding the biology of individual variation. *Frontiers in Neuroendocrinology*, *31*, 307–321.

Koolhaas, J. M., Korte, S. M., De Boer, S. F., Van Der Vegt, B. J., Van Reenen, C. G., Hopster, H., De Jong, I. C., Ruis, M. A. W., & Blokhuis, H. J. (1999). Coping styles in animals: Current status in behavior and stress- physiology. *Neuroscience and Biobehavioral Reviews*, *23*(7), 925–935. https://doi.org/10.1016/S0149-7634(99)00026-3

Koski, S. E. (2011). Social personality traits in chimpanzees: Temporal stability and structure of behaviourally assessed personality traits in three captive populations. *Behavioral Ecology and Sociobiology*, *65*(11), 2161–2174. https://doi.org/10.1007/s00265-011-1224-0

Koski, S. E. (2014). Broader horizons for animal personality research. *Frontiers in Ecology and Evolution*, *2*, 1–6. https://doi.org/10.3389/fevo.2014.00070

Krause, J., James, R., & Croft, D. P. (2010). Personality in the context of social networks. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1560), 4099–4106. https://doi.org/10.1098/rstb.2010.0216

Kudo, H., & Dunbar, R. I. M. (2001). Neocortex size and social network size in primates. *Animal Behaviour*, *62*(4), 711–722. https://doi.org/10.1006/anbe.2001.1808

Leliveld, L. M. C., Langbein, J., & Puppe, B. (2013). The emergence of emotional lateralization: Evidence in non-human vertebrates and implications for farm animals. *Applied Animal Behaviour Science*, *145*(1), 1–14. https://doi.org/10.1016/j.applanim.2013.02.002

Lehmann, J., Korstjens, A. H., & Dunbar, R. I. M. (2007). Fission–fusion social systems as a strategy for coping with ecological constraints: A primate case. *Evolutionary Ecology*, *21*(5), 613–634. https://doi.org/10.1007/s10682-006-9141-9

Llorente, M., Mosquera, M., & Fabré, M. (2009). Manual laterality for simple reaching and bimanual coordinated task in naturalistic housed *Pan troglodytes*. *International Journal of Primatology*, *30*, 183–197. https://doi.org/10.1007/s10764-009-9338-1

Llorente, M., Riba, D., Palou, L., Carrasco, L., Mosquera, M., Colell, M., & Feliu, O. (2011). Population level right-handedness for a coordinated bimanual task in naturalistic housed chimpanzees: Replication and extension in 114 animals from Zambia and Spain. *American Journal of Primatology*, *73*, 281–290. https://doi.org/10.1002/ajp.20895

MacNeilage, P. F., Studdert-Kennedy, M. G., & Lindblom, B. (1987). Primate handedness reconsidered. *Behavioral and Brain Sciences*, *10*, 247–303.

Morton, F. B., Lee, P. C., Buchanan-Smith, H. M., Brosnan, S. F., Thierry, B., Paukner, A., De Waal, F. B. M., Widness, J., Essler, J. L., & Weiss, A. (2013). Personality structure in brown capuchin monkeys: Comparisons with chimpanzees, orangutans, and rhesus macaques. *Journal of Comparative Psychology*, *127*(3), 282–298. https://doi.org/10.1037/a0031723

Murray, L. (1998). The effects of group structure and rearing strategy on personality in chimpanzees *Pan troglodytes* at Chester, London ZSL and Twycross Zoos. *International Zoo Yearbook*, *36*(1), 97–108. https://doi.org/10.1111/j.1748-1090.1998.tb02890.x

Noë, R., de Waal, F. B., & van Hooff, J. A. (1980). Types of dominance in a chimpanzee colony. *Folia Primatologica, 34*(1-2), 90-110.

Ocklenburg, S., Korte, S. M., Peterburs, J., Wolf, O. T., & Güntürkün, O. (2016). Stress and laterality – The comparative perspective. *Physiology & Behavior*, *164*, 321–329. https://doi.org/10.1016/j.physbeh.2016.06.020

Padrell, M., Gómez-Martínez, C., & Llorente, M. (2019). Short and long-term temporal consistency of hand preference in sanctuary chimpanzees (*Pan troglodytes*) for unimanual and bimanual coordinated tasks. *Behavioural Processes*, *167*, 103911. https://doi.org/10.1016/j.beproc.2019.103911

Robinson, L. M., Altschul, D. M., Wallace, E. K., Úbeda, Y., Llorente, M., Machanda, Z., Slocombe, K. E., Leach, M. C., Waran, N. K., & Weiss, A. (2017). Chimpanzees with positive welfare are happier, extraverted, and emotionally stable. *Applied Animal Behaviour Science*, *191*, 90–97. https://doi.org/10.1016/j.applanim.2017.02.008

Rogers, L., & Vallortigara, G. (2015). When and why did brains break symmetry? *Symmetry*, *7*(4), 2181–2194. https://doi.org/10.3390/sym7042181

Rogers, L. J. (2009). Hand and paw preferences in relation to the lateralized brain. *Philosophical Transactions of the Royal Society*, *364*, 943–954. https://doi.org/10.1098/rstb.2008.0225

Rogers, L. J. (2010). Relevance of brain and behavioural lateralization to animal welfare. *Applied Animal Behaviour Science*, *127*(1), 1–11. https://doi.org/10.1016/j.applanim.2010.06.008

Rogers, L. J. (2017). A matter of degree: Strength of brain asymmetry and behaviour. *Symmetry*, *9*(12), 57. https://doi.org/10.3390/sym9040057

Rogers, L. J. (2018). Manual bias, behavior, and cognition in common marmosets and other primates. In G. S. Forrester, W. D. Hopkins, K. Hudry, & A. Lindell (Eds.), *Progress in Brain Research* (Vol. 238, pp. 91–113). Elsevier. https://doi.org/10.1016/bs.pbr.2018.06.004

Salva, O. R., Regolin, L., Mascalzoni, E., & Vallortigara, G. (2012). Cerebral and behavioural asymmetries in animal social recognition. *Comparative Cognition & Behaviour Reviews*, *7*, 110–138. https://doi.org/10.3819/ccbr.2012.70006

Tomassetti, D., Caracciolo, S., Manciocco, A., Chiarotti, F., Vitale, A., & De Filippis, B. (2019). Personality and lateralization in common marmosets (*Callithrix jacchus*). *Behavioural Processes*, *167*, 103899. https://doi.org/10.1016/j.beproc.2019.103899

Úbeda, Y., & Llorente, M. (2015). Personality in sanctuary-housed chimpanzees: A Comparative approach of psychobiological and penta-factorial human models. *Evolutionary Psychology*, *13*(1), 147470491501300. https://doi.org/10.1177/147470491501300111

Uher, J. (2008). Comparative personality research: Methodological approaches. *European Journal of Personality*, *22*(5), 427–455. https://doi.org/10.1002/per.680

Uher, J., Asendorpf, J. B., & Call, J. (2008). Personality in the behaviour of great apes: Temporal stability, cross-situational consistency and coherence in response. *Animal Behaviour*, *75*(1), 99–112. https://doi.org/10.1016/j.anbehav.2007.04.018

Weiss, A., Adams, M. J., & Johnson, W. (2011). The big none: No evidence for a general factor of personality in chimpanzees, orangutans, or rhesus macaques. *Journal of Research in Personality*, *45*(4), 393–397. https://doi.org/10.1016/j.jrp.2011.04.006

Weiss, A., King, J.E., Murray, L. (Eds.) (2011). *Personality and Temperament in Nonhuman Primates.* Springer, New York, NY.

Wells, D. L., Hepper, P. G., Milligan, A. D. S., & Barnard, S. (2019). Lack of association between paw preference and behaviour problems in the domestic dog, *Canis familiaris*. *Applied Animal Behaviour Science*, *210*, 81–87. https://doi.org/10.1016/j.applanim.2018.10.008

Westergaard, G. C., Chavanne, T. J., Houser, L., Cleveland, A., Snoy, P. J., Suomi, S. J., & Higley, J. D. (2004). Biobehavioural correlates of hand preference in free-ranging female primates. *Laterality: Asymmetries of Body, Brain and Cognition*, *9*(3), 267–285. https://doi.org/10.1080/13576500342000086a

Westergaard, G. C., Chavanne, T. J., Lussier, I. D., Houser, L., Cleveland, A., Suomi, S. J., & Higley, J. D. (2003). Left-handedness is correlated with csf monoamine metabolite and plasma cortisol concentrations, and with impaired sociality, in free-ranging adult male rhesus macaques (*Macaca mulatta*). *Laterality: Asymmetries of Body, Brain and Cognition*, *8*(2), 169–187. https://doi.org/10.1080/713754484

Wiper, M. L. (2017). Evolutionary and mechanistic drivers of laterality: A review and new synthesis. *Laterality*, *22*(6), 740–770. https://doi.org/10.1080/1357650X.2017.1291658

Wolf, M., & Weissing, F. J. (2012). Animal personalities: Consequences for ecology and evolution. *Trends in Ecology & Evolution*, *27*(8), 452–461. https://doi.org/10.1016/j.tree.2012.05.001

Wright, L., Watt, S., & Hardie, S. M. (2013). Influences of lateral preference and personality on behaviour towards a manual sorting task. *Personality and Individual Differences, 54*(8), 903–907. https://doi.org/10.1016/j.paid.2013.01.005

Chapter 5. Social Network

Summary

After investigating laterality and early hemispheric specialization in the previous chapter by researching the link between laterality and behavioural style, the next objective of the thesis is to look into the relationship between laterality and intraspecific coordination. Investigating coordination in the captive group of chimpanzees studied in this thesis requires the use of Social Network Analysis. This approach allows researchers to describe and quantify aspects of the social structure of the group and the social relationships between individuals, obtaining information about social bonds that can be used to tackle the question. Chapter 5 has the objective of introducing the approach of Social Network Analysis to describe and characterize the group before tackling the final question of the thesis: investigate if laterality plays a role in intraspecific coordination by affecting the social network. In addition, a new adult chimpanzee was in the process of being introduced to the group during the process of data collection. This presented the rare opportunity to use the data both to inform management throughout the duration of the data collection as well as to offer new information about the stability of the group. The study presented in this chapter was published online in the International Journal of Primatology in October of 2020, although it is presented with minor format changes in order to better fit the structure and format of the thesis.

Introduction

Captive environments offer opportunities for researchers to study and understand primate behaviour, but they often also present numerous challenges (Hosey, 2005). A common challenge in captive management of primates is the need to integrate new members into an established group. Research on new introductions in captivity is limited and often focuses on how these events inform management decisions (Brent et al., 1997). However, research investigating how new introductions affect the animals themselves in terms of group dynamics and social relationships is scarce.

Primate relationships are well-known for being stable over time (Koski et al., 2012), but group changes can potentially alter these relationships, disrupting the group stability (Flack et al., 2006). The introduction of new individuals can alter group dynamics by creating new connections that can disrupt the already established structure of the group. For example, a study on Sulawesi crested macaques found that the introduction of a new male lead to a temporary increase in grooming among females of the group, although the grooming network reverted back to normal in the following ten weeks (Cowl et al., 2020). In addition to studying grooming networks, agonistic networks may be good indicators of disruptions after an introduction. For instance, integrations of adult male rhesus macaques are considered successful if the male remains in the group for four weeks without significant behavioural problems (e.g. severe aggression to or from the females in the group; Rox et al., 2019).

Studying the stability of a group after an introduction requires a careful consideration of other factors that can affect the position of individuals in the social network, such as early social history (Suomi, 1997), as these factors might be especially relevant during periods where new social ties are being formed. Rhesus macaques with a history of maternal deprivation show decreased social competence (Kempes et al., 2008) and often fail to reconcile after conflict (Kempes et al., 2009). Common marmosets that received reduced early care show increased signs of stress and decreased social play later in life (Dettling et al., 2002). Social deprivation also has negative effects in adult chimpanzees (Freeman et al., 2016; Murray, 1998) and presents an additional challenge in the integration of gorillas (*Gorilla gorilla gorilla*) in captivity (Burks et al., 2001). Similarly, as agonistic behaviours are particularly relevant as indicators of group stability after introductions (Rox et al., 2019), it is important to consider the possible sex differences in aggression that some primate species are known to exhibit (Bernstein & Ehardt, 1985, Fedigan & Baxter, 1984; Kulik et al., 2015, Muller & Mitani, 2005). Male capuchin monkeys, for example, display more frequent agonistic behaviours towards new individuals than females, usually shortly after the introduction but sometimes several days later (Cooper et al., 2001).

Social Network Analysis is a useful tool to investigate aspects of primate group structure such as reciprocity and stability over time and can also be used to inform the management of animals in captivity (Rose & Croft, 2015). For example, high grooming reciprocity is a good predictor of lower aggressive outbreaks in rhesus macaques (McCowan et al., 2008). Similarly, grooming reciprocity is associated with decreased aggression in male Tibetan macaques (*Macaca thibetana*, Xia et al., 2013), while females tend to show higher reciprocity with other females of adjacent ranks (Xia et al., 2012). Grooming networks are known to be highly stable in rhesus macaques (Massen & Sterck, 2013) and female baboons (*Papio* sp, Silk et al., 2012), with some research showing that wild baboon groups remain stable after group changes, showing only a limited reduction in grooming degree in the first month after an adult leaves the group (Franz et al., 2015).

Chimpanzees are an important species to focus on for the measurement of response to change in the medium-term because they are a highly social species that live in multi-male, multi-female groups with high fission-fusion dynamics (Lehmann et al., 2007). Further, in the wild female chimpanzees leave their natal community to join neighbouring communities (Foerster et al., 2015; Lehman & Boesch, 2009; McCarthy et al., 2018). For resident females, the immigrant females provide more competition for feeding, whereas for resident males, immigrant females provide new opportunities for mating (Kahlenberg et al., 2008a). Female immigrants receive higher levels of aggression than resident females (Kahlenberg et al., 2008b; Pusey et al. 2008), hold lower dominance ranks and have higher levels of physiological stress, as measured by cortisol (Kahlenberg et al., 2008a). Immigrant females form strong associations with adult males, which intervene to reduce the amount of aggression they receive (Kahlenberg et al., 2008a). Given that immigrant females have a large effect on patterns of sociality in the wild (Kahlenberg et al., 2008a; Kahlenberg et al., 2008b; Pusey et al., 2008), it is important to examine the impact of new adult females being introduced into a captive group. Thus, the aim of this study is to examine how the introduction of a new adult female into a captive group affects the stability of the group over the medium term, whilst also examining two other factors that affect patterns of sociality – early life history and sex.

Chimpanzees in captivity show strong group cohesion and distinct social roles, where each individual contributes to the overall group structure in a different way (Funkhouser et al., 2018; Kanngiesser et al., 2011). Group size has been found to relate to differences in personalities (Murray, 1998), with those living in larger groups displaying higher levels of traits associated with positive characteristics – including sociability, gentleness and intelligence – in contrast to those housed in pairs or trios. Captive groups of chimpanzees are flexible and show stable structures during changes of environment (Koyama & Aureli, 2019) and partial stability during changes in dominance (Koyama et al., 2017). The effects of rearing history on adult socialization are well studied in chimpanzees. Chimpanzees that have experienced deprived maternal contact and decreased social interactions manifest personality differences, including higher eccentricity (Murray, 1998) and show reduced grooming later in life (Freeman & Ross, 2014; Kalcher-Sommersguter et al., 2015). Although chimpanzees with different origins do not show significant differences in grooming centrality or network position in captivity (Levé et al., 2016; Rodrigues & Boeving, 2019), group density is significantly affected by the removal of wild-born chimpanzees but not captive-born chimpanzees in simulated models (Levé et al., 2016). Sex differences in chimpanzee aggression are also well documented. Males initiate aggression more often than females (Muller, 2002), although females that recently immigrated into the group tend to receive more aggression from females than from males (Kahlenberg et al., 2008a).

This study analyzed social networks based on proximity, grooming, other affiliative behaviours and agonistic behaviours of the chimpanzee group at Chester Zoo, during the first year after the introduction of a new adult female. Studies often focus on grooming as the only affiliative behaviour (Koyama et al., 2017; Levé et al., 2016) or include grooming in the affiliative network (Clark, 2011), although some studies complement these with proximity networks (Clark, 2011; Funkhouser et al., 2018). This study investigated proximity, grooming and other affiliative behaviours (embrace, social play, begging, sharing food and sexual contact) separately to obtain a more detailed picture of patterns of affiliation in the group. This study had three objectives: 1) to investigate the stability, reciprocity and cohesion of the social networks for grooming, affiliative and agonistic behaviours after the introduction of a new female in the group; 2) to investigate whether chimpanzees differed in their grooming centralities based on their early life histories, and 3) to test whether males and females differed in agonistic behaviour.

Method

Sample

The study group consisted of 19 chimpanzees, seven males and 12 females, housed at Chester Zoo, UK. Names, hours observed and rearing history of the chimpanzees are shown in Table 2, for more information on the sample and study site, see Chapter 2.

Table 1

Chimpanzees at Chester Zoo, UK, indicating hours observed and rearing history

Name	Hours observed	Rearing history
Carlos	15	Mother-reared
Eric	17	Mother-reared
Dylan	15	Mother-reared
Friday	16.7	Hand-reared
Nicky	15.7	Hand-reared
Wilson	15.7	Hand-reared
Boris	15.7	Hand-reared
Tina	15	Mother-reared
Patti	15.7	Mother-reared
Chrissie	16.3	Mother-reared
Vila	17	Mother-reared
Zee Zee	15.7	Mother-reared
Layla	15	Mother-reared
Alice	15.3	Mother-reared
Sally	15.7	Mother-reared
Sarah	15.3	Mother-reared
Mandy	17	Hand-reared
Farthing	16	Mother-reared
Rosie	16.7	Hand-reared

All the chimpanzees formed a single, well-established group. Two chimpanzees were born outside the group: Boris is wild-born and was integrated into the group in 1969 and Farthing was born in a different zoo and was integrated in 1984. No other chimpanzees had been introduced since 1984 and all other individuals were born at Chester Zoo. Vila arrived at the zoo in August 2015 with another adult female, Kiki, who subsequently passed away in October 2016. Vila was introduced gradually to the group in the off-show area under careful supervision by the keeper team before the study began. This study investigates the group structure from the moment when Vila was let into the indoor and outdoor zones to associate freely with all group members in January 2017.

Procedure

The group was observed for 301 hours from January 2017 to December 2017. Observation sessions usually lasted four hours, between 10am and 3pm, during regular zoo opening times. Data collection consisted of 20-minute sessions using 1-minute instantaneous sampling to record grooming behaviours from or directed to the focal animal and individuals within arm's reach of the focal animal. All social interactions of all individuals were recorded *ad libitum* (Altmann, 1974; Clark, 2011). Behaviours were defined using Clark´s (2011) ethogram (Table 2). Focal individuals were chosen opportunistically from those who were clearly visible, and all observations were balanced to observe all individuals for a similar amount of time. Inter-observer reliability was assessed between the main observer and two additional observers for state behaviours during the first month of data collection (Cohen's kappa *k*= 0.83). Monthly reports of the observations of grooming, affiliative and agonistic behaviours, including sociograms and centrality measures, were shared with the primate team at Chester Zoo.

Table 2

Ethogram modified from Clark (2011), showing sampling methods, affiliative, agonistic and state behaviours recorded as well as frequency and percentage of each behaviour for affiliative and agonistic behaviours

Sampling method		Description	Frequency and percentage
	Affiliative		
Ad libitum sampling	Embrace	Embrace or hug another individual	35 (11.5%)
	Social play	Tussle and chase another individual. May be accompanied by the "play face" and patting vocalizations	63 (20.3%)
	Beg	Offer hand outstretched to another individual to solicit support	99 (32.5%)
	Share food	Allow another to share the same piece or small pile of food. Handle food with another or tolerate food being taken	11 (3.6%)
	Sexual	Heterosexual mount that may be followed by thrust and intromission. Inspect genitals to solicit sexual activity	40 (13.1%)
	Other	Other affiliative behaviours not listed above	58 (19%)
	Agonistic		
Ad libitum sampling	Dominance mount	Mount another individual in a nonsexual context, or position rear-end toward another to solicit mounting	38 (13.9%)
	Displace or supplant	Approach another individual and cause their retreat. May be related to access to a resource such as food	110 (40.1%)
	Noncontact threat	Various behaviours including charge and lunge. May be accompanied by bristling hair. Display aimed at group, sub-group or one individual	47 (17.2%)
	Attack	Physical aggressive contact such as hit or bite	79 (28.8%)
	State Behaviours		
One-minute focal scan sampling	Proximity	Identity of individuals within arm's reach of the focal individual	
	Feed	Eat or drink from diet, enclosure substrate, or food-based enrichment	
	Forage	Actively search for food	
	Locomote	Move bipedally or quadrupedally	
	Explore	Investigate environment, but not in relation to food. Vigilant to visitors or keepers	
	Rest	Rest or sleep in varying postures	
	Social	Agonistic and affiliative behaviour. Specific social interactions recorded separately (see below)	
	Auto groom	Pick through own hair, examine skin, and remove dirt and detritus	
	Allo-groom	Pick through the hair of another individual, examine skin, and remove dirt and detritus. Behaviour may or may not be reciprocated	
	Other	Any behaviour not listed above	

Social Network Measures

Four separate networks were created to analyze different aspects of the group structure: proximity, grooming, other affiliative behaviours, and agonistic networks. Grooming is widely used as an indicator of chimpanzee relationships (Koyama et al., 2017; Levé et al., 2016) and proximity is often used in addition to grooming in Social Network Analyses (Funkhouser et al., 2018; Kalcher-Sommersguter et al., 2015; Schel et al., 2013). Agonistic behaviours are commonly reported in management studies, particularly during integrations (Brent et al., 1997; Schel et al., 2013). Other affiliative behaviours are also commonly reported in Social Network Analyses (Clark, 2011; Funkhouser et al., 2018) and the behaviours included in this affiliative network were embrace, social play, begging, sharing food and sexual contact (Table 2). Grooming or proximity were not reported in the affiliative behaviours network, as they are considered separately. Each network had 19 rows and 19 columns, representing the 19 total focal chimpanzees, with a total of 342 dyads.

Simple ratio indices, ranging 0–1, were used to quantify the amount of time spent together or the amount of interaction between individuals while accounting for different observation times. Simple ratio indices are useful in order to represent association matrices while accounting for different observation times (Whitehead & James, 2015). These indices were used to create an undirected (symmetrical) proximity matrix and a directed (asymmetrical) grooming matrix. Half-weight ratio indices, also ranging 0-1, were used as a more conservative estimate of association to create directed (asymmetrical) matrices for affiliative and agonistic interactions (Farine & Whitehead, 2015). Half-weighted ratios are used as a more conservative estimation of association than weighted ratios, less biased when there is a chance of missing observations of individuals (Farine & Whitehead, 2015).

In-degree (mean value of interactions received) and out-degree (mean value of interactions given) were calculated to assess how well connected each individual was (Rose & Croft, 2015). Betweenness centrality (the number of times the focal is in the shortest path connecting two other nodes) was also calculated, to determine which individuals are important in keeping the group connected (Rose & Croft, 2015). Degree is useful to measure which individuals have strong direct connections in the network, while betweenness allows the identification of individuals that play an important role in connecting isolated members of the group (Kanngiesser et al., 2010; Koyama & Aureli, 2019). Both measures work well with weighted data in both directed and undirected networks (Borgatti et al., 2013). While weighted degree is commonly referred to as "strength" centrality, this chapter will refer to it as "in-degree" or "out-degree", depending on direction, according to Borgatti et al.' (2013). All centrality measures were calculated using UciNet 6.627 (Borgatti et al., 2002).

Data Analysis

Network Stability

Changes in the group structure were explored by dividing the 12 month data collection period into three time periods of four months each: January to April, May to August and September to December. Studies have used this approach with this group of chimpanzees to examine network stability over time (Koyama et al., 2017). Quadratic Assignment Procedure (QAP) correlations were calculated in R v. 3.6.1 using the package "sna" (Butts, 2019) to test the consistency of grooming, affiliative and agonistic behaviours across the three time periods. This procedure correlates two matrices by modifying them into two columns and calculating Pearson's *r* between them. It creates a set number of random permutations with the rows and columns of the matrices to create a distribution to compare with the correlation obtained to calculate the significance of the correlation (Borgatti & Feld, 1994). The *p*-value is calculated by determining the proportion of times that the random correlations are larger than the observed correlation. All analyses used 5000 permutations and an alpha value of 0.05.

Network Reciprocity and Sub-group Detection

Network reciprocity was examined in grooming, agonistic behaviours and affiliative behaviours using Mantel Z-tests with the “ape” package (Paradis & Schliep, 2019) in R v. 3.6.1. Mantel Z-tests are a permutation-based procedure used to detect reciprocity in behaviours, obtaining a matrix correlation coefficient by correlating the non-diagonal elements of two matrices (Hemelrijk, 1990).

Hierarchical cluster analyses were calculated in UciNet 6.627 (Borgatti et al*.,* 2002), using the average between pairs method, to create a dendrogram and detect sub-groups in the proximity matrix, and in the symmetrized grooming, agonistic and affiliative matrices. This algorithm detects the strongest similarity between two elements (for example, the two chimpanzees that have spent the most time in close proximity) and clusters them together. The software repeats this step until a single cluster represents the whole group, then provides Q coefficients to measure how well-defined the sub-groups are. Q coefficients with values of 0.3 or more indicate good divisions of the network into subgroups (Newman, 2004).

Sex and Rearing History Differences

Node-level permutation t-tests were calculated using the “coin” package (Hothorn et al., 2008) in R v. 3.6.1 to test for differences in the centrality indices of the grooming matrix between hand-reared and mother-reared chimpanzees, and for differences in the centrality indices of the agonistic matrix between males and females using an alpha value of 0.05. The package “effsize” was used to calculate the effect size using Cohen’s d. Permutation-based ANOVA (Symmetry Test) was used to further investigate differences across the three periods in Out-Degree (the mean value of agonistic behaviour by the focal individual directed at other individuals) to study changes in agonistic behaviour over time. Post-hoc tests were used with adjusted *p*-values to control the false discovery rate (Benjamini & Hochberg, 1995; Benjamini & Yekutieli, 2001).

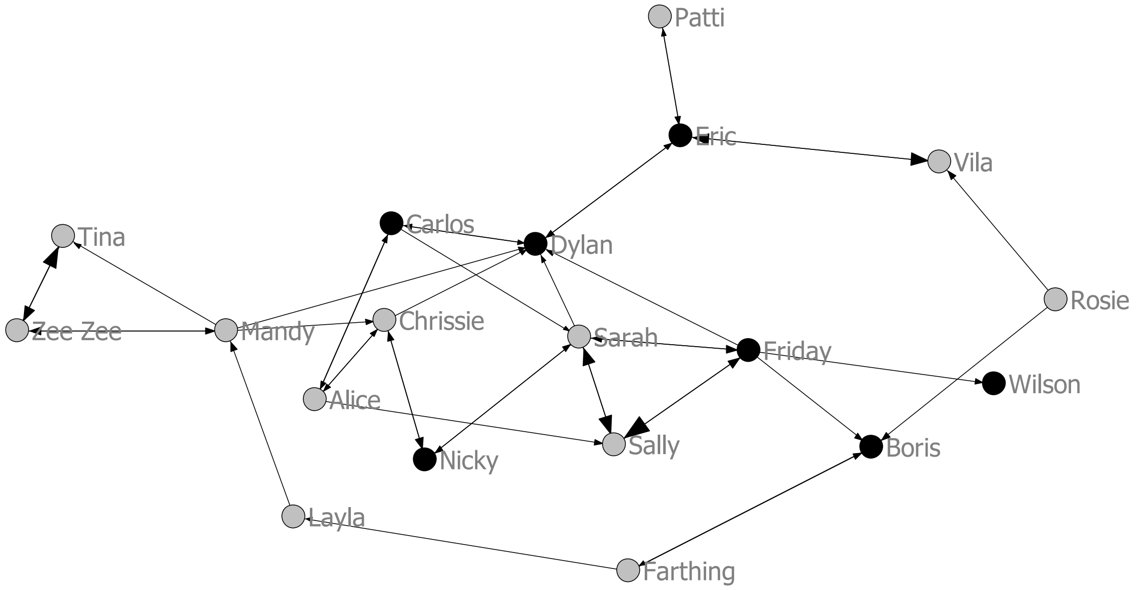
Results

Frequency of Behaviours

Each chimpanzee was involved in a mean of 0.79 (SD 0.63) affiliative interactions per hour, and in a mean of 0.50 (SD 0.77) agonistic interactions per hour. Over the three time periods, chimpanzees spent a mean of 12.1% of their time grooming (SD 5.8%). Vila, the newly integrated chimpanzee, groomed reciprocally with Eric and received grooming from Rosie (Figure 1). Vila displayed affiliative ties to Tina, the youngest female in the group, and Dylan, the alpha male, who was central to both the affiliative and grooming networks (Figure 2). However, Vila was unconnected in the agonistic network because she did not receive, or give, strong agonistic behaviour (Figure 3).

Figure 1

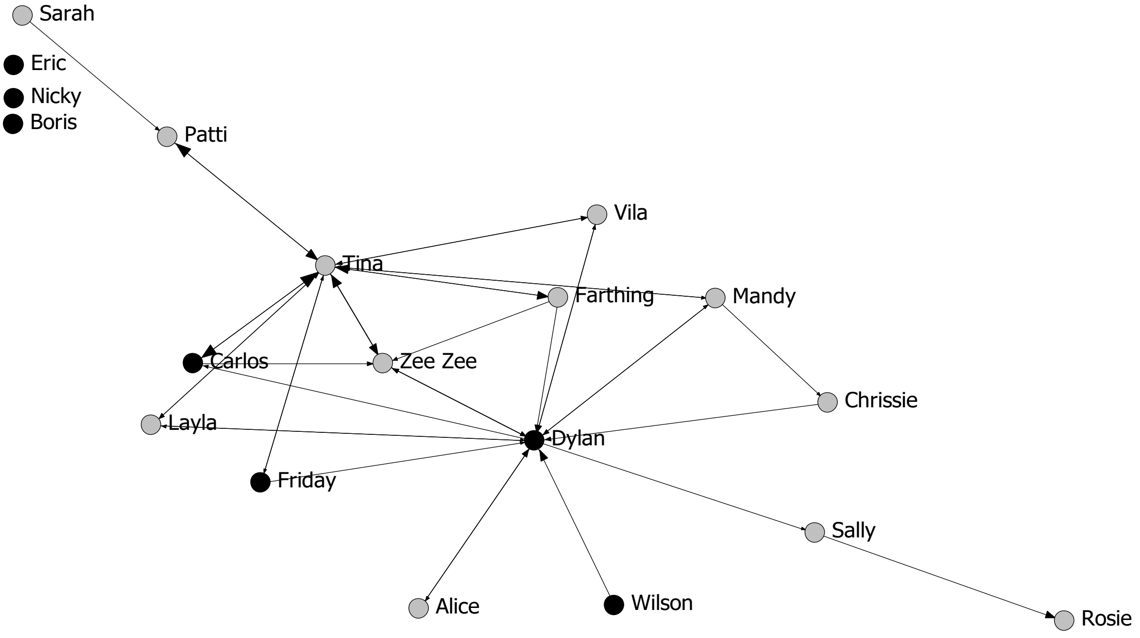
Grooming network over 12 months, showing strong grooming ties (one SD above the mean)



Note: Females are displayed in grey and males in black; arrowheads represent direction and strength.

Figure 2

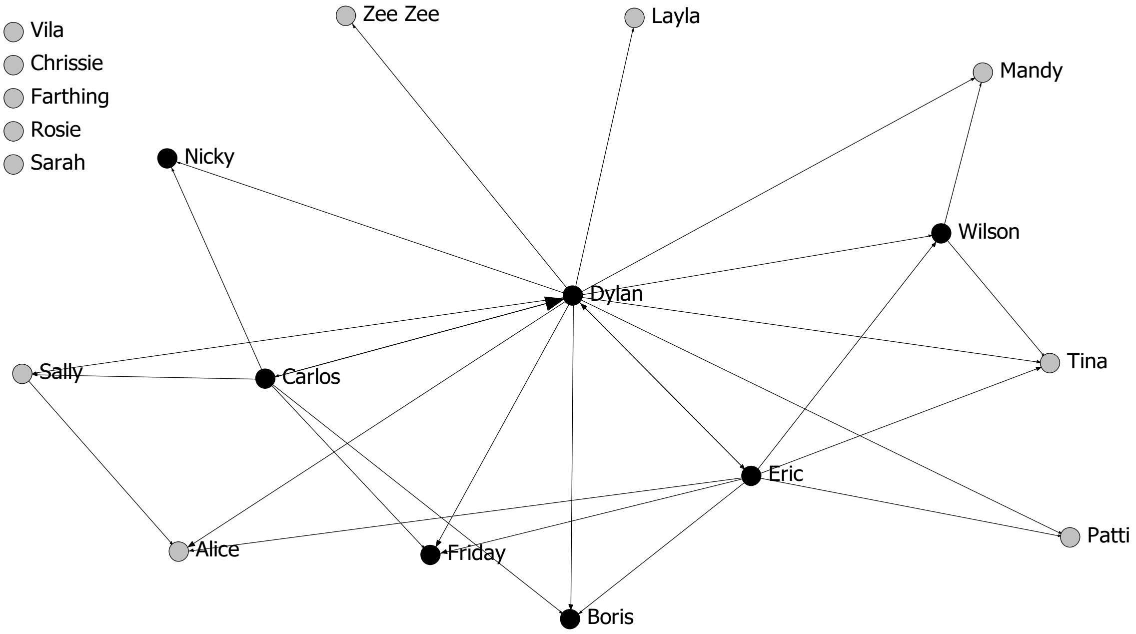
Affiliative network over 12 months, showing strong affiliative ties (one SD above the mean)



Note: Females are displayed in grey and males in black; arrowheads represent direction and strength.

Figure 3

Agonistic network over 12 months, showing strong agonistic ties (one SD above the mean)



Note: Females are displayed in grey and males in black; arrowheads represent direction and strength.

Correlations Between Behaviours

For the full year, a significant positive QAP correlation was found between grooming and proximity (*r*= 0.595, *p*< 0.001, N= 342 dyads) but the correlations between grooming and affiliative behaviours (*r*= 0.119, *p*= 0.061, N= 342 dyads) and between grooming and agonistic behaviours (*r*= 0.064, *p*= 0.130, N= 342 dyads) were not statistically significant.

Correlations Between Time Periods

The QAP correlations for grooming between the first and second periods, and between the second and third periods (Table 3) were significant. For affiliative behaviours, the data does not show a significant correlation between the first and second periods, but there was a significant positive correlation between the second and third periods. Finally, for agonistic behaviours, the QAP analysis found significant positive correlations between the first and second period, and between the second and third periods.

Table 3
Quadratic Assignment Procedure correlation coefficients between three time periods for grooming, affiliative and agonistic behaviours (N= 342 dyads)

	Grooming	Affiliative	Agonistic
Periods 1 - 2	.316**	.081	.319**
Periods 2 - 3	.415**	.391**	.411**

** Indicates correlations significant at *p* < 0.01.

Network Reciprocity

There was significant reciprocity in grooming (Mantel Z-test *p* = .001), agonistic behaviours (*p*< .044) and affiliative behaviours (*p*< .001), indicating that chimpanzees tended to reciprocate interactions.

Subgroup Detection

Hierarchical cluster analysis did not detect a good division into subgroups in grooming (Q=.228), although the adequacy of grooming clusters was close to the cut-off of Q>.3. There were no good subgroups in proximity (Q=.067), affiliative behaviours (Q=.142) or agonistic behaviours (Q=.011).

Rearing History

The data does not show significant differences between hand-reared and mother-reared chimpanzees in out-degree (Permutation *t* test *Z*= -1.18, *p*= .251, *d*=0.59, Table 3), in-degree (*Z*= -1.40, *p*= .167, *d*=0.71, Table 3) or betweenness centrality (*Z*= -1.07, *p*= 0.292, *d*=0.53, Table 3), indicating that chimpanzees with different early life histories did not differ in the amount of grooming partners they had, or in their importance as interconnecting individuals between other members of the group (Table 4).

Table 4
Mean (and standard deviation) grooming centrality for hand-reared and mother-reared chimpanzees

	Hand-reared	Mother-reared
Out-degree	0.10 (0.07)	0.13 (0.04)
In-degree	0.10 (0.04)	0.13 (0.04)
Betweenness	3.21 (2.55)	4.29 (4.72)

Sex Differences

The out-degree for agonistic behaviours was significantly higher in males than in females (*Z*=-2.29, *p*= .018, *d*=1.26, Table 5), indicating that males directed more agonistic behaviours at other individuals than females did, but there was no sex differences in in-degree (*Z*=-1.74, *p*= .077, *d*=0.88) or betweenness centrality (*Z*=-.67, *p*= .519, *d*=0.31) (Table 5), indicating that males and females did not differ in the amount of agonistic behaviour received or directed to other individuals. The data did show a significant effect of time period on female agonistic out-degree (symmetry test *T*= 2.57, *p*= .027), but pairwise comparisons with adjusted *p* values revealed no significant differences between periods (Table 6).

Table 5
Mean (and standard deviation) agonistic centrality by sex

	Males	Females
Out-degree	0.62 (0.66)	0.112 (0.11)
In-degree	0.40 (0.23)	0.241 (0.15)
Betweenness	17.07 (15.47)	12.54 (14.02)

Table 6
Mean (and standard deviation) out-degree by sex during three 4-month periods

	Males	Females
Period 1	3.29 (3.45)	1.08 (1.16)
Period 2	4.14 (5.43)	0.92 (1.16)
Period 3	7.86 (6.20)	2.58 (2.61)

There was also a significant effect of time period of male out-degree in agonistic behaviours (*T*= 2.92, *p*= .01), with pairwise comparisons revealing that male out-degree in agonistic behaviours was higher in period 3 than in periods 2 or 1 (Table 7).

Table 7
Adjusted p values for pairwise comparisons of out-degree in agonistic behaviour between three 4 month time periods

	Females	Males
Periods 1 and 2	.637	.355
Periods 1 and 3	.142	.046*
Periods 2 and 3	.087	.046*

* Indicates significant corrected *p* values.

Discussion

The findings show that the grooming network and agonistic network were stable between the three 4-month study periods in this captive group of chimpanzees after the integration of a new adult female into the group. However, the network using other affiliative behaviours was only stable between the second and third periods. The three networks showed significant reciprocity, but there were no subgroups in the group. There were no differences in network position in grooming between hand-reared and mother-reared chimpanzees. Finally, males performed significantly more agonistic behaviours than females with a large effect size, although there was no difference in in-degree, meaning that neither females nor males were more likely to be targeted in aggression, and betweenness centrality, which indicates that neither females nor males were more likely to display agonistic behaviours towards less connected individuals. Moreover, male agonistic behaviour increased significantly during the third 4-month period of the year.

The grooming network correlated moderately across the three 4-month time periods of the study, indicating that it was moderately stable during the first year after the integration of a new group member. Primate networks are highly stable over time (Franz et al., 2015; Massen & Sterck, 2013) and the results indicate that chimpanzee grooming networks retain some stability during periods where the group undergoes changes, supporting previous findings that indicate that grooming networks in captive chimpanzees correlate between periods of dominance uncertainty (Koyama et al., 2017). The agonistic network of the group also showed moderate correlations across the three time periods. These results contrast with those found in a study showing that agonistic behaviour reduced in the year following the integration of two chimpanzee groups (Schel et al., 2013). This difference in results can be explained by the fact that integrating two groups is a much bigger disruptor than integrating a single female, and it is possible that agonistic behaviour increased particularly among male chimpanzees, as males show high intergroup aggression (Muller & Mitani, 2005). The results showed only a moderate correlation between the second and third time periods for affiliative behaviours, which could be due to initial changes in the affiliative network in the first period, followed by more settled structure in the next two periods. However, the affiliative network in this study includes diverse behaviours such as play and sexual interactions and an alternative explanation for the lack of temporal stability between the first and second periods is that these affiliative behaviours serve different functions during these two periods. These results match those found in a study on dyadic interactions between newly introduced chimpanzees that showed how grooming could be observed early in the introduction but other affiliative behaviours such as play would appear later in the process (Brent et al., 1997). The lack of a significant correlation between the grooming network and the affiliative network highlights the need to consider grooming behaviours separately from other interactions and indicates that this approach might offer a more nuanced picture of primate groups.

The chimpanzee group at Chester Zoo shows high grooming reciprocity, with females reciprocating grooming even during periods of dominance instability (Koyama et al., 2017), and the results indicate that the group also shows reciprocity in other affiliative behaviours. Higher grooming reciprocity is associated with lower aggression rates in macaques (*Macaca nemestrina* Flack et al*.,* 2006; *Macaca sylvanus* McCowan et al*.,* 2008), which may reflect a positive overall group dynamic and could indicate that that the integration of the new chimpanzee into the group is going well. The results contrast with a study that did not find reciprocity in grooming in a sample of seven chimpanzees housed in a sanctuary (Funkhouser et al., 2018). This difference may have been because grooming reciprocity is higher among related than among unrelated chimpanzees (Fedurek & Dunbar, 2009). The sanctuary animals were genetically unrelated (Funkhouser et al., 2018), whereas the chimpanzee group at Chester Zoo has several maternally-related individuals (Koyama et al., 2017). The results support previous findings of reciprocity in agonistic interactions (Funkhouser et al., 2018). These data indicate that although some individuals are more central in the agonistic network (i.e. Dylan and Carlos), they do not dominate agonistic behaviours. However, it is important to consider that observations of agonistic behaviour are often limited in captivity, particularly in big groups or in situations with limited space to avoid interactions (Videan & Fritz, 2007).

Although the data shows distinct preferences in the way each individual interacts with others, hierarchical cluster analysis did not detect sub-groups. This finding supports previous findings that also did not find significant sub-groups in captive chimpanzees (Clark, 2011; Funkhouser et al., 2018), although the authors stressed the need to be cautious when interpreting a lack of sub-groups, as groups of chimpanzees might change too quickly to be reflected when studied over a period of several months (Clark, 2011). Studies of chimpanzees (Brent et al., 1997) and of macaques (Cowl et al., 2020; Rox et al., 2019) show that successful integrations might disrupt the group networks in the first four weeks. The findings indicate that, in the medium-term after the integration, the overall group structure was moderately stable, reciprocal and cohesive, showing that the group was well adapted to the new arrival and did not experience strong changes during this period. The position of Vila, the newly introduced female, in the grooming and affiliative network showed strong ties to central individuals such as Dylan, and her position in the agonistic network indicated that she did not commonly receive or give aggression. Thus, whilst immigrant females in wild groups have significant effects on patterns of female-female and male-female sociality and aggression (Kahlenberg et al., 2008a), the introduction of a single female did not appear to have a disruptive effect on the social network of a captive group. One important difference may be that whereas in wild groups there are multiple immigrant females, creating tension between resident males, resident females and immigrant females (Kahlenberg et al., 2008a; Kahlenberg et al., 2008b; Pusey et al., 2008), this study focused solely on a single new female immigrant into an otherwise stable group.

The findings did not show a significant difference in grooming centrality between hand-reared and mother-reared chimpanzees. The two hand-reared females in the group (Mandy and Rosie) are both well-connected to their daughters, and the increased reciprocity between kin might contribute to their centrality in the grooming network. Deprivation of social maternal contact during early life reduces grooming activity throughout adult life in chimpanzees (Freeman & Ross, 2014; Kalcher-Sommersguter *et al.,* 2013), while research with rhesus macaques has shown that it is associated with less reconciliation after a fight (Kempes *et al*., 2008; Kempes *et al*., 2009), although the effect on network position is still unclear. More research into the mediating effects of family relationships and, potentially, resocialization efforts in sanctuary settings, could help build a more detailed understanding of the long-lasting impact of early life on network position and social role.

Males showed significantly higher out-degree in agonistic behaviour than females with a large effect size, which is to be expected in chimpanzees, as males tend to show more aggression than females and in a wider range of contexts, from fights for dominance to food competition (Muller, 2002). In particular, three individuals held central positions in the agonistic network: Dylan, who has been identified as the dominant individual since 2002 (Koyama et al., 2017), and two young males that often display and fight with him, Carlos and Eric. In the wild, males may protect new females from aggression by resident females (Kahlenberg et al., 2008a). Nevertheless, there was no significant sex difference in in-degree or betweenness centrality, indicating that agonistic behaviours were not directed preferentially towards females or other males. In contrast to the high levels of aggression received by immigrant females in the wild (Kahlenberg et al*.,* 2008a) Vila, the new female chimpanzee, did not receive above-average agonistic behaviour from other members of the group, but did show strong grooming ties to central males in the group (Dylan during the first period and Eric throughout the year) which might have helped her avoid agonistic interaction with other females. Whilst there are important differences between patterns of sociality in captivity and the wild, for example in the fission-fusion social structure (Lehmann et al., 2007), the results suggest that new adult females introduced into captive groups may follow the strategy seen in wild chimpanzees of forming stronger associations with males than females (Kahlenberg et al., 2008a). Further research could examine whether this is a consistent finding when new adult females are introduced in captivity, whether males intervene to prevent the new female receiving aggression in captive settings as they do in the wild (Kahlenberg et al., 2008a) and whether the social network of wild chimpanzee groups also shows stability when new adult females enter the group.

Interestingly, male agonistic behaviour significantly increased during the third period of the study. Although space restriction due to bad weather was more common during the last period of the study, this is unlikely to be a determining factor in the increase of male agonistic behaviour, as studies found no differences in mutual grooming and agonistic behaviour in the same group during periods of space restriction (Koyama & Aureli, 2019). Instead, this increase in male agonistic behaviour is likely to indicate intensification of the conflict between the dominant male and the two young males that were beginning to challenge his dominance.

It is important to consider several limitations when interpreting these findings. First, the affiliative network groups together social play, begging, sharing food and sexual behaviours. This affiliative network was included to give a more comprehensive picture of affiliation in the group than relying only on grooming. However, grouping behaviours can present problems when the behaviours might have different functions and may explain why some researchers focus solely on grooming networks (Funkhouser et al., 2018; Kalcher-Sommersgutter et al., 2015; Koyama et al., 2017; Levé et al., 2016; Schel et al., 2013). Considering additional affiliative behaviours separately instead of grouping them may be a valuable approach in future. Future research could also consider the use of multi-layered approaches to the study of affiliation, which allow researchers to integrate and examine multiple indices of social interactions (Silk et al., 2013; Silk et al., 2018; Smith-Aguilar et al., 2019).

A second limitation is that the study examined the development of the group structure after the integration of a new female but did not use data prior to the integration. The data does not allow the possibility of assessing changes in the network as a consequence of the arrival of the new chimpanzee. Instead, this study focused on the medium-term stability of the group structure. Similarly, the study does not include information from before Vila had access to the full enclosure, which could be valuable in interpreting her position in the networks and her individual ties.

Despite these limitations, the findings extend previous work on social networks in primates (Clark, 2011; Funkhouse et al., 2018; Koyama & Aureli, 2019; Koyama et al., 2017; Massen & Sterck, 2013; McCowan et al., 2008; Silk et al., 2012) by examining how a chimpanzee group adapted to the integration of a new adult female, as well as investigating the effects of rearing history and sex in the social network. The group structure proved to be moderately stable and cohesive during the first year after the introduction of the female, suggesting that the integration was successful, although affiliative behaviours were only stable in the second and third periods. Rearing history did not significantly affect grooming centrality. Males were more agonistic than females, particularly during the third period. The new chimpanzee, Vila, formed strong grooming ties to central male individuals in the group and was not strongly connected in the agonistic network, indicating that she was not a common target of agonistic behaviour and that she did not direct frequent agonistic behaviours at others. Further research could examine primate social networks before new introductions to better understand changes produced by the arrival. The findings show that chimpanzee groups can adapt well to new integrations and illustrate how Social Network Analysis can be used to understand primate behaviour in captivity, potentially helping management decisions.

References

Altmann, J. (1974). Observational study of behavior: Sampling methods. *Behavior, 49*(3), 227-259.

Benjamini, Y., & Hochberg, Y. (1995). Controlling the false discovery rate - A practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society Series B (Methological)*, *57*(1), 289–300. https://doi.org/10.2307/2346101

Benjamini, Y., & Yekutieli, D. (2001). The control of the false discovery rate in multiple testing under dependency. *Annals of Statistics*, *29*(4), 1165–1188. https://doi.org/10.1214/aos/1013699998

Bernstein, I. S., & Ehardt, C. L. (1985). Age-sex differences in the expression of agonistic behavior in rhesus monkey (*Macaca mulatta*) groups. *Journal of Comparative Psychology*, *99*(2), 115–132. https://doi.org/10.1037/0735-7036.99.2.115

Borgatti, S. P., Everett, M. G., & Johnson, J. C. (2013). *Analyzing social networks*. London, United Kingdom: SAGE.

Borgatti, S. P., Everett, M.G. & Freeman, L.C. (2002). *Ucinet 6 for Windows: Software for Social Network Analysis*. Harvard, MA: Analytic Technologies.

Borgatti, S. P., & Feld, S. L. (1994). How To Test the Strength of Weak Ties Theory. *Connections, 17*(1), 45–46.

Brent, L., Kessel, A. L., & Barrera, H. (1997). Evaluation of introduction procedures in captive chimpanzees. *Zoo Biology*, *16*(4), 335–342. https://doi.org/10.1002/(SICI)1098-2361(1997)16:4<335::AID-ZOO5>3.0.CO;2-B

Butts, C.T. (2019). Sna: Tools for social network analysis. R package version 2.5 https://CRAN.R-project.org/package=sna

Burks, K. D., Bloomsmith, M. A., Forthman, D. L., & Maple, T. L. (2001). Managing the socialization of an adult male gorilla (*Gorilla gorilla gorilla*) with a history of social deprivation. *Zoo Biology, 20*(5), 347-358.

Clark, F. E. (2011). Space to choose: Network analysis of social preferences in a captive chimpanzee community, and implications for management. *American Journal of Primatology*, *73*(8), 748–757. https://doi.org/10.1002/ajp.20903

Cooper, M. A., Bernstein, I. S., Fragaszy, D. M., & de Waal, F. B. M. (2001). Integration of new males into four social groups of tufted capuchins (*Cebus apella*). *International Journal of Primatology, 22*(4), 663–683. https://doi.org/10.1023/A:1010745803740

Cowl, V. B., Jensen, K., Lea, J. M. D., Walker, S. L., & Shultz, S. (2020). Sulawesi crested macaque (*Macaca nigra*) grooming networks are robust to perturbation while individual associations are more labile. *International Journal of Primatology, 41*(1), 105–128. https://doi.org/10.1007/s10764-020-00139-6

Dettling, A. C., Feldon, J., & Pryce, C. R. (2002). Repeated parental deprivation in the infant common marmoset (*Callithrix jacchus*, primates) and analysis of its effects on early development. *Biological Psychiatry, 52*(11), 1037-1046.

Farine, D. R., & Whitehead, H. (2015). Constructing, conducting and interpreting animal social network analysis. *Journal of Animal Ecology*, *84*(5), 1144–1163. https://doi.org/10.1111/1365-2656.12418

Fedigan, L. M., & Baxter, M. J. (1984). Sex differences and social organization in free-ranging spider monkeys (*Ateles geoffroyi*). *Primates*, *25*(3), 279–294. https://doi.org/10.1007/BF02382267

Fedurek, P., & Dunbar, R. I. M. (2009). What does mutual grooming tell us about why chimpanzees groom? *Ethology*, *115*(6), 566–575. https://doi.org/10.1111/j.1439-0310.2009.01637.x

Flack, J. C., Girvan, M., De Waal, F. B. M., & Krakauer, D. C. (2006). Policing stabilizes construction of social niches in primates. *Nature*, *439*, 426–429. https://doi.org/10.1038/nature04326

Foerster, S., McLellan, K., Schroepfer-Walker, K., Murray, C. M., Krupenye, C., Gilby, I. C., & Pusey, A. E. (2015). Social bonds in the dispersing sex: Partner preferences among adult female chimpanzees. *Animal Behaviour*, *105*, 139–152. https://doi.org/10.1016/j.anbehav.2015.04.012

Franz, M., Altmann, J., & Alberts, S. C. (2015). Knockouts of high-ranking males have limited impact on baboon social networks. *Current Zoology*, *61*(1), 107–113. https://doi.org/10.1093/czoolo/61.1.107

Freeman, H. D., & Ross, S. R. (2014). The impact of atypical early histories on pet or performer chimpanzees. *PeerJ*, *2*, e579 https://doi.org/10.7717/peerj.579

Freeman, H. D., Weiss, A., & Ross, S. R. (2016). Atypical early histories predict lower extraversion in captive chimpanzees. *Developmental Psychobiology, 58*(4), 519–527. https://doi.org/10.1002/dev.21395

Funkhouser, J. A., Mayhew, J. A., & Mulcahy, J. B. (2018). Social network and dominance hierarchy analyses at Chimpanzee Sanctuary Northwest. *PLOS ONE*, *13*(2), e0191898. https://doi.org/10.1371/journal.pone.0191898

Fushing, H., McAssey, M. P., Beisner, B., & McCowan, B. (2011). ranking network of a captive rhesus macaque society: A sophisticated corporative kingdom. *PLOS ONE*, *6*(3), e17817. https://doi.org/10.1371/journal.pone.0017817

Hemelrijk, C. K. (1990). Models of, and tests for, reciprocity, unidirectionality and other social interaction patterns at a group level. *Animal Behavior*, *39*(6), 1013–1029. https://doi.org/10.1016/S0003-3472(05)80775-4

Hosey, G. R. (2005). How does the zoo environment affect the behavior of captive primates? *Applied Animal Behavior Science, 90*(2), 107–129. https://doi.org/10.1016/J.APPLANIM.2004.08.015

Hothorn, T., Hornik, K., van de Wiel, M.A., Zeileis, A. (2008). Implementing a class of permutation tests: The coin package. *Journal of Statistical Software, 28*(8), 1-23. doi:10.18637/jss.v028.i08

Kahlenberg, S. M., Thompson, M. E., Muller, M. N., & Wrangham, R. W. (2008a). Immigration costs for female chimpanzees and male protection as an immigrant counterstrategy to intrasexual aggression. *Animal Behavior*, *76*(5), 1497–1509. https://doi.org/10.1016/j.anbehav.2008.05.029

Kahlenberg, S. M., Emery Thompson, M., & Wrangham, R. W. (2008b). Female competition over core areas in *Pan troglodytes schweinfurthii*, Kibale National Park, Uganda. *International Journal of Primatology*, *29*(4), 931–947. https://doi.org/10.1007/s10764-008-9276-3

Kalcher-Sommersguter, E., Franz-Schaider, C., Crailsheim, K., & Preuschoft, S. (2013). Social competence of adult chimpanzees (*Pan troglodytes*) with severe deprivation history: a relational approach. *International Journal of Comparative Psychology*, *26*(2), 135–157.

Kalcher-Sommersguter, E., Preuschoft, S., Franz-Schaider, C., Hemelrijk, C. K., Crailsheim, K., & Massen, J. J. M. (2015). Early maternal loss affects social integration of chimpanzees throughout their lifetime. *Scientific Reports*, *5*(1), 16439. https://doi.org/10.1038/srep16439

Kanngiesser, P., Sueur, C., Riedl, K., Grossmann, J., & Call, J. (2011). Grooming network cohesion and the role of individuals in a captive chimpanzee group. *American Journal of Primatology*, *73*(8), 758–767. https://doi.org/10.1002/ajp.20914

Kempes, M. M., Den Heijer, E., Korteweg, L., Louwerse, A. L., & Sterck, E. H. M. (2009). Socially deprived rhesus macaques fail to reconcile: Do they not attempt or not accept reconciliation? *Animal Behaviour, 78*(2), 271–277. https://doi.org/10.1016/j.anbehav.2009.04.013

Kempes, M. M., Gulickx, M. M. C., van Daalen, H. J. C., Louwerse, A. L., & Sterck, E. H. M. (2008). Social competence is reduced in socially deprived rhesus monkeys (*Macaca mulatta*). *Journal of Comparative Psychology, 122*(1), 62–67. https://doi.org/10.1037/0735-7036.122.1.62

Koyama, N. F., & Aureli, F. (2019). Social network changes during space restriction in zoo chimpanzees. *Primates*, *60*(3), 203–211. https://doi.org/10.1007/s10329-018-0675-6

Koyama, N. F., Ronkainen, K., & Aureli, F. (2017). Durability and flexibility of chimpanzee grooming patterns during a period of dominance instability. *American Journal of Primatology*, *79*(11), e22713. https://doi.org/10.1002/ajp.22713

Kulik, L., Amici, F., Langos, D., & Widdig, A. (2015). sex differences in the development of aggressive behavior in rhesus macaques (*Macaca mulatta*). *International Journal of Primatology, 36*(4), 764–789. https://doi.org/10.1007/s10764-015-9853-1

Lehmann, J., & Boesch, C. (2009). Sociality of the dispersing sex: The nature of social bonds in West African female chimpanzees, *Pan troglodytes*. *Animal Behaviour*, *77*(2), 377–387. https://doi.org/10.1016/j.anbehav.2008.09.038

Lehmann, J., Korstjens, A. H., & Dunbar, R. I. M. (2007). Fission–fusion social systems as a strategy for coping with ecological constraints: A primate case. *Evolutionary Ecology, 21*(5), 613-634.

Levé, M., Sueur, C., Petit, O., Matsuzawa, T., & Hirata, S. (2016). Social grooming network in captive chimpanzees: does the wild or captive origin of group members affect sociality? *Primates*, *57*(1), 73–82. https://doi.org/10.1007/s10329-015-0494-y

Massen, J. J. M., & Sterck, E. H. M. (2013). Stability and durability of intra- and intersex social bonds of captive rhesus macaques (*Macaca mulatta*). *International Journal of Primatology*, *34*(4), 770–791. https://doi.org/10.1007/s10764-013-9695-7

McCarthy, M. S., Lester, J. D., Langergraber, K. E., Stanford, C. B., & Vigilant, L. (2018). Genetic analysis suggests dispersal among chimpanzees in a fragmented forest landscape in Uganda. *American Journal of Primatology*, *80*(9), e22902. https://doi.org/10.1002/ajp.22902

McCowan, B., Anderson, K., Heagarty, A., & Cameron, A. (2008). Utility of social network analysis for primate behavioral management and well-being. *Applied Animal Behavior Science*, *109*(2-4), 396-405.

Muller, M. N. (2002). Agonistic relations among Kanyawara chimpanzees. In C. Boesch, G. ohmann, & L. Marchant (Eds.). *Behavioural diversity in chimpanzees and bonobos*, 112-124. Cambridge University Press

Muller, M. N., & Mitani, J. C. (2005). Conflict and cooperation in wild chimpanzees. *Advances in the Study of Behavior, 35*, 275–331. https://doi.org/10.1016/S0065-3454(05)35007-8

Murray, L. (1998). The effects of group structure and rearing strategy on personality in Chimpanzees *Pan troglodytes* at Chester, London ZSL and Twycross Zoos. *International Zoo Yearbook, 36*, 97–108. https://doi.org/10.1111/j.1748-1090.1998.tb02890.x

Newman, M. E. (2004). Fast algorithm for detecting community structure in networks. *Physical Review E*, 69(6), 066133.

Paradis, E., & Schliep, K. 2019. Ape 5.0: An environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics, 35*, 526-528.

Pusey, A., Murray, C., Wallauer, W., Wilson, M., Wroblewski, E., & Goodall, J. (2008). Severe aggression among female *pan troglodytes schweinfurthii* at Gombe National Park, Tanzania. *International Journal of Primatology*, *29*(4), 949–973. https://doi.org/10.1007/s10764-008-9281-6

R Core Team (2019). R: A language and environment for statistical computing. *R Foundation for Statistical Computing*, Vienna, Austria. https://www.R-project.org/

Rodrigues, M. A., & Boeving, E. R. (2019). Comparative social grooming networks in captive chimpanzees and bonobos. *Primates*, *60*(3), 191–202. https://doi.org/10.1007/s10329-018-0670-y

Rose, P. E., & Croft, D. P. (2015). The potential of social network analysis as a tool for the management of zoo animals. *Animal Welfare*, *24*(2), 123-138.

Rox, A., van Vliet, A. H., Sterck, E. H. M., Langermans, J. A. M., & Louwerse, A. L. (2019). Factors determining male introduction success and long-term stability in captive rhesus macaques. *PLoS ONE, 14*(7). https://doi.org/10.1371/journal.pone.0219972

Schel, A. M., Rawlings, B., Claidière, N., Wilke, C., Wathan, J., Richardson, J., … Slocombe, K. (2013). Network analysis of social changes in a captive chimpanzee community following the successful integration of two adult groups. *American Journal of Primatology*, *75*(3), 254–266. https://doi.org/10.1002/ajp.22101

Silk, J. B., Alberts, S. C., Altmann, J., Cheney, D. L., & Seyfarth, R. M. (2012). Stability of partner choice among female baboons. *Animal Behaviour*, *83*(6), 1511–1518. https://doi.org/10.1016/j.anbehav.2012.03.028

Silk, J., Cheney, D., & Seyfarth, R. (2013). A practical guide to the study of social relationships. *Evolutionary Anthropology: Issues, News, and Reviews*, *22*(5), 213–225. https://doi.org/10.1002/evan.21367

Silk, M. J., Finn, K. R., Porter, M. A., & Pinter-Wollman, N. (2018). Can multilayer networks advance animal behavior research? *Trends in Ecology and Evolution, 33*(6), 376–378. https://doi.org/10.1016/j.tree.2018.03.008

Smith-Aguilar, S. E., Aureli, F., Busia, L., Schaffner, C. M., & Ramos-Fernandez, G. (2019). Using multiplex networks to capture the multidimensional nature of social structure. *Primates, 60*(3), 277–295. https://doi.org/10.1007/s10329-018-0686-3

Suomi, S. J. (1997). Early determinants of behaviour: Evidence from primate studies. *British Medical Bulletin*, *53*(1), 170–184. https://doi.org/10.1093/oxfordjournals.bmb.a011598

Truelove, M. A., Martin, A. L., Perlman, J. E., Wood, J. S., & Bloomsmith, M. A. (2017). Pair housing of Macaques: A review of partner selection, introduction techniques, monitoring for compatibility, and methods for long-term maintenance of pairs. *American Journal of Primatology, 79*(1), 1-15. https://doi.org/10.1002/ajp.22485

Videan, E. N., & Fritz, J. (2007). Effects of short- and long-term changes in spatial density on the social behavior of captive chimpanzees (*Pan troglodytes*). *Applied Animal Behaviour Science*, *102*(1), 95–105. https://doi.org/10.1016/j.applanim.2006.03.011

Whitehead, H., & James, R. (2015). Generalized affiliation indices extract affiliations from social network data. *Methods in Ecology and Evolution, 6*(7), 836–844. https://doi.org/10.1111/2041-210X.12383

Xia, D., Li, J., Garber, P. A., Sun, L., Zhu, Y., & Sun, B. (2012). Grooming reciprocity in female Tibetan macaques *Macaca thibetana*. *American Journal of Primatology*, *74*(6), 569–579. https://doi.org/10.1002/ajp.21985

Xia, D.-P., Li, J.-H., Garber, P. A., Matheson, M. D., Sun, B.-H., & Zhu, Y. (2013). Grooming reciprocity in male Tibetan macaques. *American Journal of Primatology*, *75*(10), 1009–1020. https://doi.org/10.1002/ajp.22165

Chapter 6. Laterality and Social Networks

Summary

Chapter 6 is the last empirical study of this thesis. It is primarily focused on looking into the link between laterality and coordination. In order to do this, this study applies Social Network Theory to research if there is homophily based on lateral preference, that is, if chimpanzees associate more with others that have a similar laterality as them. Although Chapter 4 did not find that laterality in hand preference was associated with behavioural style, this chapter also tackles the secondary objective of investigating if there is homophily based on behavioural style. Overall, this chapter brings the thesis to conclusion by using data from all three areas of the thesis: laterality, behavioural style and social networks.

Introduction

Laterality is a well-known characteristic widespread among vertebrates (for a review, see Rogers & Vallortigara, 2015) and invertebrates (for a review, see Frasnelli et al., 2012). Lateralisation of behaviours allows each brain hemisphere to specialise in a different function, avoiding duplication of tasks and increasing brain efficiency (Vallortigara & Rogers, 2005). However, this advantage is independent to which brain hemisphere is lateralised for each function and does not help explain why some species show population level lateralisation. One of the proposed explanations for population level laterality is that it is an evolutionarily stable strategy, where a critical proportion of the population benefit from sharing the same bias (Dominey, 1984). This theory proposes that shared lateral biases facilitate coordination with other members of the species (Vallortigara, 2006; Vallortigara & Rogers, 2005). Evidence supporting this theory comes mainly from fish: population level laterality is more common in social fish than in solitary fish (Bisazza et al., 2000; Bisazza et al., 2002), as coordinating escape responses with conspecifics can greatly increase individual fitness (Ghirlanda et al., 2009; Ghirlanda & Vallortigara, 2004). However, while this evidence comes from predator-prey contexts where lateralised escape responses have an immediate repercussion in survival, research investigating different forms of cooperation and its possible link with laterality can provide new insights into the evolution of laterality (Rogers et al., 2013). Investigating the possible link between laterality and sociality is relevant in primate research where individuals live in complex social groups.

Friendships and social bonds often involve cooperation over long periods of time and are good indicators of cooperative behaviour and, while studying social bonds does not offer a direct measure of intraspecific coordination, cooperative behaviours are often separated in time and difficult to study outside a laboratory setting (Seyfarth & Cheney, 2012). Social bonds might promote cooperation between individuals by reducing uncertainty about others' behaviours (Ebenau et al., 2018; Molesti & Majolo, 2016). Even when cooperation is studied in an experimental setting, previous social bonds between animals have a strong effect on their ability to cooperate. For example, in an experimental context, pairs of Barbary macaques that share strong social bonds are not only more likely to cooperate but also succeed more often when they cooperate than those who share weak social bonds (Molesti & Majolo, 2016). Similar results have also been found in bird species (*Corvus corax*), as pairs of ravens that shared high tolerance levels displayed higher success rates in cooperation tasks than pairs with low tolerance (Massen et al., 2015). The social network approach has proved to be of great value in explaining the emergence and maintenance of cooperation in primate groups as an evolutionary strategy (Fehl et al., 2011; Kasper & Voelkl, 2009; Voelkl & Kasper, 2009). Considering the significance of social grooming as a tool to maintain social bonds in primates (Lehmann et al., 2007a; Kudo & Dunbar, 2001; Dunbar, 2010), grooming networks are particularly relevant in the study of social bonds and cooperation. Centrality measures can be particularly useful when studying the ability of individuals to cooperate and coordinate with others, as well-connected individuals can greatly enhance cooperation in a group (Brask & Brask, 2020). In groups that show high modularity, clustering is also a relevant measure to consider, as co-operators are likely to interact with other co-operators, creating smaller clusters within a group (Kurvers et al., 2014). Social bonds in chimpanzees are particularly relevant as males often bond opportunistically, forming coalitions to help them achieve a higher status in the group (Newton-Fisher, 2004). Studying the overall social network of chimpanzees can offer more detailed knowledge into whether laterality plays a role in coordinating behaviour with conspecifics, allowing the testing of whether chimpanzees tend to associate based on laterality and if central chimpanzees tend to be more lateralised than peripheral chimpanzees.

A recent topic that has gained attention in animal social network studies is the research of homophily, that is, the tendency to form ties between individuals that share similar characteristics (McPherson et al., 2001). Recent papers have mainly focused on homophily of personality traits. For example, a study in guppy (*Poecilia reticulata*) showed how bold fish tend to interact with similar individuals (Croft et al., 2009), while research in birds (*Parus major*) found that faster explorers had higher centralities in their social networks (Aplin et al., 2013; Snijders et al., 2014). Primate research has also shown that individuals of several species have a tendency to associate more often with others that have similar personalities. For example, capuchin monkeys (*Sapajus* sp.) tend to have stronger relationships with others that have similar levels of neuroticism, independently of age, sex, kinship and rank (Morton et al., 2015). Moreover, social factors of personality have been found to be particularly relevant in some primate species. Gregariousness is a particularly important factor of personality in macaques (*Macaca assamensis*), as it can predict association in males (Ebenau et al., 2019). This body of research suggests that homophily helps further reduce uncertainty in social interactions, facilitating the creating and maintenance of social bonds (Massen & Koski, 2014; Rivas, 2009). Chapter 4 has not found a relationship between social factors of behavioural style and laterality. However, given the importance of homophily of personality in the maintenance of social bonds, it is important to consider the possible effect of behavioural style when studying the link between laterality and social networks.

Interestingly, while social factors are expected to play an important role in the presence of homophily based on behavioural style, studies have found that the shy-bold axis can have similar effects. Baboons (*Papio ursinus*) are more likely to associate with others that have similar boldness levels (Carter et al., 2015). Similarly, a study with 38 captive chimpanzees showed that chimpanzees not only had a tendency to sit in contact with others that had a similar sociability to them, but also with others with similar boldness levels (Massen & Koski, 2014). Most research has focused on identifying patterns in the social group and new studies have begun to explore how individual traits (such as behavioural style) can affect the group structure. Past studies have explored network models that attempts to explain how bold and shy individuals might have different positions in the group network (Ilany & Akçay, 2016). Specifically, the model proposes that bolder individuals will have a higher betweenness centrality, as they might establish more connections outside of their social circle (Ilany & Akçay, 2016). Given the known association between right-handedness and boldness in chimpanzees (Hopkins & Bennett, 1994), this implies that laterality might have an effect on intraspecific coordination and social networks through its link with behavioural style.

One last question that needs to be considered in order to study the possible link between laterality and social networks in chimpanzees is which measure of laterality is the most appropriate to use. Rogers (2009) has argued that, in order to measure hemispheric dominance in individuals, tasks that do not require the use of a particular process that is lateralised in a specific hemisphere are the most appropriate. This rationale leads to considering simple reaching behaviours, as they require less motor and cognitive skill compared to experimental tasks (Llorente et al., 2009; Padrell et al., 2019; Vauclair et al., 2005) and, additionally, maintain good ecological validity (Marchant & McGrew, 2013). A possible counterargument is that simple reaching tasks tend to elicit weaker laterality than bimanual tasks (Mosquera et al., 2012). However, the fact that spontaneous simple reaching tasks still elicit individual preferences while often not showing clear population level preference (as shown in Chapter 2, but also see Fletcher & Weghorst, 2005) makes them particularly interesting to study homophily, as there will be a more diverse spread of right- and left-handed chimpanzees in a group.

Previous research points towards intraspecific coordination as an important force that drives the emergence of population level laterality (Vallortigara, 2006). The present study uses social network analysis as a way to study the role of laterality in the network of a group of chimpanzees, investigating if chimpanzees show homophily based on hand preference. Additionally, this study also takes into account the effect of behavioural style in the social network (Massen & Koski, 2014) and, although a previous chapter (chapter 4) failed to find a relationship between laterality and social factors of behavioural style, said chapter did not measure boldness in an experimental context. If the link between laterality and behavioural style is mainly present in boldness, as suggested by previous research (Hopkins & Bennett, 1994), right-handedness should be associated with higher betweenness centrality. The hypotheses for this study are: 1) chimpanzees will show homophily of hand preference; 2) chimpanzees will also show homophily of behavioural style; and 3) right-handed chimpanzees will have higher betweenness centralities than left-handed chimpanzees.

Method

Sample

The sample consisted of a group of 19 chimpanzees housed at the chimpanzee colony of Chester Zoo. For more details on the individual chimpanzees, the group structure and the enclosure see Chapters 2 and 5.

Procedure

Laterality Measures

Laterality was assessed using spontaneous simple reach in quadrupedal position in two periods: from January to April 2017 and from June to August 2019 using continuous focal samples of ten minutes, switching focal subject when appropriate to maximize data collection. For more information regarding the calculation of the scores, reliability, temporal stability and other methodological aspects, see Chapter 2.

Behavioural Style Measures

Behavioural style was assessed using the behavioural style factors found in Chapter 4 (popularity, sociability and influence) using principal component analysis and regularised exploratory factor analysis from 12 behavioural variables (Koski, 2011; Massen & Koski, 2014).

Social Network Measures

The grooming network used had 19 rows and 19 columns, representing the 19 focal chimpanzees with a total of 342 dyads and was asymmetrical (directed), as one individual can groom another without being groomed back. This network used weighted data. Simple ratio indices ($E_{AB} = \frac{x}{x+yAB+yA+yB}$) ranging 0-1 were used to quantify the amount of time spent grooming (Farine & Whitehead, 2015; Whitehead & James, 2015). See Chapter 5 for more information on how the network was constructed. Laterality indices and behaviuoral style factors were converted into similarity networks using UciNET 6.708 (Borgatti et al., 2002). Similarity networks contain dyads that display the difference between two nodes on certain attributes, so that a lower score indicates that both individuals have similar values in that varaible. As an example, if Wilson has a laterality score of -0.5 and Boris has a score of 0.5, their dyad score in the network would be a 1, representing the difference of scores between them.

Centrality was assessed using betweenness centrality, defined as the number of times the focal is in the shortest path connecting two other nodes, in order to determine which individuals are important in keeping the group connected (Rose & Croft, 2015). Betweenness centrality works well with both directed and undirected data, as well as with weighted data (Borgatti et al., 2013).

Data Analysis

Hypothesis one (homophily of hand preference) and two (homophily of behavioural) were examined using Multiple Regression Quadratic Assignment Procedure (MRQAP) using the Double Dekker semi-partialling technique (Dekker, 2003). This prodecure uses a linear regression model to predict an output matrix from predictor matrices, using a set number of random permutations to calculate the significance of the model. The grooming matrix was used as the output matrix, similarity matrices for laterality and behavioural style factors, as well as age, sex and estimated relatedness coefficients were considered predictor matrices. The MRQAP analyses were conducted on UciNET 6.708 (Borgatti et al., 2002) using 5000 permutations. Relatedness was estimated from the data on parent-offsping information offered by the zoo (see Appendix I). As not all father-offsping relationships were known, chimpanzees that shared a mother but had no information on father were assumed to be half-siblings. Individuals not known to be related were assumed to have have a relatedness of 0.

Laterality indices and betweenness centrality were correlated using Spearman's *rho* in order to investigate hypothesis three (right-handed chimpanzees will have higher betweenness centrality than left-handed chimpanzees) using SPSS 26. All analysis used an alpha value of .05.

Results

Descriptive Statistics

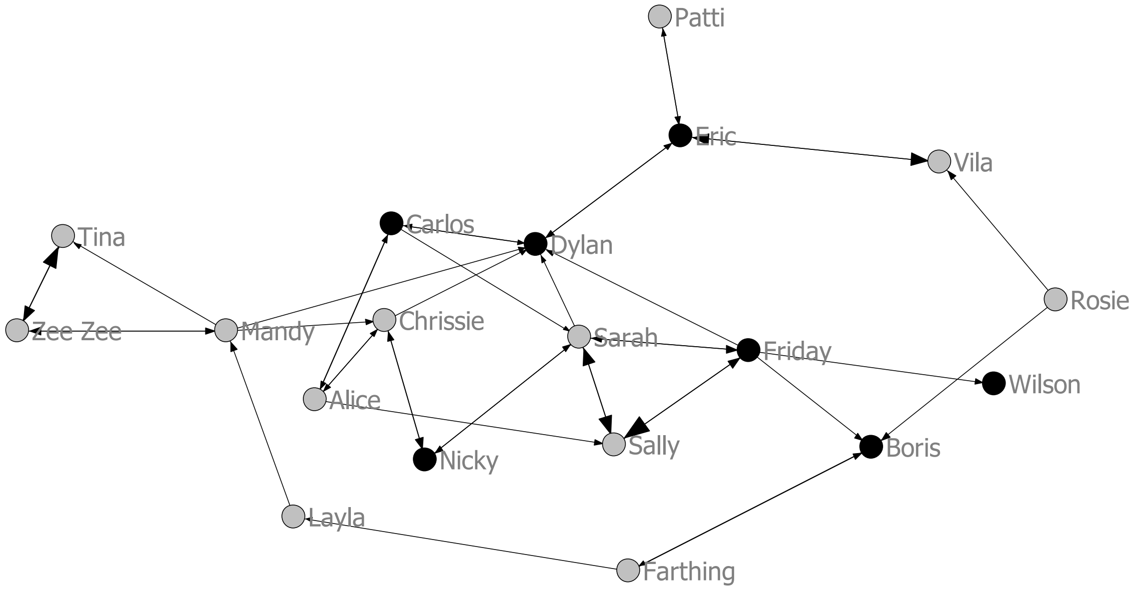
Mean and standard deviation for all variables can be seen in Table 1. A sociagram for the grooming network is displayed in Figure 1.

Table 1
Mean and standard deviation for laterality, behavioural style and centrality measures (N=19)

	Mean	Standard deviation
Strength of hand preference	0.443	0.280
Hand preference	0.030	0.533
Sociability	0	1.087
Influence	0	0.952
Popularity	0	0.997
Betweenness centrality	3.947	2.038

Figure 1

Grooming network, showing strong grooming ties (one SD above the mean) for the chimpanzee group



Note: Females are displayed in grey and males in black; arrowheads represent direction and strength.

First Hypothesis

The MRQAP model predicting homophily in grooming based on similar hand preference was significant (R^2= .103, p= .022), although similarity of hand preference did not predict grooming relationships. Relatedness did predict grooming relationships. The standarised coefficient and *p* value for all the predictors of the model can be seen in Table 2.

Table 2

Coefficients and p values for the MRQAP model (n= 342 dyads).

Outcome variable	Predictors	Standarized coefficient	*p* value
Grooming	Hand preference	-0.099	.226
	Age	0.079	.257
	Sex	0.132	.155
	Relatedness	0.286	.012

Second Hypothesiss

The MRQAP analysis for homophily of behaviuoral style showed a significant result with a small effect size (R^2= .122, *p*= .008). Again, only relatedness predicted grooming relationship (Table 3).

Table 3
Coefficients and p values for the MRQAP model (n= 342 dyads).

Outcome variable	Predictors	Coefficient	*p* value
Grooming	Popularity	0.122	.174
	Sociability	-0.100	.210
	Influence	-0.031	.396
	Age	0.142	.133
	Sex	0.132	.154
	Relatedness	0.287	.013

Third Hypothesis

The Spearman correlation did not find a significant relationship between hand preference and grooming centrality (*R*(17)=.035, *p*= .443) or between strength of hand preference and grooming centrality (*R*(17)=.062, *p*= .400).

Discussion

This study investigates the possible link between laterality and coordination (Vallortigara, 2006) by using social network analysis to study how the group structure is affected by laterality, while accounting for relevant factors of behavioural style. The results of the study do not support the first hypothesis as the data do not show homophily of hand preference. Laterality does not predict grooming, meaning that chimpanzees do not tend to spend time grooming others that have a similar hand preference. The findings also do not support hypothesis two, as the data shows that there was not a significant effect of homophily of behavioural style. Finally, the results do not support hypothesis three, as right-handed chimpanzees do not show higher centralities in the group.

The first hypothesis of this study predicted that chimpanzees would associate more (spending more time grooming) with other chimpanzees that shared similar hand preferences. The findings of the study do not support this prediction, as the MRQAP analysis did not find that grooming was predicted by similarity in hand preference. This hypothesis was based on Vallortigara's (2006) theory that sharing similar laterality facilitates coordination. While this theory has some supporting empirical evidence (Bisazza et al., 2000; Bisazza et al., 2002; Ghirlanda et al., 2009; Ghirlanda & Vallortigara, 2004) there is no current evidence in primates. The most apparent interpretation for these findings is that lateralization of hand preference does not facilitate coordination in chimpanzees. It is important to stress that this study uses hand preference in a simple reach task as a measure of laterality because the lack of population level preference in this measure (as seen in Chapter 2) offers a good distribution of left- and right-handed chimpanzees, in addition to the high ecological validity of spontaneous tasks (Marchant & McGrew, 2013). A possible critique of this choice is that measures that show clear population level preferences, mainly bimanual experimental tasks (Hopkins, 1994; Hopkins, 1995; Mosquera et al., 2012), might be more appropriate for exploring this hypothesis. Simple reaching tasks, on the other hand, do not typically show population level preferences (although some studies find a population preference when considering additional tasks, see Llorente et al., 2009). A counter argument is that simple reaching tasks are considered as more appropriate measures of overall hemispheric dominance (Rogers, 2009), making them more appropriate measures when studying an effect of laterality in more general aspects of behaviour. Nonetheless, it would be particularly interesting to see if future research finds homophily in laterality when using a bimanual coordinated task.

Hypothesis two predicted that chimpanzees would associate more with others that had similar personalities. The findings show that, while there was a significant effect size, the only significant predictor of grooming relationships was relatedness. Previous studies have shown homophily in different personality factors in primates. A study by Ebenau et al. (2019) found that macaques tend to associate with others that have similar levels of gregariousness, although authors did not account for the influence of relatedness in their analysis. Interestingly, other studies have considered relatedness and nevertheless found effects of personality. Morton et al. (2015) found that capuchins show homophily in neuroticism even when accounting for known relatedness. In chimpanzees, a past study used a very similar methodology to measure social personality factors and found that chimpanzees showed homophily in sociability and boldness, as well as an interaction between relatedness and sociability indicating that, while there was homophily in sociability among non-kin individuals, the effect was stronger for related individuals (Massen & Koski, 2014). The present study finds that relatedness, but not behavioural style, predicts stronger grooming relationships. This contrasting evidence might be explained by the measures used to determine association. Massen and Koski (2014) use contact-sitting, that is, when two chimpanzees sit maintaining physical contact, as an indication for association in chimpanzees. The present study used grooming instead of proximity and, while it is a behaviour more directly related to social bonds than spending time in proximity, it might also conflate effects of grooming used in exchange for coalitionary support (Henzi & Barrett, 1999). Grooming as a tool to maintain not only affiliative bonds but also alliances, including those between related individuals (Lehmann et al., 2007a; Kudo & Dunbar, 2001; Dunbar, 2010).

The third hypothesis predicted that right-handed chimpanzees would have higher betweenness centralities than left-handed chimpanzees. The data do not support this hypothesis, as there was no significant relationship between hand preference and betweenness centrality. While this question has not been addressed previously in primates, past research indicated that right-handed chimpanzees are bolder than left-handed ones (Hopkins & Bennett, 1994). This, together with the fact that social network models predict that bolder individuals will have roles of high betweenness centralities in their groups (Ilany & Akçay, 2016), pointed towards a possible relationship between hand preference and betweenness. It is important to keep in mind that Ilany and Akçay's (2016) model addresses the relationship between boldness as a behavioural trait and centrality, but not between hand preference and centrality. Moreover, this model explains how bold animals are expected to establish social connections with individuals outside of their immediate social circle. The discrepancy between the findings of this study and the expected predictions might be due to limitations inherent to captive context, as chimpanzees in captivity do not have the option to fully display fission-fusion communities (Lehmann et al., 2007b) due to space limitations. Additionally, the chimpanzee group at Chester Zoo displays very strong cohesion and low modularity (see Chapter 5), which indicates that the group is highly interconnected, making betweenness centrality a less useful indicator of the relative importance of each individual in keeping the group connected (Rose & Croft, 2015).

The context of naturalistic captivity of this study presents some challenges and limitations that are important to keep in mind, in addition to the limitations in space that prevent individuals from moving between communities. All the measures of this study were designed to cause no disruption for the chimpanzees, which means that experimental measures and tasks could not be used. While this is important from a management perspective, it does limit the range of variables that could be used, both in terms of behavioural style observations and laterality measures. While the objectives of the current study focused on social behavioural style factors, which can be measured without the need for experimental tasks, future research could explore boldness and exploration style introducing novel stimuli in the group enclosure (Hopkins & Bennett, 1994; Koski & Burkart, 2015; Šlipogor et al., 2016). Similarly, future research could use experimental tasks in order to explore whether there is homophily in hand preference measured using complex bimanual tasks.

In conclusion, the findings do not show homophily in hand preference, contrary to the predictions of the study. Additionally, hand preference did not show any relationship with betweenness centrality, indicating that group position of individual chimpanzees is not influenced by their laterality. Lastly, there was homophily in relatedness: chimpanzees spent more time grooming their related kin in the group. Overall, the current study set out to investigate the possible link of intraspecific coordination and laterality, applying a novel approach by using social network analysis in order to explore if hand preference plays a role in the social organization in chimpanzees. The data does not seem to indicate that hand preference influences social relationships in chimpanzees, although future research could apply this approach in order to investigate if using different measures of hand preference yield similar results.

References

Aplin, L. M., Farine, D. R., Morand-Ferron, J., Cole, E. F., Cockburn, A., & Sheldon, B. C. (2013). Individual personalities predict social behaviour in wild networks of great tits (*Parus major*). *Ecology Letters*, *16*(11), 1365–1372. https://doi.org/10.1111/ele.12181

Bisazza, A., Cantalupo, C., Capocchiano, M., & Vallortigara, G. (2000). Population lateralisation and social behaviour: A study with 16 species of fish. *Laterality*, *5*(3), 269–284. https://doi.org/10.1080/713754381

Bisazza, A., De Santi, A., & Vallortigara, G. (1999). Laterality and cooperation: Mosquitofish move closer to a predator when the companion is on their left side. *Animal Behaviour*, *57*(5), 1145–1149. https://doi.org/10.1006/anbe.1998.1075

Borgatti, S. P., Everett, M. G., & Johnson, J. C. (2013). *Analyzing social networks*. London, United Kingdom: SAGE.

Borgatti, S.P., Everett, M.G. & Freeman, L.C. (2002). *Ucinet 6 for Windows: Software for Social Network Analysis*. Harvard, MA: Analytic Technologies.

Brask, J. B., & Brask, J. B. (2020). Evolution of cooperation in networks: Well-connected cooperators can enhance cooperation but are counteracted by Trojan horses. *ArXiv:1908.05923*. http://arxiv.org/abs/1908.05923

Carter, A. J., Lee, A. E. G., Marshall, H. H., Ticó, M. T., & Cowlishaw, G. (2015). Phenotypic assortment in wild primate networks: Implications for the dissemination of information. *Royal Society Open Science*, *2*(5), 140444. https://doi.org/10.1098/rsos.140444

Croft, D. P., Krause, J., Darden, S. K., Ramnarine, I. W., Faria, J. J., & James, R. (2009). Behavioural trait assortment in a social network: Patterns and implications. *Behavioral Ecology and Sociobiology*, *63*(10), 1495–1503. https://doi.org/10.1007/s00265-009-0802-x

Dekker, D., Krackhardt, D., & Snijders, T. (2003). Multicollinearity robust QAP for multiple regression. *1st annual conference of the North American Association for Computational Social and Organizational Science*, Pittsburgh: Omni William Penn.

Dominey, W. J. (1984). Alternative mating tactics and evolutionarily stable strategies. *Integrative and Comparative Biology*, *24*(2), 385–396. https://doi.org/10.1093/icb/24.2.385

Dunbar, R. I. M. (2010). The social role of touch in humans and primates: Behavioural function and neurobiological mechanisms. *Neuroscience & Biobehavioral Reviews*, *34*(2), 260–268. https://doi.org/10.1016/j.neubiorev.2008.07.001

Ebenau, A., von Borell, C., Penke, L., Ostner, J., & Schülke, O. (2019). Personality homophily affects male social bonding in wild Assamese macaques, *Macaca assamensis*. *Animal Behaviour*, *155*, 21–35. https://doi.org/10.1016/j.anbehav.2019.05.020

Farine, D. R., & Whitehead, H. (2015). Constructing, conducting and interpreting animal social network analysis. *Journal of Animal Ecology*, *84*(5), 1144–1163. https://doi.org/10.1111/1365-2656.12418

Fehl, K., van der Post, D. J., & Semmann, D. (2011). Co-evolution of behaviour and social network structure promotes human cooperation. *Ecology Letters*, *14*(6), 546–551. https://doi.org/10.1111/j.1461-0248.2011.01615.x

Fletcher, A., & Weghorst, J. (2005). Laterality of hand function in naturalistically housed chimpanzees (*Pan troglodytes*). *Laterality*, *10*(3), 219–242. https://doi.org/10.1080/13576500442000049

Frasnelli, E., Vallortigara, G., & Rogers, L. J. (2012). Left–right asymmetries of behaviour and nervous system in invertebrates. *Neuroscience & Biobehavioral Reviews*, *36*(4), 1273–1291. https://doi.org/10.1016/j.neubiorev.2012.02.006

Ghirlanda, S., Frasnelli, E., & Vallortigara, G. (2009). Intraspecific competition and coordination in the evolution of lateralization. *Philosophical Transactions of the Royal Society*, *364*, 861–866. https://doi.org/10.1098/rstb.2008.0227

Ghirlanda, S., & Vallortigara, G. (2004). The evolution of brain lateralization: A game- theoretical analysis of population structure. *The Royal Society*, *271*, 853–857. https://doi.org/10.1098/rspb.2003.2669

Henzi, P., & Barrett, L. (1999). The value of grooming to female primates. *Primates, 40*(1), 47–59.

Hopkins, W. D. (1994). Hand preferences for bimanual feeding in 140 captive chimpanzees (*Pan troglodytes*): Rearing and ontogenetic determinants. *Developmental Psychobiology, 27*(6), 395–407. https://doi.org/10.1002/dev.420270607

Hopkins, W. D. (1995). Hand preferences for a coordinated bimanual task in 110 chimpanzees (*Pan troglodytes*): Cross-sectional analysis. *Journal of Comparative Psychology*, *109*(3), 291–297.

Hopkins, W. D., & Bennett, A. J. (1994). Handedness and approach-avoidance behavior in chimpanzees (*Pan*). *Journal of Experimental Psychology: Animal Behavior Processes, 20*(4), 413–418. https://doi.org/10.1037/0097-7403.20.4.413

Ilany, A., & Akçay, E. (2016). Personality and social networks: A generative model approach. *Integrative and Comparative Biology, 56*(6), 1197–1205. https://doi.org/10.1093/icb/icw068

Kasper, C., & Voelkl, B. (2009). A social network analysis of primate groups. *Primates*, *50*(4), 343–356. https://doi.org/10.1007/s10329-009-0153-2

Koski, S. E., & Burkart, J. M. (2015). Common marmosets show social plasticity and group-level similarity in personality. *Scientific Reports, 5*(1), 8878. https://doi.org/10.1038/srep08878

Kudo, H., & Dunbar, R. I. M. (2001). Neocortex size and social network size in primates. *Animal Behaviour, 62*(4), 711–722. https://doi.org/10.1006/anbe.2001.1808

Kurvers, R. H. J. M., Krause, J., Croft, D. P., Wilson, A. D. M., & Wolf, M. (2014). The evolutionary and ecological consequences of animal social networks: Emerging issues. *Trends in Ecology & Evolution*, *29*(6), 326–335. https://doi.org/10.1016/j.tree.2014.04.002

Lehmann, J., Korstjens, A. H., & Dunbar, R. I. M. (2007a). Group size, grooming and social cohesion in primates. *Animal Behaviour,* *74*(6), 6171–1629. https://doi.org/10.1016/j.anbehav.2006.10.025

Lehmann, J., Korstjens, A. H., & Dunbar, R. I. M. (2007b). Fission–fusion social systems as a strategy for coping with ecological constraints: A primate case. *Evolutionary Ecology*, *21*(5), 613–634. https://doi.org/10.1007/s10682-006-9141-9

Llorente, M., Mosquera, M., & Fabré, M. (2009). Manual laterality for simple reaching and bimanual coordinated task in naturalistic housed *Pan troglodytes*. *International Journal of Primatology*, *30*, 183–197. https://doi.org/10.1007/s10764-009-9338-1

Marchant, L. F., & McGrew, W. C. (2013). Handedness is more than laterality: Lessons from chimpanzees. *Annals of the New York Academy of Sciences*, *1288*(1), 1–8. https://doi.org/10.1111/nyas.12062

Massen, J. J. M., & Koski, S. E. (2014). Chimps of a feather sit together: Chimpanzee friendships are based on homophily in personality. *Evolution and Human Behavior*, *35*(1), 1–8. https://doi.org/10.1016/j.evolhumbehav.2013.08.008

Massen, J. J. M., Ritter, C., & Bugnyar, T. (2015). Tolerance and reward equity predict cooperation in ravens (*Corvus corax*). *Scientific Reports*, *5*(1), 15021. https://doi.org/10.1038/srep15021

McPherson, M., Smith-Lovin, L., & Cook, J. M. (2001). Birds of a feather: Homophily in social networks. *Annual Review of Sociology*, *27*(1), 415–444. https://doi.org/10.1146/annurev.soc.27.1.415

Molesti, S., & Majolo, B. (2016). Cooperation in wild Barbary macaques: Factors affecting free partner choice. *Animal Cognition*, *19*(1), 133–146. https://doi.org/10.1007/s10071-015-0919-4

Morton, F. B., Weiss, A., Buchanan-Smith, H. M., & Lee, P. C. (2015). Capuchin monkeys with similar personalities have higher-quality relationships independent of age, sex, kinship and rank. *Animal Behaviour*, *105*, 163–171. https://doi.org/10.1016/j.anbehav.2015.04.013

Mosquera, M., Llorente, M., Riba, D., Estebaranz, F., González-Brao, M., Lorenzo, C., Carbonell, E., & Feliu, O. (2006). Ethological study of manual laterality in naturalistic housed chimpanzees (*Pan troglodytes*) from the Mona Foundation Sanctuary (Girona, Spain). *Laterality*, *12*(1), 19–30. https://doi.org/10.1080/13576500600886754

Newton-Fisher, N. E. (2004). Hierarchy and social status in Budongo chimpanzees. *Primates*, *45*(2), 81–87. https://doi.org/10.1007/s10329-003-0064-6

Rivas, J. (2009). Friendship selection. *International Journal of Game Theory, 38*(4), 521–538. https://doi.org/10.1007/s00182-009-0168-3

Rogers, L. J. (2009). Hand and paw preferences in relation to the lateralized brain. *Philosophical Transactions of the Royal Society*, *364*, 943–954. https://doi.org/10.1098/rstb.2008.0225

Rogers, L., & Vallortigara, G. (2015). When and why did brains break symmetry? *Symmetry*, *7*(4), 2181–2194. https://doi.org/10.3390/sym7042181

Rogers, L. J., Vallortigara, G., & Andrew, R. J. (2013). *Divided Brains: The Biology and Behaviour of Brain Asymmetries*. Cambridge University Press.

Rose, P. E., & Croft, D. P. (2015). The potential of social network analysis as a tool for the management of zoo animals. *Animal Welfare*, *24*, 123–138.

Seyfarth, R. M., & Cheney, D. L. (2012). The evolutionary origins of friendship. *Annual Review of Psychology*, *63*(1), 153–177. https://doi.org/10.1146/annurev-psych-120710-100337

Šlipogor, V., Gunhold-de Oliveira, T., Tadić, Z., Massen, J. J. M., & Bugnyar, T. (2016). Consistent inter-individual differences in common marmosets (*Callithrix jacchus*) in boldness-shyness, stress-activity, and exploration-avoidance. *American Journal of Primatology*, *78*(9), 961–973. https://doi.org/10.1002/ajp.22566

Snijders, L., van Rooij, E. P., Burt, J. M., Hinde, C. A., van Oers, K., & Naguib, M. (2014). Social networking in territorial great tits: Slow explorers have the least central social network positions. *Animal Behaviour*, *98*, 95–102. https://doi.org/10.1016/j.anbehav.2014.09.029

Padrell, M., Gómez-Martínez, C., & Llorente, M. (2019). Short and long-term temporal consistency of hand preference in sanctuary chimpanzees (*Pan troglodytes*) for unimanual and bimanual coordinated tasks. *Behavioural Processes*, *167*, 103911. https://doi.org/10.1016/J.BEPROC.2019.103911

Vallortigara, G. (2006). The evolutionary psychology of left and right: Costs and benefits of lateralization. *Developmental Psychobiology*, *48*(6), 418–427. https://doi.org/10.1002/dev.20166

Vallortigara, G., & Rogers, L. J. (2005). Survival with an asymmetrical brain: Advantages and disadvantages of cerebral lateralization. *Behavioral and Brain Sciences*, *28*, 575–633.

Vauclair, J., Meguerditchian, A., & Hopkins, W. D. (2005). Hand preferences for unimanual and coordinated bimanual tasks in baboons (*Papio anubis*). *Cognitive Brain Research*, *25*(1), 210–216. https://doi.org/10.1016/J.COGBRAINRES.2005.05.012

Voelkl, B., & Kasper, C. (2009). Social structure of primate interaction networks facilitates the emergence of cooperation. *Biology Letters*, *5*(4), 462–464. https://doi.org/10.1098/rsbl.2009.0204

Whitehead, H., & James, R. (2015). Generalized affiliation indices extract affiliations from social network data. *Methods in Ecology and Evolution*, *6*(7), 836–844. https://doi.org/10.1111/2041-210X.12383

Chapter 7. Conclusions

Laterality is widespread among vertebrates and has clear advantages for individuals, as it increases brain efficiency and reduces processing redundancy (Frasnelli et al., 2012; Rogers & Vallortigara, 2015; Vallortigara & Rogers, 2005). However, individual advantages cannot explain the existence of population level biases in laterality (Vallortigara & Rogers, 2005) and thus, it is logical to assume that there is an evolutionary explanation for why some lateral biases are shared among the population. This thesis focuses on two possible evolutionary explanations for population level laterality. The first explanation is that current manifestations of laterality are likely to be built on earlier forms of sensory lateralization which has led each hemisphere to specialize in certain tasks (Fitch & Braccini, 2013; Rogers, 2009). According to this view, hemispheric dominance might influence not only motor laterality, but also other general patterns of behaviour such as personality or behavioural style (Rogers, 2009). The second explanation is that sharing lateral biases offers advantages when coordinating and competing with conspecifics (Vallortigara, 2006; Vallortigara & Rogers, 2005). This theory has been studied using mathematical and theoretical models (Ghirlanda et al., 2009; Vallortigara, 2006) and points towards a possible effect of laterality in the creation and maintenance of the social network. Investigating the link between laterality and behavioural style, as well as the effect of laterality in social relationships can offer important new insights into the evolution of population level laterality.

This thesis studied laterality in captive chimpanzees, examining different forms of motor laterality, as well as its links with behavioural style and social relationships. This thesis yielded several findings. First, while there is no population level laterality in spontaneous tasks in the sample of chimpanzees, individual laterality in simple reaching tasks is consistent over a period of two years and is more pronounced than other forms of spontaneous hand use. Second, other forms of motor laterality do not elicit individual or group preferences, and sidedness, the lateral bias on the way individuals move around their conspecifics, is not associated with group aggression. Third, laterality assessed using simple reach and motor laterality is not associated with behavioural style. Lastly, laterality does not seem to influence the overall structure of social relationships in the group, as the chimpanzees studied preferentially associate with other related individuals.

This thesis uses new approaches to explore two explanations for the evolution of laterality in chimpanzees. While the studies presented in this work must be seen as part of a large body of research that includes, but is not limited to, primates it does add new approaches to test hypotheses that are particularly appropriate for chimpanzees and other social species. The findings of this thesis contribute to three main areas of research: measures of laterality in chimpanzees, the link between behavioural style and laterality, and the link between laterality and intraspecific coordination. First, Chapter 2 offers a detailed study of widely used measures of hand use. Chapter 3 expands the current knowledge of laterality in chimpanzees by studying other forms of motor laterality and proposing the use of sidedness as a measure of laterality. Chapter 4 tackles the question of whether early hemispheric specialization influences measures of laterality by studying the role of the right-hemisphere in processing emotional and social stimuli using two different approaches. Finally, Chapters 5 and 6 use social network analysis to study intraspecific coordination in chimpanzees and its links with laterality.

Main Findings

Overall, the findings of this thesis regarding the presence of temporal stability of hand preference over a period of two years are consistent with those recently published (Padrell et al., 2019), adding further support to the idea that hand preference is stable in the medium term in chimpanzees. This thesis also presents new contributions to the study of laterality by introducing sidedness as a measure of laterality in chimpanzees. Sidedness draws from past research of lateral biases in sheep (Barnard et al., 2016; Versace et al., 2007), which allows the researcher to study the preference in the visual hemifield when avoiding obstacles and complements previous research in locomotion laterality in chimpanzees (Hopkins, 2008; Morcillo et al., 2006). However, in contrast with measures used in sheep, sidedness focuses on the social environment in order to study social biases. While this thesis did not find strong preferences in sidedness in chimpanzees in a naturalistic zoo setting, this measure might yield different results in a more controlled laboratory environment or when focused on specific contexts such as aggression.

Regarding the link between personality and laterality, this thesis builds from previous research by expanding the measures of behavioural style used in order to better understand the possible association between laterality and behavioural styles. While past research has found that right-handed and left-handed primates show consistent differences in exploration style (Braccini & Caine, 2009; Cameron & Rogers, 1999; Fernández-Lazaro et al., 2019; Hopkins & Bennet, 1994), this thesis focuses on studying if these individual differences could also be seen in other aspects of behaviour. The main contribution of this thesis to this area is the finding that, while neither laterality in hand preference nor laterality in leading arm are associated with behavioural style, congruent laterality was significantly associated with sociability. However, although the findings of the thesis in this area are compatible with the idea that a dominance of the left hemisphere is associated with approach behaviours and known stimuli, the differences between left-congruent and right-congruent chimpanzees was only a non-significant tendency. This evidence does not support the idea that an overall dominance of the right hemisphere, which is specialised in processing emotions and social stimuli, translates into an association between behavioural style and laterality.

Lastly, this thesis tackles the question of whether laterality favours intraspecific coordination by using social network analysis. Social network analysis allows us to research the relationships between individuals in a group while simultaneously considering the position of each individual in the overall structure (Borgatti et al., 2013) and it has already been used with success in the investigation of cooperation in primates (Fehl et al., 2011; Kasper & Voelkl, 2009; Voelkl & Kasper, 2009). This thesis shows that, in the sample of chimpanzees that was observed, individuals do not associate preferentially based on hand preference, which indicates that laterality is not linked with stronger social bonds. Since social bonds are an indication of the tendency of individuals to cooperate (Molesti & Majolo, 2016), this indicates that shared lateral biases do not contribute to cooperation. However, more research is needed in order to fully understand if social networks can accurately predict coordination in chimpanzees.

On the Relationship Between Laterality and Behavioural Style

A main element of this thesis is the idea that individual lateralization can be reflected in general aspects of behaviour, such as movement through a social environment (Chapter 3), individual differences in general behaviour (Chapter 4) or social structure (Chapter 5). In particular, Chapter 3 was formulated based on previous research that finds evidence of particular lateral biases in behaviour, while Chapter 4 is based on a number of studies that find a link between motor laterality and behavioural style. The field of investigating the association between motor laterality and individual differences of behaviours in animals started decades ago, with a study showing that left- and right-handed chimpanzees showed significant differences in exploration styles (Hopkins & Bennett, 1994). Since then, research has shown that lateralised behaviours are associated with individual differences in primates (Braccini & Caine, 2009; Cameron & Rogers, 1999; Díaz et al., 2021; Fernández-Lázaro et al., 2019; Westergaard et al., 2003; Westergaard et al., 2004) and other mammals (Barnard et al., 2018; Barnard et al., 2017; Goursot et al., 2019; Wells et al., 2019). While this area appears to be gaining interest among animal researchers and evidence of this association continues to grow, it is necessary to carefully examine not only the evidence, but also the evolutionary explanation for the relationship between motor laterality and individual differences in behaviour.

As explained in Chapter 1, Rogers (2009) proposes that the process underlying the association between laterality and general behaviour is the early hemispheric sensory specialization: as senses appear to be lateralised earlier in evolution, it is logical to assume that this early lateralization may have led to motor lateralization as well. While the underlying mechanisms are not well-studied, there is evidence that activity in the right hemisphere is associated with higher levels of cortisol secretion in humans (Wittling & Pflüger, 1990) and other primates (Kalin et al., 1998). The implication behind a link between laterality and general differences of behaviour is that one hemisphere might have a predominance in the control of certain types of behaviour (Rogers, 2009). This idea is similar to the concept of hemisphericity, which proposes that, since each hemisphere processes stimuli and behaviour in different ways, individuals might have a preferred mode of cognitive processing (Beamont et al., 1984). Hemisphericity was mainly studied in humans and in relation to cognitive processes and personality (Beamont et al., 1984; Vingiano, 1989) although much of the interest in this topic faded over the years. Past research in hemisphericity has been criticised for being simplistic in its notion that each hemisphere has a contrasting processing style (Corballis, 1980) and, in particular, over the lack of evidence that humans can "train" a particular hemisphere of the brain (Haapanen, 1979). It is important, therefore, to be cautious when interpreting the existing evidence of behavioural differences between left- and right-handed primates.

A key element to better understand the link between laterality and general behaviour, and that can help explain why this thesis did not find it, is in the particular context in which this link is examined. Contexts that elicit strong emotional responses, such as exploration and aggression, might be more appropriate to investigate this link in mammals, since mammal species are known to show strong lateralization in emotional processing (Fernández-Carriba et al., 2002; Leliveld et al., 2013; Salva et al., 2012) and lateralization is known to be associated with cortisol secretion (Wittling & Pflüger, 1990; Kalin et al., 1998). The fact that previous research has found differences in exploration style in chimpanzees for right- and left-handed individuals (Hopkins & Bennett, 1994) while the present thesis has failed to find such differences for behavioural styles seems to support this idea. Investigating the lateralization of specific processes, such as emotional and social responses, and their relationship to motor laterality is likely to offer more insightful results than investigating the relationship between personality and laterality in animals. However, this thesis has shown how social network analysis can take into account important aspects of the social structure, such as agonistic interactions or grooming network, and how they might impact certain measures of laterality and behavioural style. Therefore, future research investigating personality and laterality should consider using this approach to fully take into account the social structure.

Contributions

The research undertaken in this thesis contributes to existing literature in several ways. First, regarding the study of laterality and more specifically hand preference in primates, this thesis offers valuable information on several important factors. Information regarding temporal stability is valuable since it is assumed to exist in laterality measures although it is often an underreported aspect of laterality (but see Hopkins 1995a, Padrell et al., 2019). While some studies of laterality in chimpanzees have a longitudinal approach to data collection (Hopkins, 1993; 1995a; 1995b; Hopkins & Pearson, 2000; Hopkins et al, 1993; 2005; 2013; 2015), which helps avoid problems regarding stability, more knowledge regarding short- and long-term stability can help evaluate the findings of studies where the data collection was completed over short periods. The findings of this thesis, together with those reported in recently published papers (Padrell et al., 2019) indicate that, while there is significant temporal consistency of hand preference in chimpanzee groups, a minority of the individuals studied show changes in their preferred hand. This highlights the need to continue to investigate and report temporal stability, as it is still unknown which factors might contribute to lower stability.

The findings presented on sidedness adds new data to the area of social and visual laterality that is currently understudied in comparison with hand preference in primates. While there are several important limitations to the application of this concept to primates, as discussed in Chapter 3, it adds further context to past research of visual and social laterality in primates (Casperd & Dunbar, 1993; Quaresimini et al., 2014). Additionally, the approach of studying social laterality through sidedness is likely to be useful in other animal species, particularly in social species with laterally placed eyes.

Lastly, this thesis contributes to the areas of laterality and individual differences of behaviour by making use of the social networks approach to studying similarities and differences between individuals. While the findings of the thesis did not point towards homophily of hand preference or behavioural style in chimpanzees, this approach offers useful tools that can potentially contribute to both areas. In particular, given the new tools that have been developed through social network analysis, such as Network-Based Diffusion Analysis (Pinter-Wollman et al., 2014), future research using this approach could prove useful when investigating how social learning might affect laterality in hand use.

Weaknesses and Limitations

While this thesis investigates two explanations for the evolution of lateralization, focusing on chimpanzees, there are several limitations that are important to acknowledge. First, tackling evolutionary drivers behind any behaviour is difficult, as it requires examining extensive research studies in as many species as possible. In this sense, this thesis must be understood as a first exploration of these hypotheses in a single species and cannot be used to make final conclusions regarding the two explanations for the evolution of population level laterality. Moreover, these studies have been conducted in a single chimpanzee group. Repeating similar studies in other populations, both in captivity and in the wild, will offer more solid evidence, or lack of evidence, for the findings of the thesis.

Second, while the approach of using social network analysis has great potential in the study of primate behaviour, as mentioned before, it might yield more interesting results when studying laterality as a frequency dependent evolutionary strategy in non-primate species. Frequency dependent strategies propose that, while there are evolutionary advantages in having the same laterality bias as most conspecifics, there are also alternate social advantages in having a minority bias (Ghirlanda & Vallortigara, 2004; Vallortigara & Rogers, 2005). Social networks offer can greatly benefit investigations of laterality as a frequency dependent strategy by offering a more detailed analysis of how the social structure might influence the interactions between conspecifics with the same bias of laterality. While the social networks approach allows the study of how different factors affect complex social networks, it is possible that, contrary to what Rogers (2009) speculated, hand preference might not be the most appropriate measure for studying the impact of laterality in other patterns of behaviour. Additionally, social networks can help investigate how complex social behaviours might affect laterality, but it is important to highlight that this thesis did not directly measure cooperation, but rather, grooming sociality. Grooming is known to be related to cooperation (Ebenau et al., 2018; Molesti & Majolo, 2016), but it is still not a direct measure. Species that show a lateralised response directly to threatening or social stimuli (i.e. escape or attack responses) might be better candidates to study the interaction of sociality and laterality. Therefore, applying a social network approach to species commonly studied such as fish (Bisazza et al., 1999; 2000) might yield interesting results in the future.

Final Conclusions

Laterality is a complex area of research that encompasses multiple interconnected but very different phenomena and expressions. While the mechanisms that explain the advantages of a lateralised brain for individuals are well known (Rogers, 2017; Vallortigara & Rogers, 2005), explanations for the development of population level laterality are still being explored. This thesis investigated two explanations for possible advantages of population level laterality: early hemispheric specialization through the link between laterality and behavioural style and intraspecific coordination through the link between laterality and social networks. Overall, the research undertaken in this thesis found that measures of laterality such as simple reach and leading arm are not associated with either behavioural style or intraspecific coordination in one group of chimpanzees. However, there are indications that using congruent laterality might be a better approach to study the link between laterality and behavioural style in chimpanzees than studying single measures of hand preference alone. Additionally, the social networks analysis approach shows promise and could be used to further expand the knowledge of the effects of laterality on coordination in social species.

References

Barnard, S., Matthews, L., Messori, S., Podaliri-Vulpiani, M., & Ferri, N. (2016). Laterality as an indicator of emotional stress in ewes and lambs during a separation test. *Animal Cognition, 19*(1), 207–214. https://doi.org/10.1007/s10071-015-0928-3

Barnard, S., Wells, D. L., & Hepper, P. G. (2018). Laterality as a predictor of coping strategies in dogs entering a rescue shelter. *Symmetry, 10*(11), 538. https://doi.org/10.3390/sym10110538

Barnard, S., Wells, D. L., Hepper, P. G., & Milligan, A. D. S. (2017). Association between lateral bias and personality traits in the domestic dog (*Canis familiaris*). *Journal of Comparative Psychology, 131*(3), 246–256. https://doi.org/10.1037/com0000074

Beaumont, J. G., Young, A. W., & McManus, I. C. (1984). Hemisphericity: A critical review. *Cognitive Neuropsychology*, *1*(2), 191-212.

Bisazza, A., De Santi, A., & Vallortigara, G. (1999). Laterality and cooperation: Mosquitofish move closer to a predator when the companion is on their left side. *Animal Behaviour, 57*(5), 1145–1149. https://doi.org/10.1006/anbe.1998.1075

Bisazza, A., Cantalupo, C., Capocchiano, M., & Vallortigara, G. (2000). Population lateralisation and social behaviour: A study with 16 species of fish. *Laterality*, *5*(3), 269–284. https://doi.org/10.1080/713754381

Borgatti, S. P., Everett, M. G., & Johnson, J. C. (2013). *Analyzing social networks*. London, United Kingdom: SAGE.

Braccini, S. N., & Caine, N. G. (2009). Hand preference predicts reactions to novel foods and predators in marmosets (*Callithrix geoffroyi). Journal of Comparative Psychology, 123*(1), 18–25. https://doi.org/10.1037/a0013089

Cameron, R., & Rogers, L. J. (1999). Hand preference of the common marmoset (*Callithrix jacchus*): Problem solving and responses in a novel setting. *Journal of Comparative Psychology*, *113*(2), 149–157. https://doi.org/10.1037/0735-7036.113.2.149

Casperd, J. M., & Dunbar, R. I. M. (1996). Asymmetries in the visual processing of emotional cues during agonistic interactions by gelada baboons. *Behavioural Processes*, *37*(1), 57–65. https://doi.org/10.1016/0376-6357(95)00075-5

Corballis, M. C. (1980). Laterality and myth. *American Psychologist*, *35*(3), 284-295.

Díaz, S., Murray, L., Rodway, P. (2021) Limb preference and personality in donkeys (*Equus asinus*). *Laterality: Asymmetries of Brain, Behaviour, and Cognition. 26*(1-2) 186-200. https://doi.org/10.1080/1357650X.2021.1882480

Ebenau, A., von Borell, C., Penke, L., Ostner, J., & Schülke, O. (2019). Personality homophily affects male social bonding in wild Assamese macaques, *Macaca assamensis. Animal Behaviour, 155*, 21–35. https://doi.org/10.1016/j.anbehav.2019.05.020

Fehl, K., van der Post, D. J., & Semmann, D. (2011). Co-evolution of behaviour and social network structure promotes human cooperation. *Ecology Letters*, *14*(6), 546–551. https://doi.org/10.1111/j.1461-0248.2011.01615.x

Fernández-Carriba, S., Loeches, Á., Morcillo, A., & Hopkins, W. D. (2002). Asymmetry in facial expression of emotions by chimpanzees. *Neuropsychologia*, *40*(9), 1523–1533. https://doi.org/10.1016/S0028-3932(02)00028-3

Fernández-Lázaro, G., Latorre, R., Alonso-García, E., & Barja Núñez, I. (2019). Nonhuman primate welfare: Can there be a relationship between personality, lateralization and physiological indicators? *Behavioural Processes*, *166*, 103897. https://doi.org/10.1016/j.beproc.2019.103897

Fitch, W. T., & Braccini, S. N. (2013). Primate laterality and the biology and evolution of human handedness: A review and synthesis. *Annals of the New York Academy of Sciences*, *1288*(1), 70–85. https://doi.org/10.1111/nyas.12071

Frasnelli, E., Vallortigara, G., & Rogers, L. J. (2012). Left–right asymmetries of behaviour and nervous system in invertebrates. *Neuroscience & Biobehavioral Reviews*, *36*(4), 1273–1291. https://doi.org/10.1016/j.neubiorev.2012.02.006

Ghirlanda, S., Frasnelli, E., & Vallortigara, G. (2009). Intraspecific competition and coordination in the evolution of lateralization. *Philosophical Transactions of the Royal Society*, *364*, 861–866. https://doi.org/10.1098/rstb.2008.0227

Goursot, C., Düpjan, S., Kanitz, E., Tuchscherer, A., Puppe, B., & Leliveld, L. M. C. (2019). Assessing animal individuality: Links between personality and laterality in pigs. *Current Zoology*, *65*(5), 541–551. https://doi.org/10.1093/cz/zoy071

Hardyck, C., & Haapanen, R. (1979). Educating both halves of the brain: Educational breakthrough or neuromythology?. *Journal of School Psychology*, *17*(3), 219-230.

Hopkins, W. D. (1993). Posture and reaching in chimpanzees (*Pan*) and orangutans (*Pongo*). *Journal of Comparative Psychology*, *107*(2), 162–168.

Hopkins, W. D. (1995a). Hand preferences for a coordinated bimanual task in 110 chimpanzees (*Pan troglodytes*): Cross-sectional analysis. *Journal of Comparative Psychology*, *109*(3), 291–297.

Hopkins, W. D. (1995b). Hand preferences for simple reaching in juvenile chimpanzees (*Pan troglodytes*): Continuity in development. *Developmental Psychology*, *31*(4), 619–625.

Hopkins, W. D. (2008). Locomotor limb preferences in captive chimpanzees (*Pan troglodytes*): Implications for morphological asymmetries in limb bones. *American Journal of Physical Anthropology*, *137*(1), 113–118. https://doi.org/10.1002/ajpa.20834

Hopkins, W. D., Bard, K. A., Jones, A., & Bales, S. L. (1993). Chimpanzee hand preference in throwing and infant cradling: Implications for the Origin of Human Handedness. *Current Anthropology*, *34*(5), 786–790.

Hopkins, W. D., & Bennett, A. J. (1994). Handedness and approach-avoidance behavior in chimpanzees (*Pan*). *Journal of Experimental Psychology: Animal Behavior Processes*, *20*(4), 413–418. https://doi.org/10.1037/0097-7403.20.4.413

Hopkins, W. D., Cantalupo, C., Freeman, H., Russel, J., Kachin, M., & Nelson, E. (2005). Chimpanzees are right-handed when recording bouts of hand use. *Laterality*, *10*(2), 121–130.

Hopkins, W. D., Gardner, M., Mingle, M., Reamer, L., & Schapiro, S. J. (2013). Within- and between-task consistency in hand use as a means of characterizing hand preferences in captive chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, *127*(4), 380–391. https://doi.org/10.1037/a0031071

Hopkins, W. D., & Pearson, K. (2000). Chimpanzee (*Pan troglodytes*) handedness: Variability across multiple measures of hand use. *Journal of Comparative Psychology*, *114*(2), 126–35.

Hopkins, W. D., Schaeffer, J., Russell, J. L., Bogart, S. L., Meguerditchian, A., & Coulon, O. (2015). A comparative assessment of handedness and its potential neuroanatomical correlates in chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*). *Behaviour, 152*, 461–492. https://doi.org/10.1163/1568539X-00003204

Kalin, N. H., Larson, C., Shelton, S. E., & Davidson, R. J. (1998). Asymmetric frontal brain activity, cortisol, and behavior associated with fearful temperament in rhesus monkeys. *Behavioral Neuroscience, 112*(2), 286–292. https://doi.org/10.1037/0735-7044.112.2.286

Kasper, C., & Voelkl, B. (2009). A social network analysis of primate groups. *Primates*, *50*(4), 343–356. https://doi.org/10.1007/s10329-009-0153-2

Leliveld, L. M. C., Langbein, J., & Puppe, B. (2013). The emergence of emotional lateralization: Evidence in non-human vertebrates and implications for farm animals. *Applied Animal Behaviour Science*, *145*(1), 1–14. https://doi.org/10.1016/j.applanim.2013.02.002

Molesti, S., & Majolo, B. (2016). Cooperation in wild Barbary macaques: Factors affecting free partner choice. *Animal Cognition*, *19*(1), 133–146. https://doi.org/10.1007/s10071-015-0919-4

Morcillo, A., Fernandez-Carriba, S., & Loeches, A. (2006). Asymmetries in postural control and locomotion in chimpanzees (*Pan troglodytes*). *American Journal of Primatology*, *68*(8), 802–811. https://doi.org/10.1002/ajp.20280

Padrell, M., Gómez-Martínez, C., & Llorente, M. (2019). Short and long-term temporal consistency of hand preference in sanctuary chimpanzees (*Pan troglodytes*) for unimanual and bimanual coordinated tasks. *Behavioural Processes*, *167*, 103911. https://doi.org/10.1016/j.beproc.2019.103911

Pinter-Wollman, N., Hobson, E. A., Smith, J. E., Edelman, A. J., Shizuka, D., de Silva, S., Waters, J. S., Prager, S. D., Sasaki, T., Wittemyer, G., Fewell, J., & McDonald, D. B. (2014). The dynamics of animal social networks: Analytical, conceptual, and theoretical advances. *Behavioral Ecology*, *25*(2), 242–255. https://doi.org/10.1093/beheco/art047

Quaresmini, C., Forrester, G. S., Spiezio, C., & Vallortigara, G. (2014). Social environment elicits lateralized behaviors in gorillas (*Gorilla gorilla gorilla*) and chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, *128*(3), 276–284. https://doi.org/10.1037/a0036355

Rogers, L. J. (2009). Hand and paw preferences in relation to the lateralized brain. *Philosophical Transactions of the Royal Society*, *364*, 943–954. https://doi.org/10.1098/rstb.2008.0225

Rogers, L. J. (2017). A matter of degree: strength of brain asymmetry and behaviour. *Symmetry*, *9*(12), 57. https://doi.org/10.3390/sym9040057

Rogers, L., & Vallortigara, G. (2015). When and why did brains break symmetry? *Symmetry*, *7*(4), 2181–2194. https://doi.org/10.3390/sym7042181

Salva, O. R., Regolin, L., Mascalzoni, E., & Vallortigara, G. (2012). Cerebral and behavioural asymmetries in animal social recognition. *Comparative Cognition & Behaviour Reviews*, *7*, 110–138. https://doi.org/10.3819/ccbr.2012.70006

Vallortigara, G. (2006). The evolutionary psychology of left and right: Costs and benefits of lateralization. *Developmental Psychobiology*, *48*(6), 418–427. https://doi.org/10.1002/dev.20166

Vallortigara, G., & Rogers, L. J. (2005). Survival with an asymmetrical brain: Advantages and disadvantages of cerebral lateralization. *Behavioral and Brain Sciences*, *28*, 575–633.

Versace, E., Morgante, M., Pulina, G., & Vallortigara, G. (2007). Behavioural lateralization in sheep (*Ovis aries*). *Behavioural Brain Research*, *184*(1), 72–80. https://doi.org/10.1016/j.bbr.2007.06.016

Vingiano, W. (1989). Hemisphericity and Personality. *International Journal of Neuroscience, 44*(3–4), 263–274. https://doi.org/10.3109/00207458908986206

Voelkl, B., & Kasper, C. (2009). Social structure of primate interaction networks facilitates the emergence of cooperation. *Biology Letters*, *5*(4), 462–464. https://doi.org/10.1098/rsbl.2009.0204

Wells, D. L., Hepper, P. G., Milligan, A. D. S., & Barnard, S. (2019). Lack of association between paw preference and behaviour problems in the domestic dog, *Canis familiaris*. *Applied Animal Behaviour Science, 210*, 81–87. https://doi.org/10.1016/j.applanim.2018.10.008

Westergaard, G. C., Chavanne, T. J., Houser, L., Cleveland, A., Snoy, P. J., Suomi, S. J., & Higley, J. D. (2004). Biobehavioural correlates of hand preference in free-ranging female primates. *Laterality*, *9*(3), 267–285. https://doi.org/10.1080/13576500342000086a

Westergaard, G. C., Chavanne, T. J., Lussier, I. D., Houser, L., Cleveland, A., Suomi, S. J., & Higley, J. D. (2003). Left-handedness is correlated with csf monoamine metabolite and plasma cortisol concentrations, and with impaired sociality, in free-ranging adult male rhesus macaques (Macaca mulatta). *Laterality: Asymmetries of Body, Brain and Cognition, 8*(2), 169–187. https://doi.org/10.1080/713754484

Wittling, W., & Pflüger, M. (1990). Neuroendocrine hemisphere asymmetries: Salivary cortisol secretion during lateralized viewing of emotion-related and neutral films. *Brain and Cognition, 14*(2), 243–265. https://doi.org/10.1016/0278-2626(90)90032-J

Appendix I: Relatedness information

Chimpanzee	***Mother-Offspring Relationships***	***Siblings/Other***
Boris (1966)	Father to Sarah and Alice	
Wilson (22.2.68)		Uncle to Rosie Great-uncle to Sally Brother to Mandy
Nicky (21.1.69)		Half-brother to Friday
Friday (6.2.76)	Father to Dylan, Layla and Sally	Half-brother to Nicky
Dylan (9.4.87)	Mother: Farthing Father: Unknown Father to Chrissie	Half-Sister*: Layla
Eric (24.6.03)	Mother: Kankan Father: Unkown	Half-Brother* to Patti Uncle to Carlos
Carlos (6.3.05)	Mother: Whitney Father: Unknown	Nephew to Eric and Patti
Rosie (20.1.73)	Mother to Sally	Niece to Wilson and Mandy
Farthing (19.9.75)	Mother to Dylan and Layla	Half-sister to Halfpenny
Mandy (19.9.77)	Mother to ZeeZee Grandmother to Tina	Sister to Wilson Aunt to Rosie Great-aunt to Sally
Sarah (16.10.86)	Mother: Halfpenny Father: Boris	Mother Halfpenny is sister to Florin, therefore cousin to Alice and Chrissie. Mother Halfpenny is half-sister to Farthing, therefore some relatedness to Dylan and Layla.
Sally (4.6.88)	Mother: Rosie Father: Friday	Great-uncle Wilson Great-aunt Mandy
Layla (2.11.90)	Mother: Farthing Father: Friday	Half-brother*: Dylan

Alice (6.11.91)	Mother: Florin Mother to Annie Father: Boris	Half-Sister to Chrissie Mother Florin is sister to Halfpenny, therefore cousin to Sarah. Mother Florin is half-sister to Farthing, therefore some relatedness to Dylan and Layla.
ZeeZee (15.2.94)	Mother: Mandy Father: Unknown Mother to Tina and Stevie	Sister to Baby
Vila (27.2.95)	No relations in group	
Chrissie (11.3.96)	Mother: Florin Father: Dylan	Half-Sister to Alice Aunt to Annie Mother Florin is sister to Halfpenny, therefore cousin to Sarah. Mother Florin is half-sister to Farthing, therefore some relatedness to Layla.
Patti (24.7.97)	Mother: Kankan Father: Unknown	Half-sister* to Eric Aunt to Carlos
Tina (16.2.09)	Mother: Zeezee Father: Unknown Grandmother: Mandy	Sister to Stevie Niece to Baby

Siblings marked with * are assumed when fathers are unknown for one or both siblings. Siblings without * are known half-siblings.

Appendix II: Details on Rearing history

As provided by Niall Ormerod, former lead primate keeper at Chester Zoo, now retired.

Chimpanzee	***Rearing History***
Boris [1966]	Bought in a pet shop in New York, aged approx 6 months, reared as a member of a family by Hester Mundis, the book 'No he's not a monkey, he's an ape, and he's my son' tells of his first few years. Arrived at Chester 1969 and was kept in a small group of young chimps, but always had plenty of human contact up to the age of 9 –10 years old.
Wilson (22.2.68)	Hand-reared. In the 1960s at Chester most of the chimps born were hand-reared, they were very popular with visitors and therefore were displayed in a small building with a large window to allow visitors to view them. When they out-grew this building, they were moved to the monkey house. In those days it consisted of about 24 small glass fronted cages, some with access to the outside. These cages housed up to about 6 monkeys or young hand-reared apes. When they were about 3 –5 years old they were moved to either the chimp or orang houses. Wilson and Nicky were taken to the chimp house late 1972, this was the first time they would see, hear and smell other chimps since the day they were born. Once they were settled and happy with their new housing and 'noisy neighbours', they were integrated with other young chimps. It was not to the late '70s that all the chimps were combined into one group, before there were at least 4 groups, sometimes rising to 6 groups.
Nicky (21.1.69)	Hand-reared. As above.
Friday (6.2.76)	Parent-reared until 6 months, then hand-reared (following calcium deficiency) Friday's mother Jane had reared a baby before [Kate] so when Friday was born she continued raising her new baby. When he was about 6 months old it was clear that he was not growing properly. On removing after tests he was found to have calcium deficiency. He then broke a leg which was pinned back together by the vets. It was too long a period of time to put him back with Jane, and as he was already too lively to go into the nursery he went to the monkey house, where I think he was kept with a young hand-reared orang, Sibu. He came back to the chimp house and was put in with 2 other young hand-reared males. Those 2 went to other collections and so Friday was mixed with other youngsters.
Rosie (20.1.73)	Hand-reared . Rosie followed the pattern of the ones above. She grew up with another young female [Heidi] who had been mother reared up to 6 – 10 months as her mother wouldn't wean her. These 2 didn't stay long in the monkey house and came to the chimp when they were about 3 years old, where after a couple of years were mixed with Kate. These 3 were later mixed with other youngsters, before being incorporated with all the other groups a few years later.
Mandy (19.9.77)	Hand-reared. Once she was about 12 months she stayed at the chimp house, while being hand-reared she spent most days in the chimp house and at night went home with Peter Waite who was rearing her. With being in the presence of other chimps while being hand-reared her integration with a small group of youngsters was easier and quicker.
Sarah (16.10.86)	Parent-reared (hand-reared for 10 days at 6 months when ill) There had been a bad flu outbreak when Sarah became ill. After separating her from her mother [Halfpenny}, the vet

	could not even hear her breath. She was given anti-biotics and put in a human incubator and had 10 second bursts of oxygen every hour. Halfpenny had not been put back into the group as we hoped to give her Sarah back if she survived. After 5 days the vet thought that Sarah might make it, she was then taken and shown to Halfpenny, but they were not allowed to touch. This continued, but after 10 days since she was first removed when being shown to Halfpenny, Halfpenny turned her back and refused to make visual contact. As the initial plan was to put them back together our hand was forced by Halfpenny's action, ideally Sarah could have done with a few more days treatment. They were reintroduced to each other and after a couple of days the 2 of them were put back into the group.