



DEPARTAMENTO DE CIÊNCIAS DA VIDA

FACULDADE DE CIÊNCIAS E TECNOLOGIA
UNIVERSIDADE DE COIMBRA

Chimpanzee's (*Pan troglodytes*) Social Cognition and Behaviour Mediated by a Touch Panel Task

Renata Mendonça

2012



DEPARTAMENTO DE CIÊNCIAS DA VIDA

FACULDADE DE CIÊNCIAS E TECNOLOGIA
UNIVERSIDADE DE COIMBRA

Chimpanzee's (*Pan troglodytes*) Social Cognition and Behaviour Mediated by a Touch Panel Task

Dissertação apresentada à Universidade de Coimbra para cumprimento dos requisitos necessários à obtenção do grau de Mestre em Evolução e Biologia Humanas, realizada sob a orientação científica da Professora Doutora Eugénia Cunha (Universidade de Coimbra) e da Doutora Susana Carvalho (Oxford University).

Renata Mendonça

2012

Summary

Index of figures	iv
Study 1	iv
Study 2.....	v
Index of tables	vi
Study 1	vi
Study 2.....	vi
Resumo	vii
Palavras-chave	vii
Abstract	viii
Key-words	viii
Acknowledgments	ix

Index

1. Introduction	1
1.1. Early origins of primatology.....	1
1.2. Background on chimpanzee cognition and behaviour	2
1.3. Primatology in Japan	4
1.4. Chimpanzee: General considerations.....	6
1.5. Chimpanzee cognition	9
1.5.1. Chimpanzee physical cognition.....	9
1.5.2. Chimpanzee social cognition.....	12
2. Goal of the studies	17

3. Study 1

Contest competition mediated by a touch panel task: Social dynamics and spatial distribution	21
3.1. Introduction.....	23
3.2. Subjects.....	26
3.2.1. Chimpanzee’s biography and background	26
3.3. Material and Methods	30
3.3.1. Housing and apparatus	30
3.3.2. Stimuli	30
3.3.3. Procedure.....	31
3.3.4. Statistical analysis	33
3.4. Results.....	34
3.4.1. Control sessions vs. experimental sessions	34
3.4.2. Time spent around the booth vs. Time spent performing the task	34
3.4.3. Individuals around the booth when one is performing the task.....	39
3.4.4. Spatial location around the booth	40
3.4.5. Other behaviours	42
3.4.6. Male-male competition and the dynamics of the group	43
3.5. Discussion.....	50
3.5.1. High-ranking females	52
3.5.2. Low-ranking females behaviour.....	54
3.5.3. The importance of the session 8	55
3.5.4. Entrance of Ayumu/Ai in the group and agonistic events.....	57
3.5.5. Male dominance and task monopolization	58
3.6. Conclusion	60

4. Study 2

Chimpanzees are Prosocial in a Task Mediated by a Touch Panel Computer	61
4.1. Introduction	63
4.2. Subjects	66
4.3. Material and Methods	67
4.3.1. Housing and Apparatus	67
4.3.2. Stimuli	69
4.3.3. Statistical analysis	70
4.3.4. Procedure	70
4.4. Results.....	71
4.4.1. Experiment 1: Three button choice	71
4.4.2. Experiment 2: Mixed condition.....	74
4.4.3. Experiment 3: Blocked condition	77
4.5. Discussion.....	83
4.5.1. Experiment 1: Three choices button.....	83
4.5.2. Experiment 2: Mixed condition.....	83
4.5.3. Experiment 3: Blocked condition.....	84
4.5.4. Comparison with Horner <i>et al.</i> (2011)	85
4.5.5. General discussion.....	86
4.6. Conclusion	90
4.6.1. Further perspectives.....	91
5. Final considerations.....	93
6. References.....	94
7. Appendixes	109

Index of figures

Study 1

Figure 1 – Akira, the dominant male.....	26
Figure 2 – Ayumu, juvenile male, son of Ai.....	27
Figure 3 – Ai, the dominant female.....	27
Figure 4 – Reiko, the other dominant female.....	28
Figure 4 – Mari, a low rank female.....	28
Figure 6 – Pendesa, a low rank female.....	29
Figure 7 – Shape of the experimental booth.....	33
Figure 8 –Time individuals spent around the booth area: experimental sessions vs. control sessions.....	34
Figure 9 – Time individuals spent on the booth area across the sessions.	35
Figure 10 – Time individuals spent performing the task across the sessions.....	36
Figure 11 – Correlation between mean of time performing the task and spent around the booth area.....	37
Figure 12 – Time males, high-ranking females and low-ranking females spent in both conditions: around the booth area and performing the task.....	39
Figure 13 – Time individuals spent in the booth area when Akira, Ayumu, Mari and Pendesa are performing the task.....	40
Figure 14 – Time each individual spent in the 3 different areas around the booth: task, closest positions and farthest positions (< 5m)	41
Figure 15 – Index of agonistic behaviours before and after Ayumu enters in the enclosure.....	42
Figure 16 – Index of agonistic behaviours in the sessions when Ayumu enter in the enclosure during the experiment and the session when he is in the enclosure from the beginning.....	44
Figure 17 – Frequency of the first take over by males.....	45
Figure 18 – Time individuals spent performing the task in three different conditions given by the sessions when Ayumu enter in the enclosure during the session ,when Ayumu is present since the the sessions Ayumu is absent in the area.....	47

Figure 19 – Time Mari and Pendesa spent in the sessions before and after session 8.....	48
Figure 20 – Mean of time spent in the booth area by all the females in the sessions when the frequency of displays were higher (given by the entrance of Ayumu in the enclosure) and in the session where displays occurred at a lower rate (Ayumu was in the enclosure from the beginning)	49
Figure 21 –Time Mari and Pendesa spent close to Ayumu (around the booth) when he was performing the task, before and after session 8.....	50

Study 2

Figure 1 – Pan and Pal performing the prosocial experiment.....	68
Figure 5 –Proportion of choices regarding the three different options: prosocial, selfish and altruistic (experiment 1).....	72
Figure 3 – Distribution of the choices across the trials (experiment 1).....	73
Figure 4 – a) Proportion of mean-spirited versus prosocial choices. b) Distribution of the mean-spirited and prosocial choices (experiment 2).....	75
Figure 5 – a) Proportion of mean-spirited versus altruistic choices. b) Distribution of mean-spirited and altruistic choices (experiment 2)	76
Figure 66 – a) Proportion of prosocial and altruistic choices. b) Distribution of the prosocial and altruistic choices (experiment 2).....	76
Figure 7 – a) Proportion of prosocial and mean-spirited choices. b) Distribution of the prosocial and mean-spirited choices (experiment 3)	78
Figure 8 – a) Proportion of prosocial and mean-spirited choices. b) Distribution of the mean-spirited and altruistic choices (experiment 3).....	79
Figure 97 – a) Proportion of prosocial and mean-spirited choices. b) Distribution of the prosocial and altruistic choices (experiment 3).....	79
Figure 80 –Proportion of the choices chosen by mothers and their juveniles in the tree different conditions (experiment 3)	81
Figure 11 –Distribution of the choices across the trials in the three different conditions referred to juveniles (experiment 3).....	82
Figure 12 –Distribution of the choices across the trials in the three different conditions. On the top the plots are referred to adults /mothers (experiment 3)	82

Index of tables

Study 1

Table 1 – Summary table with the information about the subjects regarding their biography and experience on touch panel tasks.....	29
Table 2 – Matrix with the positions around the booth area (< 5 m)	33
Table 3 – Presence of Ayumu and Ai in the sessions and the % of time they present in the enclosure.....	36
Table 4 – Time individuals spent in the booth area and performing the task with the respective standard error, and results of the Pearson correlation between the two variables.....	38
Table 5 – Percentage of take over. Am> Ak means Am taking over Akira, Ak > Am means the opposite tendency.....	45
Table 6 – Resume table indicating the first individual to approach first to the task across the sessions (S) with the respective proportion of time they spent performing the task and the number of takeovers per session.....	46
Table 7 – Agonistic events represented by the absolute number per session and index (agonistic events/min).....	49

Study 2

Table 1 – Stimuli assignment across individuals in all three different conditions.....	69
Table 2 – Mean of the proportion of choices for each individual P-prosocial, A-altruistic, MS-mean-spirited in each sessions S1- session 1, S2- session 2, S3- session.....	74
Table 3 – Proportion of choices across all the individuals in the three different conditions.....	77
Table 4 – Distribution of the conditions given to chimpanzees in 3 different days.....	78
Table 5 – Mean of choices by each individual in the three different given conditions.....	80
Table 6 – Values of the chi-square test, for the juveniles and mothers, comparing the choices in the three different conditions.....	80
Table 7 – Chi-square test comparing the choices of the mother with the choices of the juveniles in the three different conditions.	81

Resumo

O chimpanzé (*Pan troglodytes*) é o parente vivo mais próximo do Homem (juntamente com o bonobo - *Pan paniscus*). Características genéticas anatómicas, comportamentais e cognitivas fazem deste género um óptimo modelo parcimonioso para estudos cognitivos e comportamentais, elucidando-nos acerca da evolução do Homem. Os chimpanzés vivem em grupos sociais hierarquizados. A vida em grupos apresenta inúmeros desafios sociais. Tópicos relacionados como competição e comportamentos prosociais vão ser explorados: consequências da vida em grupo.

O estudo 1 foca-se na observação do comportamento dos chimpanzés numa situação de *contest competition*, num ambiente controlado, que requer a realização de uma tarefa num monitor Touch screen para a obtenção de recompensa. O objectivo é perceber qual dos indivíduos monopoliza a tarefa e como os restantes indivíduos se comportam. O presente estudo revelou-se uma situação de competição entre machos. Os indivíduos dominantes não são os que exercem mais a tarefa. A fêmea dominante raramente se aproxima da área do *booth* e o macho dominante realiza tarefa por menos tempo comparado com o macho juvenil, Ayumu, filho da fêmea dominante. As fêmeas subordinadas aproveitaram a ausência de Ayumu para realizar a tarefa. As sessões em que o macho juvenil entrou no recinto da experiência coincidiram com as sessões em que se verificou uma maior taxa de comportamentos agonísticos. Os resultados sugerem que a dominância não é o principal factor a influenciar a monopolização da área e que o Ayumu é o principal responsável pelos comportamentos agonísticos.

O estudo 2 foca o comportamento prosocial numa situação experimental mediada por computadores *Touch panel* em três díadas mãe-cria(juvenil). Os indivíduos foram dados a escolher entre três opções “prosocial”, “mean-spirited” e “altruistic”, em três condições distintas. Os chimpanzés escolheram, significativamente, nas três condições, a opção prosocial em relação às restantes opções e demonstraram entender as funções das opções entender ao objectivo. As crias demonstraram um comportamento mais altruísta que as respectivas mães, como estratégia para evitarem conflitos com as mesmas. Os resultados do presente estudo são confrontados com estudos anteriores.

Palavras-chave: competição, prosocialidade, cognição social em chimpanzés, ecrã táctil.

Abstract

Chimpanzee (*Pan troglodytes*) is the human closest living relative (as well as the bonobo - *Pan paniscus*). Genetic, anatomical, behavioural and cognitive traits make this genus a parsimonious role model for human evolution. Chimpanzees live in large and hierarchized groups. Life in groups holds many social challenges, Hereby we focus on two topics: competition and prosociality, as a consequence of life in groups.

Study 1 aims to observe chimpanzees' behaviour in contest competition situation in a controlled environment mediated by a touch-panel. The study focuses on understanding which individual is more likely to perform the task to obtain a reward and understanding other individuals' behaviour facing this contest competition scenario. The current study turned out to be a situation of male-male competition. The dominant individuals were not the ones that had performed for longer time. The dominant female rarely approach the booth area and the dominant male performed less than a juvenile male, Ayumu, son of the dominant female. Low ranking females took advantage and performed the task in the absence of Ayumu. The entrance of Ayumu in the enclosure where the experiment was ongoing increased the rate of agonistic behaviours. Results suggest that dominance is not the main factor accounting for the monopolization of the area, and Ayumu is the responsible for the increase of agonistic behaviours.

Study 2 aimed to understand if chimpanzees are prosocial in an experimental situation mediated by a touch-panel and improve the old paradigms to test prosocial behaviour. 3 Mother-offspring dyads were requested to choose between, 3 choices across three different conditions: prosocial, mean-spirited and altruistic.

Chimpanzees chose the prosocial option significantly above all the options in the three conditions and seemed to understand the function of the key prosocial and mean-spirited key. In condition 3, when chimpanzees faced the dyadic choice of mean-spirited and altruistic continuously for 96 trials, altruistic choice was chosen more frequently by the juveniles compared to the mothers, as a strategy to avoid conflict with the mother. Results are discussed and compared to the previous studies.

Key-words: contest competition, prosociality, chimpanzee social cognition, touch-panel task.

Acknowledgments

First of all I want to thank to Doctor Susana Carvalho, Professor Claudia Sousa and Professor Eugénia Cunha for accepting to supervise my thesis, for all the patience and support and for making possible the connection with Professor Tetsuro Matsuzawa, Primate Research, Kyoto University. I also want to thank to all my Professors in the Master Course, for contributing with their knowledge and making me even more fascinated for the Human Evolution area, and of course, Primatology.

In Japan, I want to thank to Professor Matsuzawa for all the support and for accepting me as his student, to Professor Ikuma Adachi for supervising my thesis, for all the knowledge he transmitted to me and patience he had, as well as, Doctor Christoph Dahl for sharing his ideas and knowledge with me and for collaborate in the study of prosociality, study 2 described in current the thesis. I also want to thank to Primate Research Institute staff, especially to Mami Shikuwa, without her, life in Japan would have been much more difficult and to all of the students and professors that received me so well and shared their knowledge with me.

Last, but not the least, I want to thank to my family, especially my mother and grandparents, for the “endless” support they gave me at distance, and to my friends and colleagues, Joana Prieto and Ricardo Gomes to keep sharing ideas and giving me advises, João Marchante for helping me with statistics and giving me his opinion and to Wilson Mália to help me revising the english.

“If we look straight and deep into a chimpanzee's eyes, an intelligent self-assured personality looks back at us. If they are animals, what must we be?”

Frans de Waal

1. Introduction

1.1. Early origins of primatology

The study of cognitions in animals, other than humans, was, and still is, a very controversial issue. For more than 2000 years, humans were believed to be the unique species that had developed mental capacities, and other animals, such as their close relatives, chimpanzee/bonobo, were underestimated (Tomasello and Call, 1997).

Experts say primatology was born with the father of biological naturalism, Aristotle (384–322 BC), the first man mentioning the word “ape” and documenting the resemblances between humans and non-human primates, with Barbary macaques (*Macaca sylvanus*; Atkinson, 1964). He was the first greatest biologist and evolutionist. The founder of comparative anatomy, and besides that, he was the pioneer of systematic studies of animal behaviour (Gross, 1997)

Galen (130-200 A.D.) was “*the most eminent of the ancient physicians and one of the greatest biologists history has ever known*” (Atkinson, 1964: 597). He also focused his studies in comparative anatomy by performing dissections in ungulates and in non-human primates, being his favorite subject the Barbarian Macaque (Singer, 1949; Ginn and Lorusso, 2008). He distinguished the primates which were “Dog-like”, the baboons, from those which had a human form, the macaques. Among the latest he differentiated those who had tails from those who didn't (Singer, 1949).

Centuries later, in 1641, Nicolaes Tulp, a Dutch surgeon was the first western person to draw and describe a human-like-animal in his “Book of Monsters” (Goldwyn, 1961; Corbey, 2005). Years later, in 1738, the name chimpanzee was used to denominate this human-like-animal “*A most surprising creature is brought over... that was taken in a wood in Guinea. She is female of the creature which Angolans call chimpanzee or the mockman*” (London Magazine, 1738: 465 in Goodall, 1986:6).

In 1749, a French naturalist, de Buffon referred to African and Southeast-Asian apes, as creatures “*which does not speak, nor think, nevertheless has a body, members, senses, a brain and a tongue entirely similar to those of man, for it can initiate or imitate all human behaviours, and... yet it never really performs any action of man*” (de Buffon, 1749: 61 in Corbey, 2005:7).

In the following two centuries chimpanzees were acquired by various zoological gardens in Europe and by some noblemen as pets (Goodall, 1986; Corbey, 2005).

Despite of Aristotle being the first scientist giving attention to non-human primates, his focus was mainly directed to the anatomical and physiological aspects of them. One of his great weaknesses was to mention that the brain was devoid of any sensation and was as a secondary organ, less important than the heart, considered the main organ (Atkison, 1964; Gross, 1997). For centuries, other following scientists also neglected the cognitive capacities of those that would be known, later, as our closest living relatives (Tomasello and Call, 1997).

1.2. Background on chimpanzee cognition and behaviour: from the laboratory to the wild

Primate cognition studies were born with Charles Darwin: "*Origin of man now proved. Metaphysic must flourish. He, who understands baboon, would do more towards metaphysics than Locke.*" (Darwin, 1838 in Tomasello and Call, 1997:3). After the publication of Darwin's Natural Selection and Evolution Theories, the interest for animal's behaviour and cognition bloomed (Tomasello and Call, 1997; Goodall, 1986).

In the last decade of the XIX century, R. L. Garner went to the West African Jungle, where he observed chimpanzees' wild behaviour for the first time. Six years later, Victor Meunier, a Frenchman, recognized the ease of taming non-human primates, and decided to domesticate monkeys and apes, in order to use them as servers (Goodall, 1986).

In the early XIX century, the primate cognition started to develop with the pioneer works of the scientists Wolfgang Köhler and Robert M. Yerkes. Wolfgang Köhler was a German psychologist who focused his study in apes' intelligence, during four years (1913-1917). Most of his experiments consisted in trying to understand the chimpanzee intelligence, going beyond the blind trial and error learning, by presenting them with problems to solve, and food as a reward. On the other side of the Atlantic Ocean, Robert M. Yerkes, an American psychologist, was also developing his studies on great apes' cognition. He shared much of Köhler's research interest, and besides performing captive experiments, he intended to expand his research to wild animals (Tomasello and Call, 1997).

In 1930, Henry Nissen, a Yerks' student and collaborator, went to French Guinea. Taking together the results from wild and experimental settings in captivity,

both pioneer researchers concluded that chimpanzee showed an “intelligent behaviour” (see: Goodall, 1986).

After the mid-twentieth century, the number of chimpanzee field study sites increased exponentially: A. Kortland, H. Albrecht and J. Koman in Guinea (1968-1969) and in Bossou, Sugiyama and collaborators (1976- ongoing); J. Goodall and collaborators in Tanzania, Gombe National Park (1960-ongoing); Y. Sugiyama and A. Suzuki in Uganda, Budongo Forest (1966); W. McGrew in Senegal, Nikiolo Koba National Park (1976-1979); C. Boesch and H. Boesch in Ivory Coast, Thäi Forest (1979-ongoing); J. Itani and T. Nishida, in Tanzania, Mahale Mountains (1966-ongoing), and etc... (see: Goodall, 1986; Matsuzawa, 2003; Stumpf, 2007; W.C. McGrew 2010, for an updated view on current chimpanzee field sites).

Regarding the cognition area, some experiments with chimpanzees elapsed in the sequence of Köhler's and Yerkes' work, in 1947. Examples are the well-known works of the couple Keith and Cathy Hayes in 1950's (see: Goodall, 1986), and later Gardner and Gardner (1969) that focused on teaching human language to chimpanzees. One chimpanzee was taught to pronounce some words, in which she could only learn how to “speak” (in a very imperceptible way) “papa”, “mama”, “cup”, and “up”. The latest study had more success; the human reared chimpanzee learnt more than 30 signs of American Sign Language (ASL) and used them spontaneously and appropriately at the end of the 22th month (Gardner and Gardner, 1969). This project was very important and caused widespread interest in chimpanzee cognition (Goodall, 1986).

Other relevant works regarding cognition were developed by Ann and David Premack, who design for the first time an “artificial language” with symbols. They tested a young chimpanzee that showed she could read and write vocabulary of about 130 words and claimed her understanding include also the concepts of class and sentence structure (Premack and Premack, 1972). Following the previous works, Duane Rumbaugh and his team, at the Yerkes Regional Primate Research Center, developed a computer-controlled situation, called “Lana Project”, for training language capacities using an infant chimpanzee able to perceive, organize and complete lexigrams, in order to get a reward (Rumbaugh *et al.*, 1973).

Nowadays, chimpanzees' studies include researchers spread all over the world , being the main institutions located in the USA, for example, The Yerkes Regional Primate Work Center and National Primate Research Center in Wisconsin, University of Madison; in Europe, with the Max Plank Institute for Evolutionary Anthropology:

Asia, Primate Research Institute, Kyoto University and Yunnan National Laboratory, Primate Center of China, and many others (see for a review of primate centers, labs and research programs: <http://pin.primate.wisc.edu/idp/idp/org/cen>, accessed in 25-06-2012).

1.3. Primatology in Japan

It is important to mention the historical background of primate research in Japan, the country where this study was conducted. Japan gave and has been giving a great contribution for the primatology, as we know it today. Unlike other developed countries, it has its own endemic primate species, the Japanese macaque (*Macaca fuscata*), therefore primates have been part of Japan's culture since very ancient times (Matsuzawa, 2003).

Japanese researchers were the pioneers of non-human primate's field work with the study of Japanese macaques. However, the fact that their publications were initially published in Japanese, made it difficult to spread their knowledge (Matsuzawa, 2008).

The study of primates' behaviour in Japan started in the middle of the XX century, after the Second World Wide war, with the pioneer work of Kinji Imanishi (1902-1992) on Japanese Macaques, and posteriorly with two of his students, Itani and Nishida (Matsuzawa and McGrew, 2008; de Waal, 2011). They started socio-ecological studies and developed an original method that consisted in a 1) long term observation, 2) feeding animals to accelerate the process of habituation, 3) assigning to each individuals names instead of numbers (Matsuzawa, 2008).

The contemporary scientists, Syunzo Kawamura (1956) and Masao Kawai (1965), developed studies in Japanese macaques focusing on the propagation and acquirement of sweet potato washing pre-cultural behaviour. By describing the first cultural behaviour in non-human primates, their observations changed the perception of culture, once thought to be unique to humans. Besides cultural behaviour, Japanese researchers were the first to document the existence of ranked, matrilineal kin groups in the society of Japanese Macaques. After their work, similar studies were expanded to other primate and non-primate species (Matsuzawa, 2008).

In 1966, Itani and Nishida established a field study site in the Mahale Mountains, Tanzania (Goodall, 1986; de Waal, 2011). The work developed by Nishida was very important. He has documented the importance of power struggles for male dominance in chimpanzees, through his studies of male social relationships (Nishida,

1983) and the use of *Aspilia* spp leaves as medicinal plants for the first time in wild chimpanzees (Wrangham and Nishida, 1983).

In 60's and 70's, other contemporary Japanese researcher, Y. Sugiyama described for the first time infanticide behaviour in a population of Hanuman langurs (*Semnopithecus entellus*; Sugiyama, 1965). Eleven years later, he started a long term-research of chimpanzees in Bossou and published many papers about social behaviours among the Bossou population and population dynamics (Sugiyama, 1981, Sugiyama, 1988) detailed descriptions of the tool use behaviour (Sugiyama and Koman, 1979, Sugiyama, 1995), etc.

He was the only primatologist carrying out field research in Bossou from 1976 to 1985, when Matsuzawa joined him in 1986. One year later the team was established with the third researcher, Osamu Sakura. Gen Yamakoshi and Tatyana Humle, the first foreigner, were the next researchers entering in the team in 1994, 1995 respectively. Until today, more than 50 researchers from all over the world had conducted their works in Bossou (Sugiyama and Fujita, 2011; Matsuzawa, 2003). In the beginning of the XXI century a new research field site started also in Guinea, close Nimba Mountains, 6 Km away from Bossou (Matsuzawa, 2003; Koops, 2011).

Nowadays, the research in Bossou and Nimba continues and is directed by Professor Matsuzawa, and his non-international and international team of collaborators, who also developed parallel laboratory studies on cognition and behaviour. These two strands, captive and wild studies, belong to the so-called "Ai Project", that became known worldwide and is ongoing for more than 30 years (Matsuzawa, 2003).

The focus of "Ai Project" is on the comparative research of humans and chimpanzees (subjects in similar tasks) by the application of psychophysics' methods (Matsuzawa, 1985, 2006, 2009). It focuses mainly on understanding the mechanisms of acquisition of the knowledge and skills, and how they are transferred to the next generations (Matsuzawa, 2008). This project was the precursor of a new research paradigm called "Comparative Cognitive Science", combining psychophysics and ape-language, by using computer-controlled apparatus, comparing perception, memory, and cognition in humans with chimpanzees, their closest relatives (Matsuzawa, 2009).

The current studies concerning this thesis are conducted on the behalf of Ai's project. Recently experiments using a touch panel computer started to be performed in a social context (Martin *et al.*, 2011) and our goal was to expand it regarding different topics.

1.4. Chimpanzee: General considerations

“*Pan* - spirit of the nature rural god of Greek mythology; so chimpanzee genus was named. And the species and races were labeled in kind troglodytes dwellers in dark caves...” (Goodall, 1986: 5).

Before focusing this introduction on important aspects of cognition, related to the current study, it seems relevant to mention some general aspects of chimpanzees' behaviour, ecology and phylogeny, that may be useful to understand the development and value of their cognitive skills and what makes this species so important in the scope of human evolution.

About 60 Ma ago, the primate lineage emerged as a distinct order of mammals (Klein, 2009), evolving from an insectivore ancestor which resembles more the current prosimians than the monkeys or apes (Fleagle, 1999). However, it was only around 6 million years that human and chimpanzee lineages split (Sibley and Alhquist, 1984, Chen and Li, 2001, Cheng *et al.*, 2005, Patterson *et al.* 2006), which makes the chimpanzee (*Pan troglodytes* spp.) and the bonobo (*Pan paniscus*) our closest living relatives (Goodman *et al.*, 1990; Won and Hey, 2005). These two great apes species are grouped in the same subtribe than humans: Hominina (Goodman, 1990) and they share 98.7% of their non-repetitive DNA (Fujiyama *et al.*, 2002). According to Goodman (1990) the genetic resemblance and the marked phenotypic changes between chimpanzees and humans, has to do with incongruence between the two levels of evolution: morphological evolution appears to have speeded up in higher primates, with more emphasis in humans' lineage, while molecular evolution has slowed down.

Currently, through molecular data analyses four subspecies are recognized: *Pan troglodytes vellerosus* (or *P. t. ellioti* according to Oates *et al.*, 2008), *P. t. verus* in Western Africa, *P. t. schweinfurthii* in Eastern Africa and *P. t. troglodytes* in Eastern and in Central Africa (Gonder *et al.*, 1997; 2006; Bjork, 2011). Nevertheless, there is still some controversy, Fisher *et al.* (2006) defend that the differences among the four subspecies are too small to warrant the four subdivisions.

Chimpanzees inhabit only the African continent, occupying from the tropical forest to the woodland savannahs (Suzuki, 1969; Chapman and Wrangham, 1993). They can be found in several African countries, such as: Cameroon, Congo, Ivory Coast, Democratic Republic of Congo, Gabon, Guinea, Guinea Bissau, Nigeria, Rwanda, Tanzania, Uganda etc (see Nishida *et al.*, 2011 for an updated review). They have a

large home range, being the male's range larger than females' (Goodall, 1986; Chapman and Wrangham, 1993; Newton-Fisher, 2003).

Chimpanzee, as verified in most of the primate species, is a very sociable species, living in a hierarchical society (Goodall, 1986; Nishida and Hosaka, 1996; Wittig and Boesch, 2003) composed by multi-male, multi-female groups, ranging from 20 to 150 individuals (Goodall 1986; Nishida 1990; Watts 1998; Boesch and Boesch-Achermann, 2000). Males are more gregarious, the bonds established among them are stronger and long lasting compared to female-female bonds (Symington, 1990; Mitani *et al.*, 2002). This seems to make sense, since in the chimpanzee communities males are the philopatric individuals, while females are the one who emigrate from their natal communities to others, at adolescence, between 9 and 14 years old (Goodall, 1986; Symington, 1988; Nishida *et al.* 2003). Females experience the first estrus around the time they leave the group; however around the period they emigrate to other communities there are evidences of infertile periods (Goodall, 1986; Nishida, 2003).

The hierarchy in males is mostly linear across different communities (Muehlenbein *et al.*, 2004, Watts, 1998; and Boesch and Boesch-Achermann, 2000, but see: Goodall), meanwhile regarding females the hierarchy seem to be presented in different structures (Nishida, 1989; Pussey, 1997). A more recent study reported a linear hierarchy among females in a situation of contest competition (Wittig and Boesch, 2003).

Chimpanzees have been described to live fission-fusion societies (Goodall, 1986; Symington, 1990; Boesch, 1996). This strategic behaviour have been described along the chimpanzee communities: they tend to associate in temporary parties that vary in size and composition (Goodall, 1986; Symington, 1990; Chapman *et al.*, 1994; Lehman and Boesch, 2004, Chapman *et al.*, 1995; Doran, 1997; Matsumoto-Oda *et al.*, 1998; Sakura, 1994; Wrangham *et al.*, 1992) to forage around different places (Symington, 1990; Lehman and Boesch, 2004). This flexible party size of chimpanzees is thought to be an adaptation to reduce the competition for food among the community (Symington, 1990). Party sizes can vary from 4 to 10 individuals on average (Sakura, 1994; Chapman *et al.*, 1995; Boesch, 1996; Wrangham, 2000; Mitani *et al.*, 2002) and their size number can be affected mainly by the abundance and distribution of the fruits, presence of predators and differences in the sex ratio as well the number of infants and estrous female (Goodall, 1986; Anderson *et al.*, 2002).

Chimpanzees are recognized as a species with high diverse behavioural patterns, part of them, also defined, as different cultures, by some authors (McGrew and Tutin, 1978, McGrew, 1992; Wrangham *et al.*, 1994; 1996; Whiten *et al.*, 1999; Boesch and Tomasello, 1999; Nishida *et al.*, 2009; Langergraber *et al.*, 2010). These different behavioural patterns described for the chimpanzee populations included use of tools (each population of chimpanzee has been describe to use its own unique tool kit (McGrew, 1998)), grooming techniques, courtship behaviours, and seem to be common in some communities, and completely absent in others (see: Whiten *et al.*, 1999). The differences among cultures cannot be supported entirely by ecological constraints. In some places that are known to have similar ecological conditions (e.g. same stones), do not always allow the development of certain behaviour (e.g. nut cracking; McGrew *et al.*, 1997; van Schaik *et al.*, 1999; Whiten *et al.*, 1999). Cultural transmission is the underlying aspect of the behaviour diversity and it's known as another way to acquire behaviour, besides through individual learning or genetic transmission (Wrangham *et al.*, 1996).

Chimpanzees, as all primates in general, have a long lifespan (Charnov and Berrigan, 1993). Individuals can live in the wild up to 50 years (see: Hill *et al.*, 2001). Female chimpanzees have a higher lifespan when compared to males. One explanation for males' case is due to higher mortality that males experienced through their lifespan (Hill *et al.*, 2001). Mortality can be cause by injuries they suffer while they compete for females (Allman, 1998), although, data shows that males are in a disadvantageous situation since they are born. Life expectancy is 3 times higher in females (Hill *et al.*, 2001). In the case of Bossou population the life span of females can be explain by the low rate of female competition due to lack female immigration (Sugiyama and Fujita, 2011). Also in Gombe the rates of transfer are lower than in Mahale (Nishida, 2003). Another reasons taking into account to explain the low transfer in Gombe, are the small number of individuals and the isolation of the community (Goodall, 1986; Nishida, 2003) and the presence of human cultures in the area (Sugiyama and Fujita, 2011). Females may benefit more by staying in the community then emigrating to neighbour groups (Nishida *et al.*, 2003). There is some evidence of the cessation of giving birth and sexual swelling in females at a later age suggesting the existence of menopause in this species (Nishida *et al.*, 2003; Sugiyama and Fujita, 2011). Although, Emery Thompson (2007), by reviewing all long term data, concluded that there is no solid evidences to claim that menopause is typical of chimpanzee life history.

Chimpanzees and all great apes, have a slower life history compared to other non-human primates and a longer immature phase in which they have to learn about their physical and social environment, in order to survive and produce offspring. Since an early stage of their ontogeny, they are learning about how to survive in their own environment, where, they have to be able of locating food, identify conspecifics, and avoid predators (Tomasello and Call, 1997).

1.5.Chimpanzee cognition

1.5.1. Chimpanzee physical cognition

For many animal species the most challenging problem relates to successfully foraging (Wrangham, 1994). According to Tomasello and Call (1997), primate foraging can be divided into three cognitive problems:

- 1) First of all they need to find food;
- 2) They have to obtain or process the food;
- 3) Finally they have to identify, categorize and quantify the amount of food available.

Following these three important steps to obtain food, in this topic, I will revise and describe the more important and latest cognitive experiments regarding physical cognition in chimpanzees, complemented by examples of the behaviour in the wild. Following the previous order: (1) “first of all they need to find food”, experiments on spatial mapping will be described, (2) “then they have to obtain or process the food”, for that, tool use behaviour will be describe and (3) “finally they have to identify, categorize and quantify the amount of food”, studies regarding categorization, quantities and numerical experiments will be revised.

For primates that feed mainly on sparse vegetable foods (fruits or leaves) in a very complex environment, their main problem is related to remember the exact location of the food resource (Milton, 1981). As chimpanzees have large home ranges, and as they travel in smaller groups in order to forage food, it is expected that they would form cognitive maps, in order to find resources and cognitive strategies to extract and manipulate them (Tomasello and Call, 1997). Because they also travel selectively to some sites, they should be able to remember the exact location of the desired items in their habitat, based on their previous experience. If chimpanzees know where they are in

the environment, they will have the ability to travel towards the desired places by using new routes (i.e. shortcuts) in order to minimize travel distances (Tomasello and Call, 1997).

Early captive experiments by Menzel (1973) showed that chimpanzees have spatial memory organization, since they can remember the places where the food was hidden if they have previously seen it. This experiment was run in captivity, at a small scale. Bennett (1996) mentioned that his data was not conclusive on proving that chimpanzees possess cognitive maps. They could have used landmarks to reach the food, as mentioned by the the author. However, studies in wild chimpanzees demonstrate that chimpanzees show excellent mental maps of their home ranges and know exactly where they are going. They are aware of the distance they have to walk and the exact location of resources, so they can visit the place repeatedly using different paths (Normand and Boesch, 2009; Normand, 2009). According to Normand and Boesch (2009) chimpanzees seem to use Euclidean maps, the most efficient and flexible mechanism to forage, instead of using only just landmarks as a clue. Normand, 2009 pointed out that their results suggest that the spatial memory in the wild chimpanzees in T ai Forest was many times greater than what was demonstrated with the previous captive works. According to him in captive studies it is difficult to know if such abilities are required, given the constraints of the captive environment.

Other evidence of an evolved mental map was previously described by Boesch and Boesch (1994). Wild chimpanzees incorporate the weight of the hammer in their choice and combine it with the transport distance, even though they can only see either the stone or the tree at the same time. This requires the following mental operations: 1) measurement and conservation of distance: they have a system of distance measurement between two objects, 2) comparisons of several distances, and relate them to the ultimate goal to find the shortest one 3) the permutation of objects in this map, the stones transported are placed in their mental maps with reference 4) permutation of the point of reference, the distances associating a stone with one can be exchange by a set relating the same stones to another tree (See: Boesch and Boesch, 1984).

Another example of the chimpanzee high cognitive skills is given by the evidence of tool use both in captive (Tonooka *et al.*, 1997, Celli *et al.*, 2004) and wild conditions, such as, for nut cracking (Sugiyama and Koman 1979; Boesch and Boesch, 1991, Matsuzawa, 1994), ant-dipping (McGrew, 1974; Boesch and Boesch, 1990; Humle and Matsuzawa, 1992), drinking water (Tonooka, 2001; Sousa *et al.*, 2009) or

hygienic of agonistic behaviours (Goodall, 1986, Boesch and Boesch, 1990). Other evidence of tool use in wild was described by Pruetz and Bertolani (2007), in which chimpanzees were reported capturing bush-babies using tools.

If chimpanzees are able to understand the causality of using tools, it is a difficult concept to understand and there is much disagreement on this subject (Tomasello, 1997). Causality requires the animal to understand the association of three events: space, time and also the mediating force that binds the early two (Visalberghi and Tomasello, 1998). Some studies indicate that individuals understand not only the association between two objects that visually interact, but also, they predict and understand the relation between the objects and the final goal (Visalberghi *et al.*, 1995; see also: Tomasello and Call, 1997).

Relatively to ant dipping and honey fishing tool behaviour, chimpanzees show an understanding about the properties of the tools by choosing specific tool for different tasks (Bermejo and Illera, 1999; Boesch *et al.*, 2009). Also, with regard to nut cracking behaviour, chimpanzees combine certain hammers with anvils, in order to perform a specific task, and they show the most complex tool for nut cracking, composed of four stones (Carvalho *et al.*, 2008).

To discriminate and categorize objects are also useful skills in the context of foraging and social behaviours (Tomasello and Call, 1997). Captive studies regarding this matter point out that, chimpanzees can also categorize and group different, but related, exemplars in the same category; once they receive they are trained (Fujita and Matsuzawa, 1986, Tanaka, 2001). The results might suggest that chimpanzees are capable of doing an abstract representation of the categories (Tanaka, 2001). In the wild they also seem to choose selectively the type of fruits they want to eat, based on their color, degree of softness and odor and the location of numerous tree fruits (Goodall, 1986).

To forage efficiently, besides locating the resource, manipulating and identifying the food, chimpanzees should be able to estimate the amount of food quantities, or in other cases, as fights, estimate the number of potential opponents (Tomasello and Call, 1997). Captive chimpanzees show skills to solve challenges involving conservation of discrete (e.g. solid food) and continue quantities (e.g. liquids). They seem to select the larger quantity of cereals above chance levels and their performance was better in experiments using liquid conservation (continuous; Suda and Call, 2004; 2005). Muncer (1983) have previously tested the capacity of understanding changes in quantity in

different shaped recipients. In the same study she also seems to discriminate the addition and subtraction of M&M's in two rows.

Many studies regarding numeral tasks have been developed in captivity (e.g. Matsuzawa, 1985, 2009; Biro and Matsuzawa, 1999; 2001; Inoue and Matsuzawa, 2007; 2009). Chimpanzees not only seem to be able to indicate the right numeric sequence (Tomonaga and Matsuzawa, 2000; 2002; Biro and Matsuzawa, 2001) but also show an amazing performance in memorizing numeric sequences, even better than humans (Kawai and Matsuzawa, 2000; Inoue and Matsuzawa, 2007, but see: Silberberg and Kearns, 2009). Young chimpanzees show a higher performance than the older ones, in memory tasks with numerals (Inoue and Matsuzawa, 2007). Besides objects and colours, chimpanzees were capable of labelling (with more than seven numerals), a set of dots displayed in different patterns (Murofushi, 1997). Gomes *et al* (2009) showed that wild chimpanzees are able to remember at least during one week about relationships on a long-term basis.

1.5.2. Chimpanzee social cognition

Not only ecological constraints seem to shape their cognitive capacities. Living in large groups (See next topic), especially in hierarchical systems also requires high cognitive skills. To succeed in the social domain, strategic intelligence is required (Tomasello and Call, 1997). Although, the size of the brain seems to be correlated to the size of the group: Larger groups have with larger brains (see: Dunbar, 2003).

Unlike the fruits on the tree, living preys or social partners react to others' behaviours and behave spontaneously. Animals that can predict conspecifics' behaviour quickly and efficiently and, particularly, in novel situations, are more likely to show higher skills compared to animals that don't (Call, 2001).

The acquisition of tool behaviour, for example, to obtain food depends essentially on learning processes that are prominent during the individual's infancy (van Schaik and Pradhan, 2003), period in which, the infant spends most time with his/her mother (horizontal transmission: Biro *et al.*, 2003; Lonsdorf, 2006). Wild observations concluded that chimpanzee's mothers may influence infant's nut cracking behaviour by stimulating, facilitating the younger (Boesch and Boesch, 1990). Boesch and Boesch (1990) reported one of active teaching by a mother towards her offspring. Hence, they concluded, based on their anecdotal observation, that mothers seem to show the

capacities to anticipate offspring's actions, and to compare their actions with the idea of how the behaviour should be performed. During the period that young chimpanzees remain close to their mother, once they reach the social and motor maturity, they start to play and practice by observing their mothers, and other conspecifics using tools (Boesch and Boesch, 1991; Tomasello, 1994, Biro *et al.*, 2003, Hirata and Celli, 2003). At a later stage, the infant may emulate the mother's behaviour, without understanding the final goal of the tool behaviour (Biro *et al.*, 2003). Vertical transmission seems also to play an important role in shaping younger's behaviour (Matsuzawa *et al.*, 2001; Hirata and Celli, 2003). The mechanisms and processes involved in the transmission of tool behaviour are yet not fully understood (Tomasello, 1994; van Schaik *et al.*, 1999) and how chimpanzees acquire social learning has been debated and tested (Call *et al.*, 2005).

A study conducted by Whiten *et al.* (2005) wanted examine how the tool use behaviour was transmitted in a group of captive chimpanzees. They trained high-ranking females to use different tool use technique and reintroduce them later in the group. Almost all the chimpanzees living in the group females were reintroduced mastered the new technique. The individuals in other groups, where females were not introduced, did not show the technique. Also Tonooka *et al.* (1997) reported the transmission of tool use behaviour within a group of chimpanzees. Two females chimpanzee started to use one type of tool to perform the task, a more efficient one, other individuals started to use the same technique, despite of having other options.

The main factors favoring the transmission of tool use behaviour are tolerance and a certain level of gregariousness, that might allow individuals to acquire the behaviour by emulation or/and imitation (van Schaik *et al.*, 1999). In wild it seems difficult to understand which mechanisms underlie the social transmission of certain behaviour. Captive studies have been conducted in order to understand if the learning processes are acquired through emulation or imitation (Visalberghi and Fragaszy, 2002; McGrew, 2004). Some experimental studies reveal that chimpanzees show insights of emulation rather than imitation, (Tomasello, 1996; Horner and Whiten, 2005; Tennie *et al.*, 2005; 2010). However, chimpanzees that were human reared are more likely to show higher degree of imitation (Tomasello *et al.*, 1993). They show some evidence of imitation arbitrary actions after an initial phase of tuition (Custance *et al.*, 1995) and they can imitate a sequential structure of actions used by the demonstrator to perform tasks related to foraging (Whiten *et al.* 1996; 2009; Whiten 1998). Imitation involves more complex understanding about the not only the ultimate goal but the authors

intention (Boesch and Tomasello 1998). An important procedure to perform imitation is to understand other individual's goals. Taking that in account, this behaviour shows the same meta-representational basis than theory of mind (Whiten, 1996).

Before assessing the topic on understanding the behaviour of other individuals, it is important to understand if chimpanzees have self-concept. To approach this topic, Gallup (1970) pioneered the experiments using a mirror to see if chimpanzees have self-recognition. In the presence of a mirror, chimpanzees tested started to direct the behaviour towards them: like grooming some parts of the body that were not visible in other circumstances, picking pieces of food from between the teeth. He also marked the subjects after anesthetized them with red colour in the upper part of the eye brow. The rate of self-directed behaviour was much higher in this condition (with the eye brow marked) compared to phase before the test and compared to control animals. He argued that, if individuals can recognize themselves on the mirror, means they are aware of their own mental states, implying they are aware of mental states of other individuals (Gallup, 1982).

The topics addressing the meta-representational domain in non-human animals always generate a lot of controversy among researchers. Theory of mind is another example (Heyes, 1998; Povinelli and Vonk, 2003, 2004; Call and Tomasello, 2008). First discussed by Premack and Woodruff (1978) and, 30 years later, Call and Tomasello (2008), reviewing the main literature about the topic, affirmed that chimpanzees have a theory of mind although they do not understand others in terms of a "fully human-like belief-desire psychology". Some other authors claimed that there is no evidence that chimpanzees reason about mental states of other individuals, for example, what others see or not (Heyes, 1998; Povinelli and Vonk, 2003, 2004).

Another topic to address and strongly related to theory of mind, is the deceptive behaviour. It is necessary to understand others intentions, in order to behave in a deceptive way (Call, 2001). Menzel (1971, 1973) pioneered the use of competitive situations to investigate social tactics and deception. He found that captive young chimpanzees can suggest to other individuals of the group about the presence, direction, quality and relative quantity of hidden objects, even if they are not visible at the moment (Menzel, 1971; see also Woodruff and Premack, 1979, for intentional communication). In the following study he showed, subordinate chimpanzees learned to avoid hidden food in the presence of dominants (Menzel, 1973). However, it is still hard to tell if they act intentionally and if they understand the motivations and perceptions of

other individuals (Woodruff and Premack, 1979, de Wall, 1986). Later studies, replicating and improving Menzel's (1973), also reported that subordinate chimpanzees know what the dominant have seen or not seen in the immediate past, and use the information to develop an efficient social-cognitive strategy to reach the food, that was hidden from the dominant. The preference to reach the food decreased when the dominant had seen the food being hidden (Menzel, 1973, Hare *et al.* 2000, 2001; Call, 2001). The same happens if the competitor is a human (Hare *et al.*, 2006). Other study that reveal chimpanzees use deceptive tactics to avoid competitors and obtain food was conducted by Hirata and Matsuzawa (2001) where two chimpanzees were released in one outside enclosure after one has seen the food being hidden. Both of them were observed to using tactics to avoid the other to reach the food.

Nishida (1990) reported an event of deceptive behaviour performed by juvenile chimpanzee who wanted to be nursed by his mother and was rejected (instead the mother preferred to groom an adult male). The young chimpanzee produced gestures and vocalizations simulating an attack by other juvenile. According to Call (2001), this behaviour showed that the chimpanzee has insight into social problems, since he developed an intelligent strategy based on past experiences, applying this in a novel situation. Nishida (1996) described another example of deception by observing a male grooming a female, which had lost her offspring, and was keeping the dead body close to her. After a few minutes the female became distracted and the male stole the dead body. Nishida interpreted the behaviour, as the male wanted to groom the female so that she became more distracted and he could steal the dead body from her.

Regarding communication, studies reveal that chimpanzees use visual gestures when other conspecifics are looking to at them, they use are able to use same gestures in different contexts, and different gestures in the same context (Tomasello *et al.*, 1994). They follow the direction of the head from humans and other conspecifics, when they look to a certain object, as well as, they are able to follow the gaze direction independent of the direction of the head, even when the target is not immediately visible to them (behind or above; Itakura and Tanaka, 1998; Call *et al.*, 1998, Tomasello *et al.*, 1999; 2000; Bräuer *et al.*, 2005). In general, these experiments support that chimpanzees understand that others are looking at something specific in a particular location (Call *et al.*, 1998).

Hare and Tomasello, (2004) found out that chimpanzees are more skillful to perform cognitive tasks in which they have to compete with the conspecifics, compared

to the tasks in which they have to collaborate. They achieved better results when the experimenter was competing than when he was collaborating with the chimpanzees. However, recent studies on cooperative and prosocial behaviour showed that chimpanzees act aiming to help the conspecific (Hirata and Fuwa, 2007; Warnecken *et al.*, 2007; Melis *et al.*, 2008; 2011a, Yamamoto *et al.*, 2009; Horner *et al.*, 2011), although other studies failed in showing prosocial behaviour (Silk *et al.*, 2005; Vonk *et al.*, 2008). This topic will be further explored in the introduction of study 2.

On the other hand, economic decision making tasks showed that chimpanzees acted more according to their self-interest, instead of other's interest (Jensen *et al.*, 2007). Bräuer *et al.*, (2006) stated chimpanzees might not be deeply inequity averse. Since they did not reject the reward when the partner received a better one, they waited longer instead. Contrary to what was previously found in Brosnan *et al.* (2005) study: chimpanzees rejected the reward and refused to perform the task. Similar findings (to Brosnan and collaborators) were achieved for capuchin monkeys (Brosnan and de Waal, 2003, Wynne, 2004).

In wild, several of prosocial behaviours have been described. Chimpanzees are known to form coalitions and alliances among the group individuals (de Waal 1982; Nishida and Hosaka, 1996, Watts, 1998, Duffy *et al.*, 2007) with or without any kinship relation (Mitani *et al.*, 2000; Langergraber *et al.*, 2007). This behavioural strategy aims to protect the group from predators, or other chimpanzees' groups (Tomasello *et al.*, 2005).

Coalitions are also formed when chimpanzees want to build up a higher position in the rank (de Waal, 1982, Goodall, 1986). Lower ranking males also adopt some strategies to access copulation (de Waal, 1982; Goodall, 1986, Watts, 1998). They form two-male coalitions, in order to guard the mating and preventing her to copulate with others (Watts, 1998). Non-dominants are sometimes seen copulating with a female through transaction and out of the sight of the dominant male (de Waal, 1982). This kind of coalition also requires strategic tactics to achieve the main goal. However, according to Tomasello *et al.* (2005), in these interactions, the same thing is done by the each individual, without coordinating their plans and is less complex than hunting, for example. Chimpanzees are also known for capturing different kinds of small mammals, including primates, being the red colobus one of their favourite (Goodall, 1968, 1986; Nishida *et al.*, 1979; Stanford, 1994). In order to do so, strong cooperative strategies among the individuals are required for the hunting behaviour (Boesch and Boesch,

1989; Boesch, 1994; Watts and Mitani, 2002). Each male participant has to play a distinct role, coordinately and synchronized in space and time with the other members of the group to succeed in capturing the prey (Boesch and Boesch, 1989; Boesch, 1994; Watts and Mitani, 2002). After hunting the prey, male chimpanzees can share it with other individuals for social purposes, e.g. with a female in exchange for sex (Gomes and Boesch, 2009; Gilby, 2006, but see: Gilby *et al.*, 2010) or with other males to form male-male coalitions for agonistic confrontations (Mitani and Watts, 2000).

The introduction focuses mainly on chimpanzee's cognitive skills, since the current study aims to investigate aspects of chimpanzee social cognition. However, there is no intention of overestimating chimpanzee's skills, over all the other non-human animals. They are our closest living relatives, so we could expect that they should show higher cognitive skills. Nevertheless, it is important not to forget that some phylogenetically more distant animals may have evolved similar strategies to solve similar problems (convergent evolution; Emery and Clayton, 2004). Cognitive experiments have been also developed with other primates species (e.g., Chevalier-Skolnikoff *et al.*, 1982; Tomasello and Call, 1997, Albiach-Serrano *et al.*, 2010), some birds species (e.g., tool use in corvids: Emery and Clayton, 2004; Taylor *et al.*, 2007), marine mammals (e.g., self- recognition in dolphins: Reiss and Marino, 2001), or elephants (they seem to understand the emotions and predict the goals of others: Bates *et al.*, 2008). Those animals also have been showing to possess high cognitive skills, regarding the proposed experiments.

2. Goal of the studies

Chimpanzees are a great parsimonious model to study human behaviour, as they live in larger and hierarchized groups, as we humans do, and they are our closest living relatives, meaning, by looking deeply into their behaviour we can somehow understand our ancestors' behaviour and strategies used to evolve in a demanding and challenging environment. As we already know, life in groups holds many social challenges and at same time that can be beneficial for the individuals, costs can also be entailing, for example, intra-specific competition for food resources or females (Clutton-Brock and Harvey, 1978). On the other hand individuals seem to engage in many kinds of

prosocial behaviours that tend to benefit other conspecifics and somehow mitigate the effect of competition (e.g. food-sharing, Wrangham, 1980).

As I mentioned before, for more than 30 years, “Ai Project” has been developing studies in which chimpanzees are tested with regard to social and physical cognition mediated one touch panel monitor, in an individual context. Only recently, different paradigms to test chimpanzees in a social context were implemented, with the work of Martin *et al.* (2011). These experiments consisted in two chimpanzees interacting with each other via touch panel computers.

The current project also pretended to test chimpanzees in a social context, by involving more than one chimpanzee performing a computer touch panel task. It comprises two different topics regarding social cognition: competition and prosociality, involving food rewards as the ultimate outcome.

In study 1, we want to focus in a topic of intraspecific competition: contest competition, in a controlled environment, by using all the chimpanzees as subjects to compete for a shared food resource provided by a touch panel computer. We want to understand the role of the dominant and the subordinate individuals. Which one is more likely to approach and monopolized the task. Studies report the dominant of the group is the one monopolizing a resource in a scenario of contest competition (e.g. Wittig and Boesch, 2003). However in our study we have to take into account other factors, such as, experience on performing touch panel tasks. We hypothesize that the dominance is not the most important factor, given the conditions of our study and we created conditions to test it. This experiment was run in the chimpanzees’ outside enclosure (comprising a more complex environment, compared to the indoor booths), giving the opportunity to all the individuals, with different backgrounds, to participate.

Competition is not the only consequence of living in social groups (Murray *et al.*, 2007), social animals engage in many cooperative and altruistic behaviours, aiming to help one another (Hamilton, 1964; Trivers, 1971) for the benefit of their group (see: Hamilton, 1963). In order to examine closely their prosocial behaviour we conducted study 2. The aim of the study was to run a prosocial choice test (PCT) mediated by touch panel computer, using mother-offspring paired chimpanzees. Taking into account the poor results on prosociality using this paradigm (PCT), the goal was to understand if chimpanzees acted prosocially (shared the reward) towards the other conspecific when given a mean-spirited option (selfish: give reward only to him/her) and an altruistic

option (providing reward only for the conspecific). Prosociality was tested across three different conditions and how their behaviour was modulated given different scenarios.

Studies on prosociality or altruism help us to understand the evolution of altruistic behaviours in the human lineage. Humans are known to be a very altruistic species (Fehr and Gaechter, 2002), however our closest living relatives, chimpanzees, are a great potential to be the target of altruistic studies, taking into account many of their characteristics, previously revised.

3. Study 1

**Contest competition mediated by a touch
panel task: Social dynamics and spatial
distribution**

3.1.Introduction

Life in groups holds many positive aspects, such as, increasing the individuals' survival and their reproductive success (Wrangham, 1980; Boesch, 1996; Byrne and Bates, 2007). Individuals that live in large groups can benefit from greater protection from predators (higher vigilance and dilution of the risk, Byrnes and Bates, 2007; Alexander, 1974; Hamilton, 1971). Living in groups also allows improving the access to food resources (Clutton-Brock, 1974; van Schaik, 1983; Boesch and Boesch, 1989) and benefits individuals in terms of assistance of others in protecting and rearing their offspring (Wiley and Rabenold, 1984).

In the case of chimpanzees, they engage in very complex cooperative behaviours, such as hunting (Boesch, 1994; Boesch and Boesch, 1989) and patrolling (Watts and Mitani, 2001), and other types of male-male coalitions for agonistic confrontations (Mitani and Watts, 2000). Nevertheless, it also incurs costs with regard to parasites' transmission and intra-specific competition (Boesch, 1996; Byrne and Bates, 2007). An individual that lives in large groups has to compete for the same resources against their partners, which means that their reproductive success, food acquisition and spatial patterns are influenced by others' behaviour (Clutton-Brock and Harvey, 1978; Eisenberg, 1992).

Competition has been receiving prominent attention among biologists because "it forms the basis for the unifying, organizing principle of biology" (Muller and Mitani, 2005: 1). There are two main types of intraspecific competition for food resources and they depend on the distribution of the food and number of individuals in the group (Isbell, 1991).

If the distribution of the food is scattered and many individuals are able to obtain an equitable amount of food, they are dealing with a scramble competition. In this case, the food is non-monopolizable and this competition is typical to a non-linear hierarchy (Wittig and Boesch, 2003). When individuals are dealing with a monopolizable food resource which, instead of being scattered, is located in an area where only one individual can take over and monopolize it, they are facing a contest competition (See: Isbell, 1991).

In the wild, chimpanzees rarely fight over plant foods, but dominant individuals tend to occupy the prime feeding sites. Monopolizable food, such as meat, seems to increase the rate of contest competition (Goodall, 1986; Wittig and Boesch, 2003). However, in situations in which food can be monopolized by only one individual, the

conflict rate of the group does not seem to increase, as it happens when individuals compete for a non-monopolizable resource (Wittig and Boesch, 2003). When individuals engage in a competition for the same food resource or for a monopolizable area where the food resource is located, usually only one individual will be able to possess it. Dominants of the group are most likely to be the ones monopolizing the resources (Parish 1994; Pusey *et al.*, 1995; Wittig and Boesch, 2003; Murray *et al.*, 2007). In males, contest competition seems to be more important than in females, once they engage more frequently in this type of competition (Pusey *et al.*, 1997). Females of Thai Forest seem to be an exception, once they engage more in contest competition than females of other sites. Wittig and Boesch (2003) argue that this happens because they have more access to monopolizable resources: meat and tools. When the rates of the encounter with food are low, contest competition seems to be more severe (Sterck *et al.*, 1997). During this competitive strategy, animals that cannot gain access to the food and monopolize it have to travel to forage until they can find another food resource. This requires costs for them: more waste of energy and time (Goodall, 1986).

Studies regarding food provisioning in captive environments showed that agonistic conflicts between individuals did not happen frequently but seemed to increase compared to other scenarios. Aggressive behaviour might be a strategy adopted in order to defend and claim the food (de Waal, 1982).

In wild situations, when chimpanzees were provisioned with extra food, the aggregation rate increased, as well as the rates of aggressive interactions (Wrangham, 1974).

As it was mentioned before, chimpanzees live in a fission-fusion society and individuals split in small groups from the community in order to forage. As they travel through the forest they may face different types of resources, according to their distribution in the environment. They can face scramble or contest competition (Isbell, 1991).

The current study aims to create a controlled situation where a group of chimpanzees has to gain access to one shared food resource: contest competition. As in the wild chimpanzees have to solve many challenging problem in order to obtain the food (Tomasello and Call, 1997), hereby we pretend to substitute their ecological constraints regarding foraging, using a touch panel numerical task, where they have to use their skills, in order to solve the task and receive a reward, instead of freely provide food to the chimpanzees. For that purpose, a touch panel was set in the outdoor compound booth

(Tonooka *et al.*, 1997) located in the chimpanzees enclosure. Other two studies regarding tool use transmission and ecological factors that affect tool use behaviour were conducted in the same area (Tonooka *et al.*, 1997; Celli *et al.*, 2004).

The reason why we chose numerical touch panel tasks was because most of all the individuals were familiar with it. Several studies were previously conducted focusing on numerical tasks using a touch panel (Matsuzawa, 1985; Murofushi, 1997; Tomonaga and Matsuzawa, 2000; for a review, see: Biro and Matsuzawa, 2001). However, chimpanzees have been previously selected according to their past experience and participation in similar types of tasks. Experiments were run in indoor compounds devoid of social context and interactions.

Recently, with the work of Martin *et al.* (2011), touch panel tasks in social contexts were performed, in order to understand how chimpanzees use the information presented on the screen of the other conspecific.

In the current study, we want to test chimpanzees mediated by a touch panel computer, with a very simple task, allowing all the individuals to participate. This experiment was performed in a more complex social and physical environment, compared to the environment chimpanzees are used to.

Once chimpanzees live in a hierarchical society, we might expect the dominance status and rank (Drews, 1993) of the individuals to be a crucial factor influencing the monopolization of the task. We expected males to be the ones who have more access to food resources and the dominant male to monopolize more the task. However, besides dominance we have to take into account individuals' experience performing similar touch panel tasks. This factor, as well as the presence of certain individuals on the area, might also play an important role in accessing and performing the current task.

Which chimpanzees are more willing to perform the task and how others behave towards them, with especial attention for the agonistic conflicts and dispersion around the booth area, are the most important aspects we focused on.

3.2. Subjects

3.2.1. Chimpanzee's biography and background

Primate Research Institute, Kyoto University (KUPRI) houses two groups of chimpanzees. One group comprises 8 individuals: two males, Gon and Reo (the latter was separated from the group, due to rehabilitation programs), and 6 females, Puchi, Popo, the mother-offspring dyads Pan-Pal, and Chloe-Cleo. The other group, the one tested in the current study, is constituted by 6 individuals: two males, Akira and Ayumu, and 4 females, Reiko, Ai, Mari and Pendesa (figure 1 to 6).

Below we give a short introduction on the biography and background of all the individuals in Akira's group and housing conditions (see also table 1).

3.2.1.1. Males

Akira (36 years old)



Figure 1 – Akira, the dominant male. Photo taken from <http://www.pri.kyoto-u.ac.jp/ai/en/friends/index.html>, accessed on 24-07-12.

He is the dominant male of the group. He was born in 1976 in Africa and has arrived to KUPRI (Kyoto University Primate Research Institute) when he was 2 years old. He is the father of Ayumu and Pal (both by artificial insemination; Matsuzawa, 2006). Akira participated in many cognitive experiments (see: Matsuzawa,

2006) concerning tool use (Tonooka *et al.*, 1997) and also mediated by touch panel (Inoue and Matsuzawa, 2009)

Ayumu (11 years old)

Ayumu is an 11 years old juvenile male chimpanzee that was born in the Institute (Matsuzawa, 2006). He is Ai and Akira's infant, by artificial insemination (I. Adachi personal communication) who has been observing his mother



Figure 2 – Ayumu, juvenile male, son of Ai.
Photo taken by Renata Mendonça.

experiments since he was born (Matsuzawa, 2006). Ayumu has been showing higher accuracy in some cognitive tasks, such as temporary memorize numerals presented in a screen (Inoue and Matsuzawa, 2007; Matsuzawa, 2009). Recently, he started his struggle for the dominant male position, confronting Akira more.

3.2.1.2. High-ranking females

Ai (36 years old)



Figure 3 – Ai, the dominant female. Photo taken from <http://www.pri.kyoto-u.ac.jp/ai/en/friends/index.html>, accessed on 24-07-12.

Ai is a female chimpanzee that was born in Africa in 1976 (estimated birth-date) and brought to KUPRI in 1977 (Matsuzawa, 2006). She is Ayumu's mother with whom he is tested in different cognitive experiments, as a partner (Martin *et al.*, 2011) or just individually (Inoue and Matsuzawa, 2007). She gave the name to the "Ai project". Ai is the

best trained chimpanzee in KUPRI and the dominant female in the group. Ai was the first chimpanzee to be trained in cognitive controlled tasks, at age of 2 (Asano, 1982). She is being trained to perform cognitive tasks using Arabic numerals since she was 5, which she started by labeling the number of objects by pressing numbered keys (Matsuzawa 1985, Murofushi 1997).

Reiko (46 years old)

Reiko was the first chimpanzee arriving to KUPRI and she is the oldest female in Akira's group. She was born in 1966 (estimated age) in Africa and brought to the institute with 2 years old (Matsuzawa, 2006). She used to be the dominant female, and she is still one of the higher ranking females in the group. She has an infant called Reo, who is currently receiving rehabilitation programs due to a health problem.



Figure 4- Reiko, the other dominant female. Photo taken from <http://www.pri.kyoto-u.ac.jp/ai/en/friends/index.html>, accessed on 24-07-12.

3.2.1.3. Low-ranking females

Mari (36 years old)



Figure 5 - Mari, a low-ranking female. Photo taken from <http://www.pri.kyoto-u.ac.jp/ai/en/friends/index.html>, accessed on 24-07-12.

She is the other low-ranking female of the group. She was born also in Africa in the year of 1976 and brought to KUPRI in 1978 (Matsuzawa, 2006). Mari also participated in experiments, but her performance is also lower when compared to Ai (Tanaka, 2001).

She had also participated in many cognitive experiments (See: Matsuzawa, 2006). She has a good relationship with Ayumu (Keeper personal communication).

Pendesa (35 years old)



Figure 6 - Pendesa, a low-ranking female, Photo taken from <http://www.pri.kyoto-u.ac.jp/ai/en/friends/index.html>, accessed on 24-07-12

This female chimpanzee was born in 1977 in Japan Monkey Center and was brought to KUPRI with 2 years old. She is one of the lowest ranking females in the group, and the only hybrid in the group (*P. troglodytes verus* x *P. troglodytes troglodytes*).

Pendesa was also tested in some perceptual and cognitive tasks (e. g., Tomonaga, 1998; Sousa and Matsuzawa, 2001). She showed less accurate performance than Ai in matching-to-sample tasks, which she had begun to perform at the age of 21 (Matsuno *et al.*, 2003). She has a lesion in the brain that is reflected in her vision field (Kaneko, in prep).

Table 1 – Summary table with the information about the subjects regarding their biography and experience in the tasks: using touch panel computer and performing experiences in the outdoor compound.

Group	Name	Sex	Birth date	Rank	Experience using touch panel Touching screen	Experience in outdoor compound	
						Tool use ²	Tool use ³
Akira's group	Akira	M	76/06/--	H	Yes	Yes	Yes
	Ayumu	M	00/04/24	H ³	Yes	No	No
	Ai	F	76/10/--	H	Yes	No	No
	Reiko	F	66/12/--	H	No	Yes	Yes
	Mari	F	76/06/--	L	Yes	No	Yes
	Pendesa	F	77/02/02	L	Yes	Yes	Yes

¹Tonooka *et al.*, 1997

²Celli *et al.*, 2004

³ He is among the dominants, however he is lower ranking than Akira.

3.3. Material and Methods

3.3.1. Housing and apparatus

The experiment was carried out in the chimpanzee outdoor enclosure at the Primate Research Institute, Kyoto University (KUPRI), where two other previous studies, focused on tool use behaviour, have been conducted in the past (Tonooka *et al.*, 1997; Celli *et al.*, 2004). This enclosure houses two groups of chimpanzees, Gon's group and Akira's group, in alternative days from 10 am to 5 pm. After 5 pm they remain indoors, in smaller compounds with 8 interconnect walled rooms. Chimpanzees enter and leave the outside enclosure using small corridors on the ceiling.

Chimpanzees are fed three times per day (9am, 2 pm, 4pm) with a variety of fruits, vegetables and chow, and freely available water (Celli *et al.*, 2004).

The outdoor enclosure comprises an area of 770 m² and is enriched with artificial streams containing fishes and more than 400 species of plants, ropes and climbing structures with 15 m high (Celli *et al.*, 2004).

An experimental booth with an octagonal shape delimited by walls made of acrylic panels is located inside the enclosure connected to the main building by an underground tunnel. One 17-inch monitor with touch-sensitive screen (Microtouch SMT2) was embedded outwards in one of the booth faces, so after approaching to it, chimpanzees could easily initiate the task by touching the screen. The screen was protected with a metal panel that was only removed when the experiment started.

To provide reward for the individuals, inside the booth, one food tray with 40 spaces for the food was *set along* with its respective universal feeder (Bio Media Co. Ltd.) in front of each touch panel monitor. The reward consisted of 1 piece of apple (1cm x 1cm x 1cm) for each trial.

In this experiment chimpanzees were not invited indoors to perform the task, as usually happens. Researchers were the ones entering in the chimpanzee area, in order to run the experiment.

3.3.2. Stimuli

To initiate the task, a circular button was presented in the bottom of the screen as stimuli. Once the button had been touched by an individual, the number one appeared in the screen, randomly distributed in the screen matrix across the trials. A task presenting

only the number one was chosen to allow all the individuals to perform it, or in case they didn't know, to learn it. The number of the task sessions per day varied and each session was divided in 48 trials. As long as the session lasted, we kept running the task. After performing the task by touching the number one, a reward was delivered. There was not an incorrect answer in these trials.

3.3.3. Procedure

The experiment consisted in 17 sessions for Akira's group: 4 control sessions + 13 experimental sessions. Experimental sessions had an average duration of 52 min (+/- 10min 18 sec), with the total time of 11h42 min (N=13). Time started to count as the session began, after starting to run the program and removing the metal panel in the front of the screen.

The control experiments conducted had an exact duration of 1h each. Control was performed to ascertain the effects of the apparatus on chimpanzee's behaviour. In this phase, the same conditions were kept, although the experiment did not run (and the touch panel remained protected).

Sessions were conducted around 1.30 pm, during the months of November – December 2011 and March to June, 2012. To avoid the coldest months, the experiment was not conducted in January and February.

3.3.4. Social behaviour: Sampling methods

The observational methodology was divided in two phases. During the course of the experiment we accessed individual's behavior by using a combination of ethological methods to observe the behaviour, followed by *a posteriori* analysis of sessions that were video recorded.

Both for the control and experimental phases, the study of social behaviours, among the individuals, was recorded using a combination between focal and *ad libitum* sampling (see: Martin and Bateson, 1993). Focal sampling was used to record all the occurrences of a specified behaviour (See ethogram in the appendix) of an individual, or groups of individuals, during each sampling period. In this study, the sample period was defined as the time an individual spent performing the task. The sample period of the focal animal ends once he/she leaves the task and another individual replaces it, being the new focal

animal. With this record we obtain not only the behaviours of focal subjects, but also the behaviours directed to them by other individuals (Martin and Bateson, 1993).

Ad libitum sampling was used to record the behaviour of other individuals around the booth (< 5 m): the actor, the behaviour, the receptor, actor's location in the area (see the topic below) and the duration of the behaviour.

In the experimental phases, we record the changes of the group's behaviour, noting the entry/exit of a chimpanzee that comes/leaves from/to the inside experiments.

In order to assure the reliability of the observation, 3 cameras (Sony HDR-CX560) were used to digitally record the sessions. One camera was placed above the monitor, recording all the events happening immediately in front of it, other was placed outside the enclosure, on the first floor, covering 50% of area around the booth perimeter, and the third camera was a "hand held camera", used in order to record more conspicuous behaviour.

3.3.5. Spatial distribution around the booth

In order to record more precisely the location of the individuals when they are present around the booth area (less than 5 m), numbers were given to each line of the octagonal booth (figure 7). Number 0 corresponded to the line where the touch panel computer was set and from there to left side numbers given were negative and to right side numbers were positive. The distance from each line of the booth was also recorded and they were given the values 1 from the adjacent areas (from 0 m to 1 m), 2 for the close area (from 1 m to 3 m) and 3 for the farthest area (from 3 m to 5m; table 2). For example, if an individual was seated 2 meters in front of the line -1, the position recorded would be (-1,2).

All the high positions in the considered area, up in the trunk, or in the tower platforms, are counted as positions on ground. If an individual is 4 meters distanced from the line 3, sited in the trunk 3 meters high, the position recorded is (3,3). The value 10 was given when the individuals were located on the top of the booth.

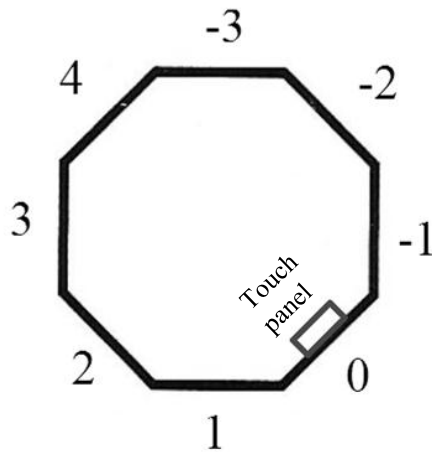


Table 2 – Matrix with the positions around the booth area (< 5 m)

Value	0	1	2	3
-3	-	-3,1	-3,2	-3,3
-2	-	-2,1	-2,2	-2,3
-1	-	-1,1	-1,2	-1,3
0	Task	-	-	-
1	-	1,1	1,2	1,3
2	-	2,1	2,2	2,3
3	-	3,1	3,2	3,3
4	-	4,1	4,2	4,3
10	-	10,1	-	-

Figure 7 – Shape of the booth viewed from the top represented with an octagon. Position (10,1) is not indicated in the picture but its location is on the top of the booth.

3.3.4. Statistical analysis

Statistical analyses were performed using the system IBM SPSS Statistics v. 20. (IBM Corp., <http://www-01.ibm.com/software/analytics/spss/>), and R software version 2.14.2 (<http://www.r-project.org/>). Microsoft Office Excel 2010 (<http://office.microsoft.com/pt-pt/excel/>) and Graphpad Prism 5 (<http://www.graphpad.com/prism/>) were used to plot some results. The statistical tests used were non-parametric: Mann-Whitney U tests to compare two groups, Kruskal-Wallis H test to compare three or more groups, and Spearman correlation to calculate the correlation of 2 variables (Motulsky, 1995; Fay and Proschan, 2010). We are dealing small samples sizes and unexpected with outlying observations that make problematic a parametric approach (Whitley and Ball, 2002). We used exact tests according to the threshold values suggested by Mundry & Fisher (1998). The P-value significance was set as < 0.05 with the confidence interval of 95%, to confirm H0. The error bars present in the following plots are set as the standard error of the mean.

3.4. Results

3.4.1. Control sessions vs. experimental sessions

First of all we wanted to compare the control sessions with the experimental sessions, to understand how the apparatus were influencing subjects' behaviours. Taking the mean of time the 6 individuals spent on the booth area (within 5 m around the booth, figure 8) across the experimental sessions (N=13) and control sessions (N=4), results show individuals spent significantly more time in the booth area, 35% of time, compared to control sessions, 5% (Mann-Whitney, N=17, U= 436,5, p(2-tailed)=0.000). The presence of the apparatus had influence on individuals' behaviour, since they approached more to the area around the booth, place, they barely used to approach on in the absence of the task (confirmed by the control sessions).

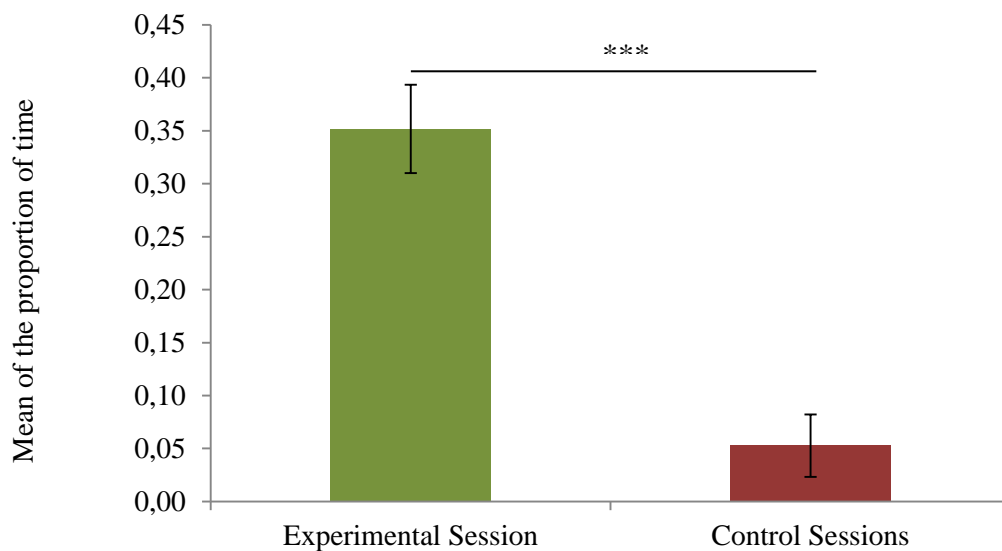


Figure 8 – Mean of the proportion of time individuals spent around the booth area in the experimental sessions and control sessions. *** indicates a P-value <0,000.

3.4.2. Time spent around the booth vs. Time spent performing the task

We measured the time individuals spent in the booth area (<5 m, figure 9) and the time they spent performing the task (figure 10, see detailed information in the appendix, table 1-5). The following plots are presented to give an overall idea, across all sessions, of the individuals that approached the area of the booth and performed the task, before going into details. The plots show that there is not a consistency in the time the chimpanzees spent in the area across the sessions; it varies a lot for all the individuals. Regarding

figure 9, Ai showed the most constant behaviour (she was almost all the time absent from the area). Reiko spent less time compared to Pendesa and Mari. The less dominant females seem to be present more time when Ayumu spent less time in the area (S6) or when he was absent (S8). After session 8 there was a clear increase of Pendesa, Mari and Reiko presence in the area, more evident in Pendesa and Mari. Regarding males, we can see a clear dominance of Akira and Ayumu, and initially we could not see which individual was monopolizing more the area. After session 8, it became more evident the dominance of Ayumu in the area and also performing the task (figure 10).

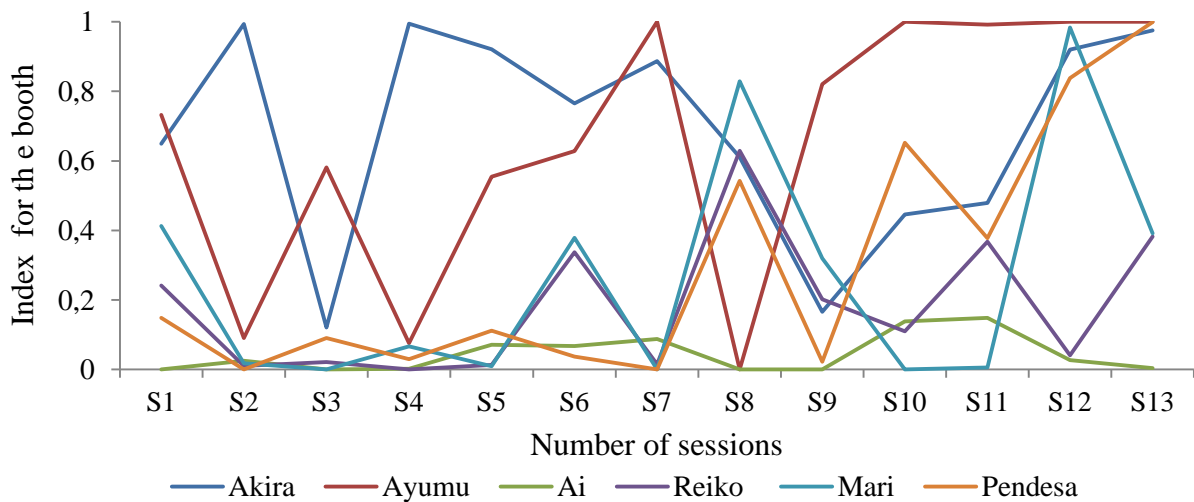


Figure 9 – Time spent by individuals on the booth area across the sessions. The y axis is given by the following index: the total time individuals spent in the booth for each session divided by the duration of each session. In the cases of Ayumu and Ai, the denominator of the index is not the duration of the session, but the time they spent in the outside enclosure, since they were absent for some time in the sessions. The time they were absent was not included.

Comparing the plot of the time spent around the booth with the plot showing the time individuals spent performing the task (figure 9 and figure 10) we can see a clear trend between the two plots, for Akira in the first 6 sessions and for Ayumu across all the sessions. After session 6, Akira was present in the booth area (<5 m around the booth), but did not perform the task (with the exception of the session 8, when Ayumu was absent). Other individuals, as Pendesa and Mari, were present in the booth area, but had lower opportunities to perform the task, as we can see by comparing the two graphs. Despite of being one of the dominants in the group, Reiko did not perform the task, and Ai, the other dominant, almost never approached the booth area and only performed the task once, for 33 seconds in the session 5.

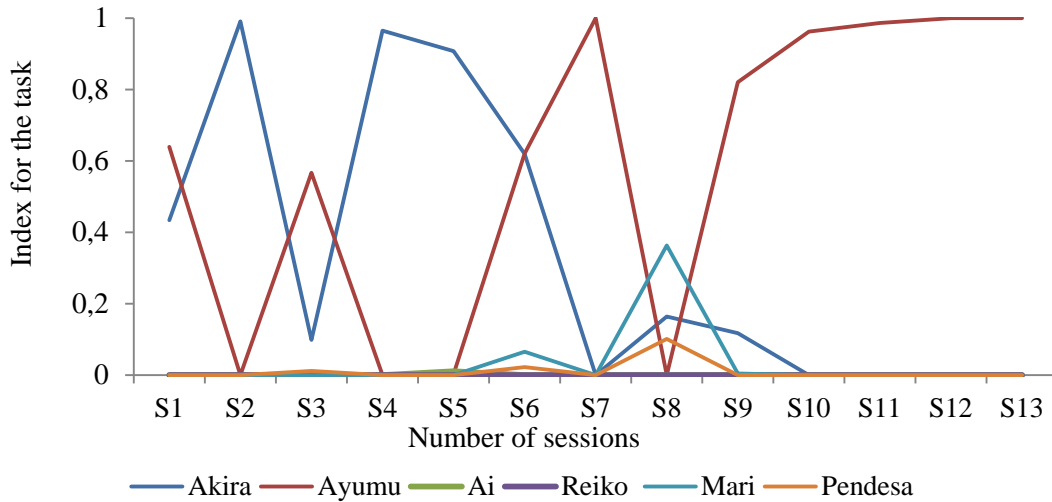


Figure 10 - Time individuals spent performing the task across the sessions. The y axis is given by the following index the total time individuals spent in the booth for each session divided by the duration of each session. In the case of Ayumu and Ai, the denominator of the index is not the duration of the session, but the time they spent in the outside enclosure, since they were absent for some time in the sessions. The time they were absent was not included.

It is important to note that, in sessions 1, 4, 6 and 9, Ayumu and Ai were not present during all the sessions from the beginning (table 3), because they were performing experiments indoors, which might be a reason why their time around the booth declined in these sessions (table 2). In session 8, they were absent during all the session. The influence of the exits/entrances of/in the group and the way they change the dynamics of the group are further analyzed in more detail. For Mari and Pendesa, the time spent in the area around the booth increased in session 8, compared to the previous sessions (1-7). They might have taken advantage of Ayumu's absence and performed the task during 30% and 10 % of the time of the session, respectively.

Table 3 – Presence of Ayumu and Ai in the sessions and the % of time he was present in the enclosure. E – entered when the session was ongoing, P- is present from the beginning, A- is absent during all the session.

	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	S11	S12	S13
Am/Ai Presence	E	P	P	E	P	E	P	A	E	P	P	P	P
Time spent (%)	69	100	100	92	100	36	100	0	79	100	100	100	100

Considering the time they spent in the booth area and performing the task in all the sessions, the results show that, despite the fact that Ayumu and Akira spent approximately, on average, the same time around the booth (69% and 69% respectively), Ayumu is the one who spent more time performing the task (figure 11). Looking to figure

11, we see that females barely (or never in the case of Reiko) performed the task compared to the time they spent on the booth area.

Results show there is a significant correlation between the mean of time individuals spent in the area with the time they spent performing the task (Spearman, $\rho=0,912$, $N=6$, P-value (2-tailed) $P=0,011$).

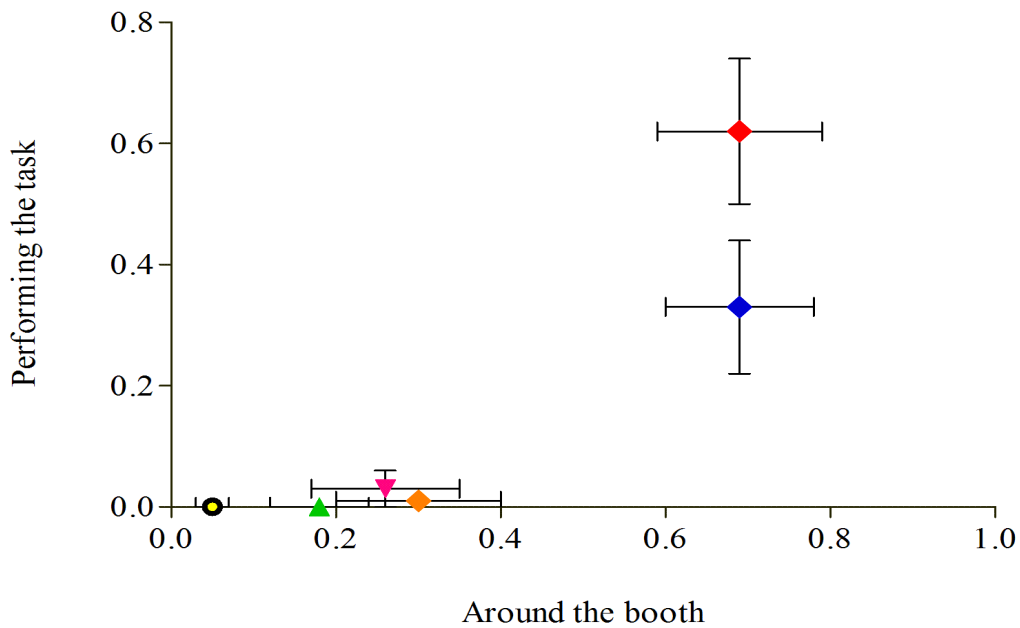


Figure 11 – Mean of time individuals spent performing the task (YY) and spent around the booth area (<5 m, XX). Horizontal error bars represent the standard error for the mean around the booth and the vertical error bars indicate the standard error for the mean of the time performing the task. Red – Ayumu, Blue – Akira, Orange – Pendesa, Pink – Mari, Green – Reiko and Yellow – Ai.

Comparing now the differences for each individual on the two different conditions (around the booth area and performing the task), results showed no significant correlation between the time they spent in the area and the time they performed the task, for all the individuals, with the exception of Ayumu (table 4, Spearman correlation $=0,984$, $p=0,000$). This means almost all the time he was in the booth area (69%) he was performing the task (62%).

Table 8 – Time individuals spent in the booth area and perform the task with the respective standard error, and results of the Pearson correlation between the two variables. Pearson correlation show non-significant differences in the time spent around the booth and performing the task for all individuals, except Ayumu.

Individuals	Descriptive statistics				N	Spearman correlation	
	Mean Task	Mean Booth	Stderror Task	Stderror Booth		rho	p-value (2 tailed)
Akira	0,33	0,69	0,11	0,09	13	0,418	0,155
Ayumu	0,62	0,69	0,12	0,1	12	0,984	0,000
Ai	0	0,05	0	0,02	12	0,220	0,492
Reiko	0	0,18	0	0,06	13	-	-
Mari	0,04	0,28	0,04	0,09	13	0,418	0,155
Pendesa	0,01	0,3	0,01	0,1	13	0,030	0,923

Taking in account only Ayumu and Akira, we compared the time they spent performing the task. We excluded the other individuals once they had performed just for a short time. We found no significant differences, regarding the mean of time Ayumu and Akira spent performing the task 62% and 33% respectively (Mann Whitney U=4 , P=0,088). However, if we look into the tendency of the plot showing individuals' performance, we observe, after session 7, that Ayumu is the only individual that performs the task. If we had run more trials, probably the tendency would be kept and we could get significant results.

Considering now the three groups (figure 12): males, high-ranking-females and low-ranking females we see that there is a clear difference among the three groups both as in the condition of time spent performing the task (Kruskal-Wallis H test, $\chi^2=22,646$, df=2, p=0,000), as in the time they spent around the booth area (Kruskal-Wallis test H, $\chi^2=32,779$, df=2, p=0,000). Males dominate the two conditions, followed by and low-ranking males, with a great disadvantage. High ranking females approach the booth area but don't perform the task.

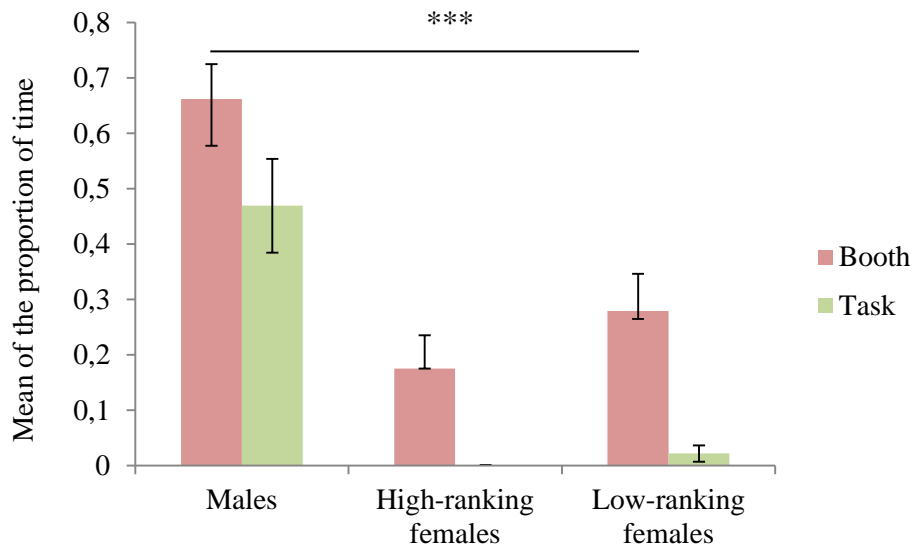


Figure 12 – Mean of proportion of time males, high-ranking females and low ranking females spent in both conditions: around the booth area – Booth, and performing the task. ***indicates a P-value <0,000.

3.4.3. Individuals around the booth when one is performing the task

Analyzing the time individuals spent around the booth area, when one is performing the task, results showed that Ayumu was the subject who had more individuals spending time close to him when performing the task and Akira was the one who spent more time in the area, almost 90% of the time (figure 13). However, he spent most of the time in the farthest position (see appendix, table 8). Pendesa is the female who spent more time in the area when Ayumu was monopolizing the task (figure 13). Regarding Akira, results show that there is a decrease in the time individuals spent around him. The individual spending more time in the area was Ayumu, followed by Reiko and Mari, with roughly the same percentage of time. Ai was the individual who spent less time when Akira and Ayumu were performing the task. This was expected, once she is absent in the area most of the time. Akira was present in the area during 77% of the time Mari was performing the task, and 29% of the time during Pendesa’s performance and did not take over them. Ayumu was not present when the females were performing the task, once Mari and Pendesa approached the task during his absence or in the periods he was not around. Reiko and Mari were the individuals spending more time close to Pendesa, 33% and 32%, respectively. In Mari’s case, the fact that Reiko was absent is due to the fact that, when she approached Mari, the subordinate female immediately stopped performing the task.

During the time Ayumu was performing the task females stayed close to him around 19%, on average, of the time, while Akira had female's presence for 8% of his time performing the task. However statistical analysis showed no significant results on the time females spent close to Akira and Ayumu when they are performing the task. (Mann-Whitney $U=474$, $N=68$, $p(2\text{-tailed})=0,116$). Females in general had no preference to stay close to any male. In the appendix to see table 7 to 10 with the time each individual spent each defined position around the booth area.

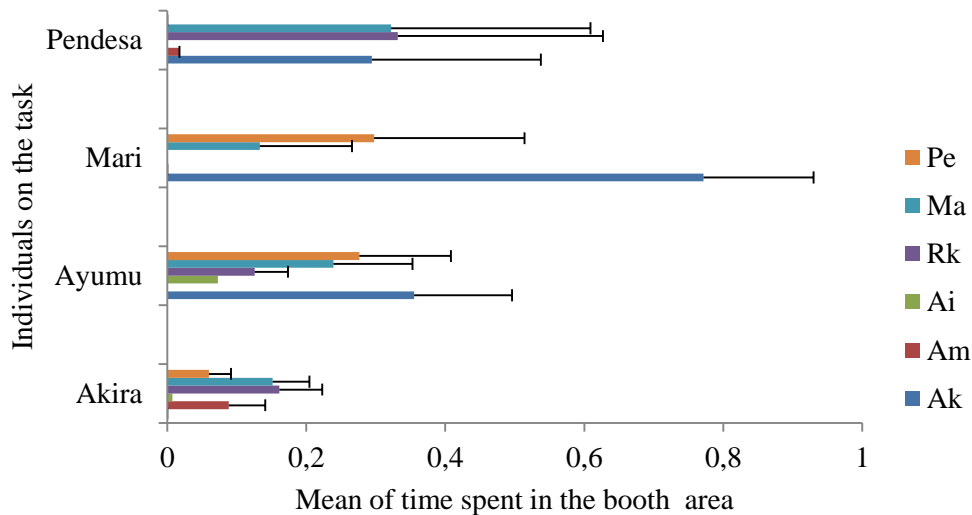


Figure 13 – Mean of time individuals spent in the booth area when Akira, Ayumu, Mari and Pendesa were performing the task (yy axes). The proportion of time is given by the time individuals spent around the booth (< 5m) divided by the by the time the individual on yy axes performed the task.

3.4.4. Spatial location around the booth

We recorded the time individuals spent in each position around the booth area (> 5 m) across all the sessions (figure 14, and for more detailed information see table 5, in the appendix). We grouped the positions in three main categories given by the names “closest area”, “farthest area” and “task”. “Closest area” is given by the positions closer to the monitor: (1,1), (0,1) and (-1,1). Individuals in this position can observe closely the behaviour of the individual performing the task and quickly takeover once the performer leave. These were the main criteria of this division. “Farthest area” is given by all the other positions. “Task” refers to the time individuals were performing the task. In the appendix more detailed information is given with the exact positions of the individuals.

The plots give an overall idea about the individuals' location on the booth area. During the time individuals were in the booth area, all the females with exception of Ai (2%), spent a great amount of their time in the closest positions, being Reiko the individual which spent more time in the closest area (71%). This can be explained by the time she spent in front of the monitor without performing the task. Ai, as we can see, almost never approached the closest positions. Mari and Pendesa spent the same time in the farthest area (41%), and the difference between them lies in the time spent performing the task, which in Mari's case is higher than in Pendesa's. Ayumu and Akira only spent, respectively, 2% and 8% of the time in the closest area.

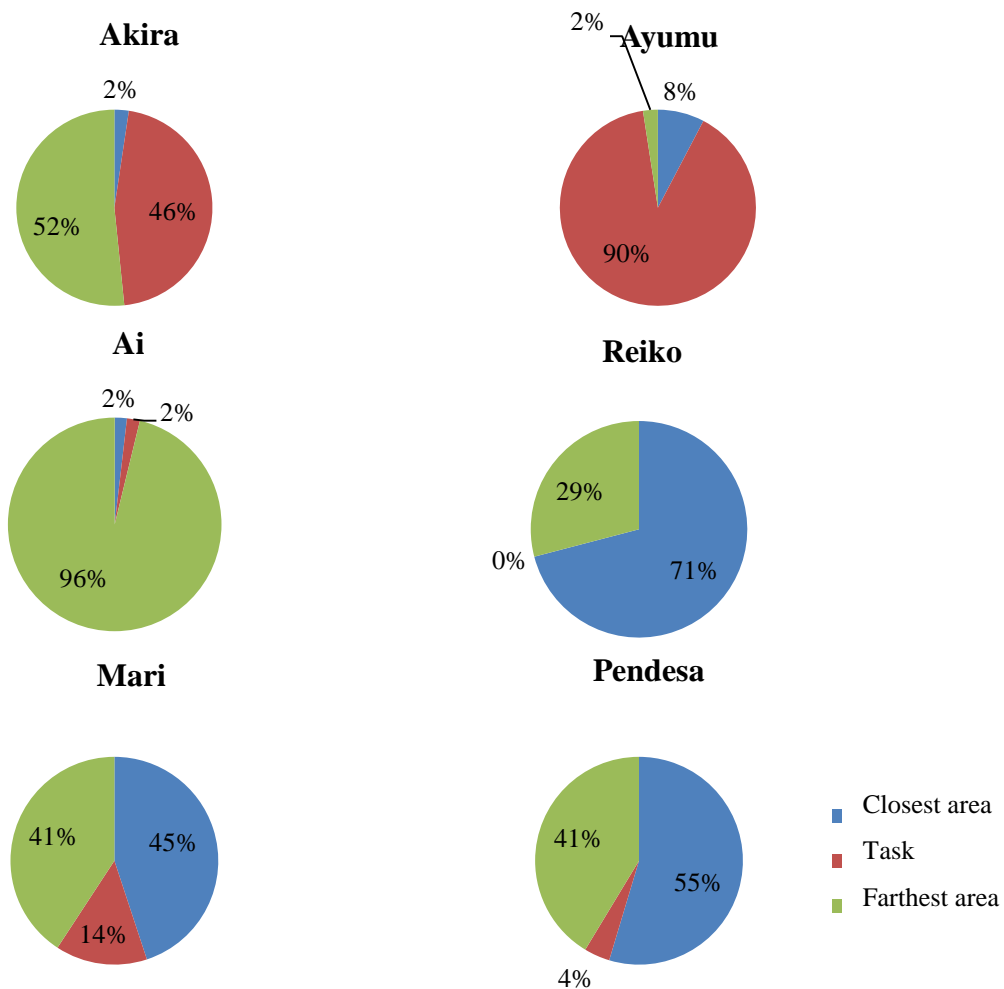


Figure 14 – Total time each individual spent in the 3 different positions. The time spent performing the task is given by time spent in the booth across all sessions divided by the time spent in the enclosure across all sessions; time spent in closest area = time spent in the positions (1,1), (0,1), (-1,1) across all sessions divided by the time spent in the enclosure across all sessions; time spent in the farthest area = time spent in the rest of the positions divided by the time spent in the enclosure across all sessions.

3.4.5. Other behaviours

Besides sitting around the booth, all the other behaviours did not occur so often. We recorded some events of grooming, solitary play, performed by the individuals that were present in the area around the booth (<5 m).

Grooming

The occurrence of grooming behaviour happened among the dyad Mari and Reiko for 402 seconds (N=2), being Mari the groomer and Reiko the groomee. One event happened after Reiko approached Mari when she was performing the task. Mari stopped doing it and left the position in front of the monitor. After a while, once Reiko could not perform the task, she left and approached Mari, who was seated close to her, and the grooming session started. The other grooming session occurred when Ayumu was performing the task. Mari approached Reiko and initiated the grooming. Pendesa groomed Akira for 401 seconds (N=2). At the same time, Akira reciprocated grooming to Pendesa for 391 seconds (N=1) in one session. Akira rejected the first attempt by Pendesa, but later he allowed her to groom him and reciprocated. The other session lasted only a few seconds: Pendesa started and quickly gave up.

Solitary play

Solitary play was defined in this case as grabbing and playing with branches and sticks. This behaviour occurred among the individuals that were close to the one who was performing the task. However, these events did not occur so often. Mari played for 194 seconds (N= 5), Pendesa (N= 4) for 148 seconds and Ayumu for 16 seconds (N=1).

Social play

This behaviour never occurred explicitly during the current experiment. However, there was one event in which Akira chased Ayumu, and he came in the direction of the booth displaying a play-face. We interpret this as an attempt to initiate play behaviour, however Ayumu did not respond to Akira.

The fact that the sessions lasted only for one hour and individuals were almost all of the time absent in the booth area (except the one who was performing the task) may justify the absence of some behaviours and little number of occurrences.

3.4.6. Male-male competition and the dynamics of the group

3.4.6.1. *Influence of the entrance of Ayumu in the enclosure*

In order to understand how the entrance/exit of the individual that performs more time the task - Ayumu - influences the rate of agonistic behaviour, we calculated the proportion of agonistic behaviour before and after Ayumu entered in the outdoor enclosure. We took the 4 sessions he entered when the session was ongoing and we compare the proportion of agonistic behaviours in two different conditions: when he was absent in the area (before he entered) with the proportion of agonistic behaviours after he entered.

To have more data and because the entrance of the individual might have affected the dynamics of all group, we considered agonistic events, as all the display and direct confrontations from all the individuals.

After Ayumu entered the area, the rate of agonistic displays increased significantly (Mann-Whitney, $N=8$, $U=16$, $p(2\text{-tailed})=0.03$) and it was almost inexistent before he entered the area, 0.01, as we can see in figure 15. In the appendix all the agonistic events are better described (table 11 to 13).

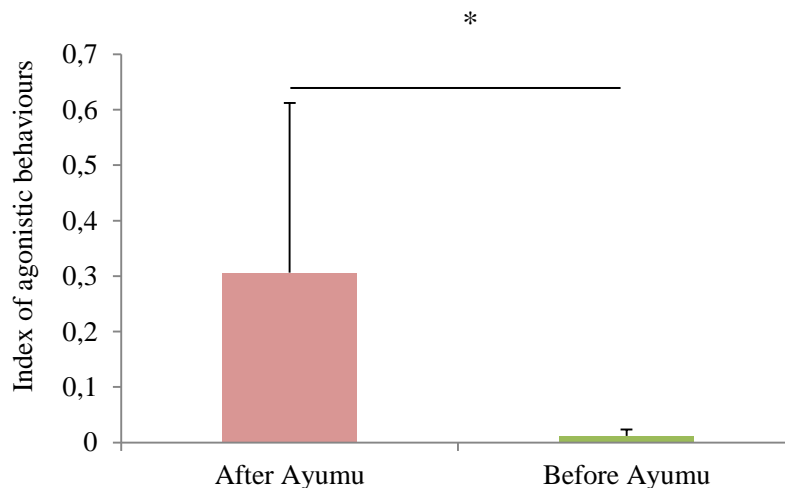


Figure 15 – Index of agonistic behaviours given by the frequency of agonistic behaviours in each condition divided by the time length of each condition (min) in the conditions: after Ayumu enters in the enclosure and before Ayumu enters the enclosure. * indicates a $P<0,05$

Across all the 12 sessions (in one session Ayumu was absent all the time, so we are not considering that in this analysis), we also measured the agonistic behaviour in the sessions where Ayumu was present from the beginning (N=8) and compared it with the sessions in which he entered (N=4, figure 15). Results show, the rate of agonistic events was significantly higher in the sessions he entered compared to the sessions in which he was present from the beginning (Mann-Whitney $U=31$, $N=12$, p (2-tailed) = 0.008). Taking together with the previous analysis, the results suggest that his entrance in the area was the reason why agonistic events increase.

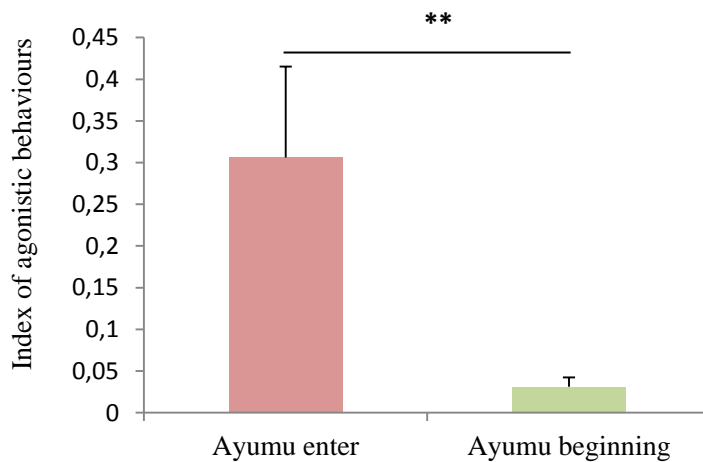


Figure 16 – Index of agonistic behaviours given by the frequency of agonistic behaviours in each condition divided by the time length of each condition (min) in the conditions: sessions when Ayumu enters the enclosure during the experiment and session in which he is in the area from the beginning. **indicates a P-value <0,01.

3.4.6.2. *Male-male takeover*

All the male takeovers were passive, there was no direct confrontation between the individual that took over and the individual that was performing the task. They usually occurred after one individual displays, by hitting the glass, or when one gave up the task. There was only one case when Akira caused the displacement of Ayumu, by chasing him after Ayumu replaced him when he left the task. The event occurred in the first session. Considering all the male-male takeover events (N=7), across the 12 sessions we verify that Ayumu was responsible for taking over Akira, 5 times, while Akira only took over Ayumu 2 times (table 5). In one session Akira took over Ayumu after he replaced him in the task. Overall, the rate of takeover was higher for Ayumu.

Table 5 – Percentage of take over. Am > Ak means Am taking over Akira, Ak > Am means the opposite tendency.

Direction of take over	Absolute frequency	Relative frequency (%)
Am > Ak	5	71
Ak > Am	2	29

We also measured the frequency of the first takeover. Considering all the sessions both individual were present (N=8), in 75% of the sessions the first individual to approach was Ayumu. All the individuals were considered; however, only the males were the first to approach the task in the beginning of the sessions. The sample size is small and did not show significant differences, but in 8 sessions Ayumu took over first than Akira, 6 times (table 6). Considering the sessions Ayumu and Akira were present from the beginning, when Ayumu was the first individual to approach the task (S3, S7, S10 - S13), he spent more time performing the task (70%), compared to the sessions Akira starts (0%). In the sessions Ayumu is not present from the beginning he performs (52%) almost the same as Akira (54%). This suggests if Ayumu is the first individual to take over he has higher probability of performing the task, compared to Akira. Only in two sessions Akira started first he was not taken over from his position. These sessions corresponded to the sessions Ayumu was present in the enclosure since the beginning.

It is important to mention that in all the sessions when Ayumu was the first to approach, Akira was in the booth area (<5 m around the booth).

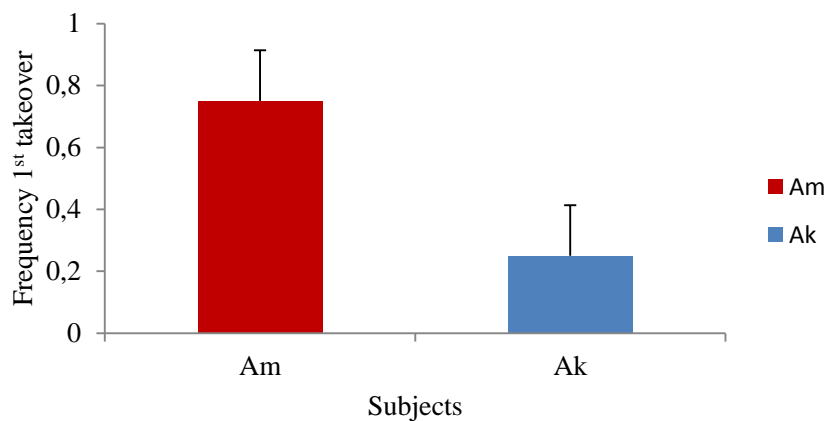


Figure 17 – Frequency of the first take over by the males across the sessions when both individuals are present from the beginning (N=8).

Table 6 – Resume table indicating the first individual to approach first to the task across the sessions (S) with the respective proportion of time they spent performing the task and the number of takeovers per session.

	S1 ¹	S2	S3	S4 ¹	S5	S6 ¹	S7	S8 ²	S9 ¹	S10	S11	S12	S13
1st Approach	Ak	Ak	Am	Ak	Ak	Ak	Am	Ak	Ak	Am	Am	Am	Am
Ak	0,43	0,99	0,10	0,97	0,91	0,62	0,00	0,16	0,12	0,00	0,00	0,00	0,00
Am	0,64	0,00	0,57	0,00	0,00 ³	0,62	1,00	0,00	0,82	0,96	0,99	1,00	1,00
Am > Ak	2	0	0	0	1	1	0	0	1	0	0	0	0
Ak > Am	1	0	1	0	0	0	0	0	0	0	0	0	0

3.4.6.3. *Ayumu influence on the group's dynamic*

Taking into account the sessions when Ayumu enters (N=4), when he is in the enclosure since the session started until the end (N=8), and when he is absent in the area, we wanted to analyze the influence of Ayumu in the performance of the others (figure 17).

As expected, the proportion of the task performance by the other individuals, Pendesa and Mari, is low when the two males are present in the area (2% for Pendesa and 0.4 % for Mari). Considering the 4 sessions when Ayumu entered, in the period when he was absent from the area, Akira completely monopolized the task during this period. Only after Ayumu entered Mari and Pendesa had opportunity to perform it.

Mari and Pendesa performance slightly increased in the sessions Ayumu entered in the enclosure (2% for Pendesa and 6% for Mari). The entrance of Ayumu when the task was ongoing corresponded to the sessions when the rate of agonistic conflicts was higher. During these sessions, and due to a higher rate of agonistic events, individuals left the task position more often allowing others to approach.. In the sessions in which Ayumu enters (N=4) the average of approaches to perform the task is higher (4.25) compared with the sessions when Ayumu is in the area from the beginning (2.25, N=12). More exchanges in the individuals performing the task happened because individuals left the task more, once active takeover did not occur. The instability created in the sessions when Ayumu entered gave some opportunity to other individuals to perform the task. This might explain why the time spent by the females performing the task increased

In the sessions Ayumu entered, he performed almost the same time than Akira, as previously seen. This means after he entered he took over him and his takeovers were successful.

In the sessions Ayumu is absent, Mari and Pendesa took advantage and performed the task for 20 % and 10% of the time, respectively. Akira was the first to take over, then, when he left Mari approached and Pendesa was the last to perform it.

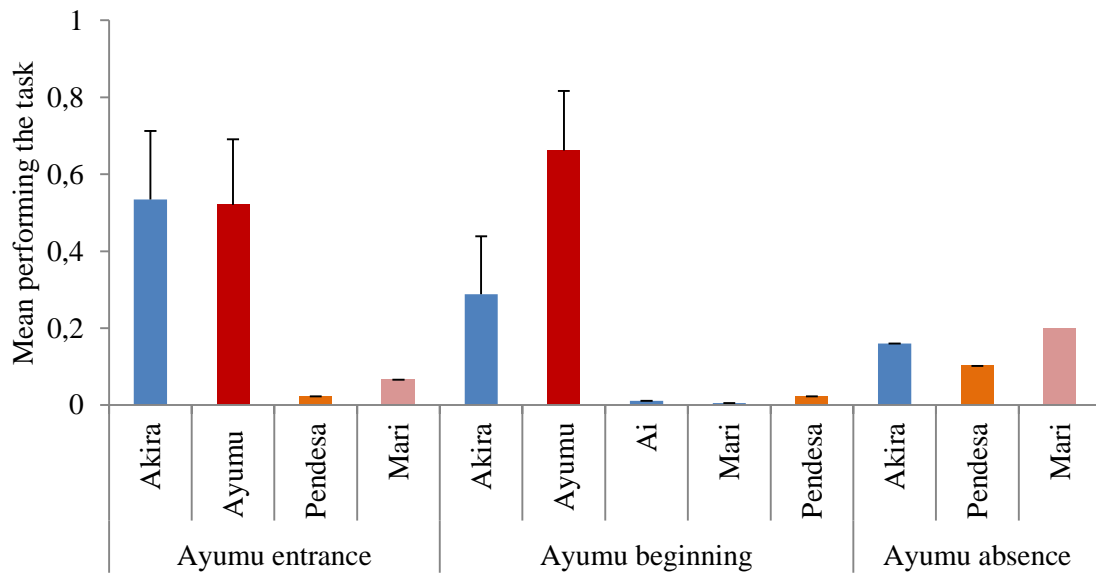


Figure 18 – Mean of the time individuals spent performing the task in three different conditions given by the sessions in which Ayumu enters in the enclosure during the session (N=4) (Ayumu entrance), the session in which Ayumu is present since the beginning of the session (N=12) (Ayumu beginning) and the sessions in which Ayumu is absent in the area (N=1)(Ayumu absence).

3.4.6.4. *Ayumu influence on the group's dynamic*

By observing the overall plot of the time spent around the booth (figure 2), we can see a clear increase in the time individuals spent around the booth (with the exception of the session 9). Ascertaining the differences, we compared the mean of time spent in the task by Mari and Pendesa in the sessions before performing the task (session 1 to session 7) and sessions after they performed the task (session 9 to session 13; figure 18). The two females spent significantly more time in the booth area in the sessions following the session 8 (Mann-Whitney U= 35, N=12, p (2-tailed) = 0.04).

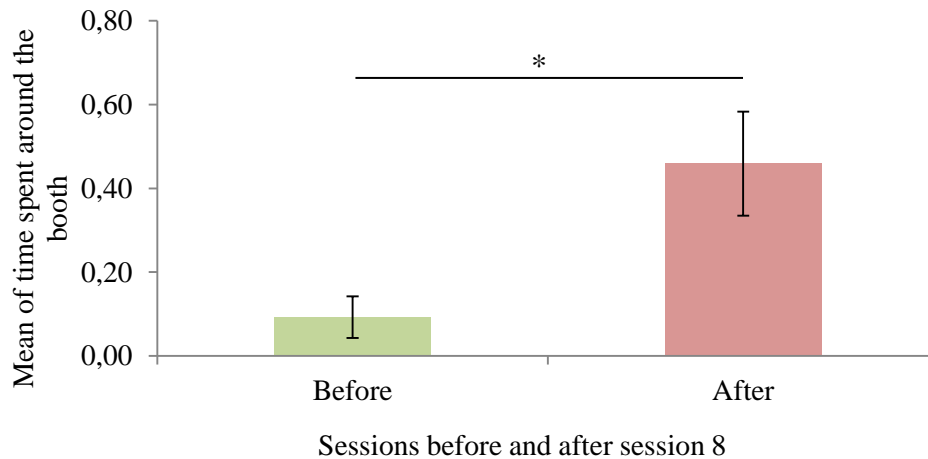


Figure 19 – Mean of time Mari and Pendesa spent in the sessions before session 8 and after session 8. * indicates a P-value >0.05 .

It is not clear if the increase of the time spent around the booth area after session 8, by Pendesa and Mari was due to the fact that Ayumu was the one who performed the task more, and the low-ranking females just prefer to be around him, or if the increase is due to the fact that in session 8 they had experienced more time performing the task. After that they understood it was more advantageous for them to stay in a closer area if their main goal was to perform the task.

There is other factor that must be taken into account to understand if what was affecting the presence of the females in the booth area is the instability of the group, as a result of Ayumu entering in the area and consequently increase the rate of agonistic events. The sessions before session 8 revealed to have more agonistic events, compared to sessions after session 8. In the previous 7 sessions, 4 of them were marked by the entrance of Ayumu in the outside enclosure, causing some instability, reflected in the increasing of the rate of agonistic interactions. After session 8, only the session 9 was marked by high rates of agonistic interactions, probably caused by the entrance of Ayumu in the area. In the same session, as we can see in figure 2, there was a decrease of the time females spent around the booth area. Table 4 resumes the agonistic events and the presence of Ayumu in the booth area.

Table 7 - Agonistic events represented by the absolute number per session and index (agonistic events/min). Ayumu presence in the booth area is given by the letters E – enters when the session is ongoing, Y- is in the area since the beginning of the session, N- is absence during all the session.

	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	S11	S12	S13
Agonistic absolute no	16	1	3	5	2	6	0	2	14	4	1	0	1
Agonistic events/min	0,5	0,03	0,05	0,09	0,04	0,15	0	0,03	0,44	0,10	0,02	0	0,02
Am Present	E	Y	Y	E	Y	E	Y	N	E	Y	Y	Y	Y

To see if the agonistic interactions had influence on the time females spent around the booth area, we compared the mean time they spent in the area with the rates of agonistic display. We found no correlation between the two variables (Spearman rho= -0.116, N= 4, P-value (2-tailed) = 0.721). However a negative r indicates that there is a negative tendency on the correlation between the two variables. By comparing the time females spent on the area in the sessions when Ayumu enters (sessions with higher rates of display: session 1, 4, 6 and 9) with the sessions in which Ayumu was present from the beginning (sessions with lower rate of agonistic events), the results don't show any significant differences (figure 19; Mann-Whitney, U= 243, N=48, P (2-tailed)=0,775). The rate of agonistic events does not seem to have a strong influence on the time females in general spent around the booth area, neither for Pendesa and Mari in particular (Mann-Whitney, U= 58,5, N=24, P (2-tailed)=0,578)

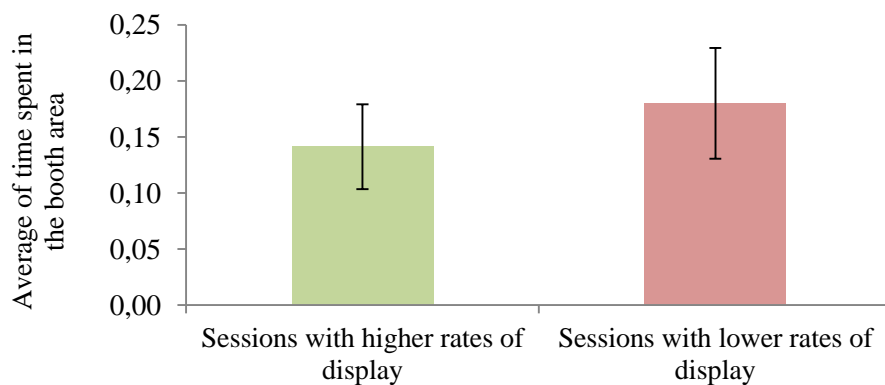


Figure 20 – Mean of time spent in the booth area by all the females in the sessions when the frequency of displays were higher (given by the entrance of Ayumu in the enclosure) and in the session where displays occurred at a lower rate (Ayumu was in the enclosure from the beginning).

To understand if Ayumu's performance on the task is the factor that influences the higher rate of the time Mari and Pendesa spent around the booth after session 8, we compared the time they spent close to Ayumu (in the booth area) in the sessions before and after the session 8. If that was the case we would expect Mari and Pendesa to spend approximately the same amount of time in before and after session 8. This was not verified. There was a significant increase, from 9% to 45% of the time they spent close to Ayumu after session 8 (figure 20, Mann-Whitney, $U= 14,5$, $p(2\text{-tailed})=0,021$).

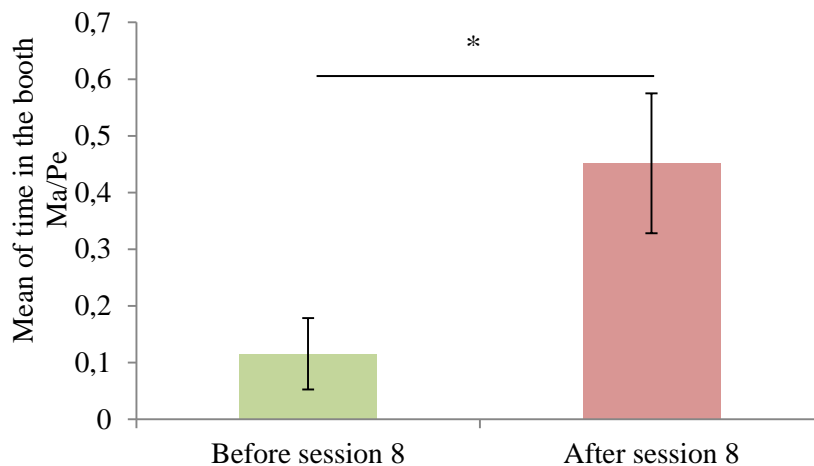


Figure 21 – Mean of time spent in the booth area by Mari and Pendesa, during Ayumu's performance, in the sessions before and after session 8. * indicates a P-value <0.05.

3.5. Discussion

This was the first experiment in which all the chimpanzees in the group were tested simultaneously with a touch panel computer task. We expected the presence of the apparatus to change the dynamics of the group and to allow all the individuals to come around the booth area. In order to test the effect of the apparatus, we conducted control experiments. By comparing the control sessions with the experimental sessions, results showed the time individuals spent in the area around the booth increased in the latest condition. However, the results would have been more accurate if we had run the same numbers of controlled experiments compared to the experimental sessions.

Previous studies, in which competition for food resources were analyzed showed the rate of interactions, agonistic and affiliative, seem to increase when chimpanzees were provided with food resources (Wrangham, 1974; de Waal, 1989). In the current study, we cannot affirm that, once we did not measure the interactions of the individuals in the

control phase. However, it is clear that, at least, when the experiment is running, the individuals approach and spend more time in the area around the booth. The approaches that happened might have occurred because they were expecting to perform the task or because they were curious about the presence of the observer. Less time spent around the booth area means fewer opportunities to have encounters with other individuals and interact in this area.

In the experimental sessions we were expecting to observe more strategic behaviours from individuals that wanted to perform the task. However, it turned out that individuals seem to understand the role of the dominant individuals, and the strategic and agonistic behaviours occurred only in a context of male-male competition. In cases of contest competition, the rate of agonistic displays is expected to be lower compared to scramble competition (Wittig and Boesch, 2003), the dominant individuals monopolize the food resources and the less dominant cannot take over them (Parish 1994, Pusey *et al.*, 1995; Wittig and Boesch, 2003, Murray *et al.*, 2007). We verified in our study that low-ranking females, also, did not try to take over dominant individuals when they were performing the task, they just approached and sit in the booth area.

We expected Akira or Ai to be the ones monopolizing the task. However, it turned out, that Ayumu, less dominant than Ai and Akira, was the individual that monopolized more the task, followed by Akira. According to Pusey *et al.* (1997) males are dominant regarding monopolizable resources, besides females being the ones who compete more for food resources (Goodall, 1986; Muller, 2002; Wittig and Boesch, 2003). In the current study, males were also dominant regarding monopolizable resources, provided by the touch panel task.

Melis *et al.* (2011b) tested chimpanzees in two different situations resembling scramble competition and contest competition scenario. The goals were different from our study, once they wanted to analyze the patterns of food sharing. However, they found out that dominant individuals monopolized the food in the contest competition scenario, and also individuals that arrived first had advantaged in the acquisition of food. This was verified in our study. Dominant individuals, the males, had access to the monopolizable area more, although the alpha male of the group performed less than the juvenile. Also, the individual that approached first to the task was the individual performing the task during more time (or during entire session), this was verified with Ayumu. In Akira's case, when he arrived first than Ayumu, Akira was more frequently taken over from the position.

Low-ranking females, Mari and Pendesa, were the female individuals that spent more time in the area. They took advantage and performed the task in situations when the males were not close to the monitor area. The peak of their performance happened when Ayumu was not present in the enclosure, in session 8.

The results showed a significant correlation between the mean of the time spent in the area and performing the task. This seems logical because, the more time they spent in the enclosure, the more opportunities they had to perform the task. Nonetheless, what could have happened instead with most of the individuals was that they could have spent much time in the area without having any opportunity to perform the task. This happened, for example, with Reiko. The only individual that showed a significant correlation between the times spent in the booth area and the time performing the task was Ayumu. The time he spent in the booth area corresponded mainly to the time spent performing the task.

3.5.1. High-ranking females

Ai, the dominant female, rarely approached the area that we defined as booth area. She approached and sit mainly in farther areas from the monitor position, as if she was monitoring the group's behaviour.

We expected Ai to approach more during the time Ayumu was performing the task. Previous experiments with Ai and Ayumu showed she monitored more her son behaviour than the opposite, since she was better responding to her son behaviour than vice-versa (Martin *et al.*, 2011). However, this happened in a smaller compound indoors when both individuals were performing the task simultaneously. In the current experiment, Ai did not monitor from a close distance Ayumu's behaviour. The time she spent close to Akira was less compared to the time she spent close to her son, although she was the individual spending less time with Ayumu.

The only time she was observed performing the task had the duration of 33 seconds. This event occurred when Akira left the task and Ai approached and initiated it. Once Ayumu approached, she had given away the place to him. Taking into account that Ayumu had not performed the task before in that session, and that Ai almost never approached to the monitor area, we interpret this event as Ai acting in order to save the

position for Ayumu , that was not around at that time. The fact that, when he approached, she immediately gave away her position, helps to support our argument.

The participation of Ai in the outdoor enclosure in other experiments (Tonoka *et al.*, 1997; Celli *et al.*, 2004) regarding tool use was also less evident compared to other individuals in the group. In the current study, we expected Ai to play a more active role, once she is used to participate in touch panel experiments both in an individual and social context (see review: Matsuzawa, 2009). This was not verified in the study, suggesting that the social context is accounting for that.

How does the social context modulate her behaviour is clearly difficult to tell. However, there might be some explanations we deduce from the current results. Ai could have been acting in a way that did not harm the performance of her son, Ayumu, by replacing him on the task. The event of Ai saving the place to Ayumu can help supporting this argument. Besides having no advantage in replacing her son, Ayumu is probably physically stronger than his mother and Ai would not have any advantage on having conflicts with him.

The current experiment turned out to be a case of competition between two males for a shared food resource. The distance Ai kept from the area might have worked as a strategy to avoid conflicts with the two males. We observed one event where Ai directly intervened in one agonistic event between Akira and Ayumu and ceased the confrontation. This behaviour showed her position as dominant female.

Reiko, the other dominant female, was the only individual on the group that did not perform the task, due to lack of knowledge, in spite of some opportunities that emerged. Our idea was to prevent this from happening with more individuals; that was the reason why we used a simple task that could be easy to learn in case of individuals' lack of experience. However, it was not easy enough to allow all the individuals to participate.

When Mari was performing the task, for two times, Reiko approached her and Mari stopped performing the task in her presence and gave away the place for her. Reiko approached the task position (in front of the monitor), but she was not able to start the task. These two events might be evidences of dominance from Reiko towards Mari. Reiko also approached Pendesa, but she had not any influence on Pendesa's behaviour (at least, she kept performing the task).

The age of the individual might be a factor that we should take into account when we try to understand why Reiko did not perform the task, or did not learn how to do it. It is known that, in humans, cognitive speed and memory performance decline with the age (Christensen, 2001). Also an experiment testing chimpanzees with touch panel computer showed that juveniles have a better work memory capability compared to older individuals (Inuo and Matsuzawa, 2007). However, we ran sessions with the other group, and a dominant female with a similar age, called Puchi, who had not any experience with touch panel tasks, after observing a juvenile chimpanzee performing it, learnt how to press the start and the initial button and the key "1".

The fact that she could not perform the task did not prevent her from approaching the booth area and to approach the closest positions from the monitor, and take over other individuals from the position. Nonetheless, the short time she spent in front of monitor, observing other individuals performing the task, might also have accounted for her failure on learning. Individual differences on personality and motivation could also explain the differences, however, that we cannot discuss here because. They are complicated to measure, although they are possible to quantify. Some studies reported measurements of personality of chimpanzees (e.g. Dutton *et al.*, 1997)

3.5.2. Low-ranking females behaviour

Subordinate individuals seldom possess the food resource after a conflict for a monopolizable food resource (Wittig and Boesch, 2003). In the current study, both low ranking females had few opportunities to perform the task.

Mari approached and performed the task 3 times across the 13 sessions, as well as Pendesa, however the proportion of time spent on the task was higher for Mari.

Pendesa showed to have a clear preference to stay close to Ayumu compared to Akira, contrary to Mari, that spent almost the same time close to Ayumu and Akira. We expected Mari to approach more to Ayumu than any other female, once they are known to have a good relationship (Keeper personal communication).

The time Mari and Pendesa spent close to Ayumu and Akira when they were performing the task showed females spent more time close to Ayumu than to Akira, although the differences were not significant. Pendesa was the female contributing more for this difference; she was the individual spending more time close to Ayumu. The fact that Ayumu performed for longer periods compared to Akira might have given more

opportunities for other individuals to approach. Akira seemed to be more intolerant towards Pendesa compared to Mari, and evidences on aggressive behaviour help to support that. We have not observed any other agonistic interaction by Akira towards other female, besides Pendesa. However, we observed for two sessions grooming events among Akira and Pendesa, when Ayumu was performing the tasks. We cannot conclude anything based on this few data. It was not enough to collect more events of social interactions, in order to understand preferences of the individuals.

The short duration of the experiment did not allow having more data on individual's interactions and other behaviours, in order to clarify the current position of the individuals in the ranking and their relationships

Akira showed some tolerance towards Mari and Pendesa when they were performing the task. He stayed close to them, around the booth area during their performance without taking over. Some social and ecological factors, such as demography, the degree of relatedness, and the availability of alternative living situations influence the degree of tolerance dominants show towards subordinates (Flack and de Waal, 2004). In the current study, the tolerance towards the subordinates might have occurred once Akira had other opportunities of obtaining food (he is fed three times per day) and performing the task was not the only way to obtain food.

3.5.3. The importance of the session 8

The drop in Ayumu's presence/performance in the session 8 is explained by his absence in the enclosure. His absence caused the increase of time spent in the booth area by other individuals, as well as the increase on the time performing the task. After session 8, Pendesa, Mari and Reiko spent more time in the booth area compared to the other sessions.

We try to understand the factors that are responsible for the increase of time spent in the area by these two females. Many factors can account for that, they had the opportunity to spend more time performing the task, in the session 8; Ayumu was the only individual performing the task after session 8, and the rate of agonistic events also decreased in the latest 5 sessions (with the exception of session 9).

We hypothesize three main factors that can be influencing Mari and Pendesa's behavioural changes: 1) Mari and Pendesa prefer to stay close to Ayumu and since he is

the only performing the task, the time they spent on the area increased 2) the sessions before session 8 were more unstable due to the changes in the group, and this would have affected the time females spent in the booth area; 3) once they had performed the task for a larger period of time they could have “understood” they had more advantages and opportunities to take over if they stayed in the surrounding area. This last statement implies that individuals might predict future events. Evidences in other contexts suggest chimpanzees plan for the future (Osvath, 2009)

To understand if the changes on the dynamics of the group (given by the entrance of Ayumu and the agonistic events) dictated the changes on their behaviour, we correlate the time individuals spent on the booth area with the rate of agonistic events before and after session 8. Results showed correlation between the conflict rate with the time females spent in the booth area. This suggests that the decrease of agonistic events was not the reason why they have changed their behaviour.

If Ayumu is the main reason why the two females spent more time after session 8, we would expect the time they spent in the two different conditions (before and after session 8) to be similar. By comparing the mean of the time Mari and Pendesa spent close to Ayumu, when he was doing the task before and after the session 8, results showed there was a clear increase after session 8. This means, before that, Mari and Pendesa rarely approached Ayumu, suggesting no preference for Ayumu since the beginning.

The results did not support that the change in the females' behaviour was due to the instability of the group or the presence of Ayumu, more data would make this statement clearer. It is, indeed, difficult to show how session 8 changes the time they spent on the task. There must have been other factors accounting for that, such as the presence of other individuals in the area around, and their will or motivation to perform the task. However, the increase of the time spent in the enclosure is evident after they experienced performing the task for a longer period. Session 8 should be taken as an important factor accounting for this increase.

Other explanation could be that this is their common behaviour when facing a situation similar to this and in the beginning, when the experiment started they were just hesitant, due to the novelty of the task in their enclosure. But since the increase happened in the following sessions after the session they participate more in the task, we suggest that, they understood they have more advantages to stay in the closer area, if the goal was to perform the task.

The time Reiko spent in the booth area after session 8 also increased. We suggest that is due to the presence of the other females in the group, mainly due to Mari's presence. We can see in the plot indicating the time individuals spent in the booth area, a clear increase in the time Reiko spent in the area in the sessions in which Mari spent more time.

It is hard to tell how individual's presence affects others in the surrounded area of the booth. Individuals may approach others not because they want to approach specifically that individual, but because they are curious about the task. However, if we had collected more data, we could make this statement clearer and we probably would have found some tendency in the individuals' behaviour.

3.5.4. Entrance of Ayumu/Ai in the group and agonistic events

De Waal (1989) suggested that aggressive behaviour can be an effective method when one individual wants to claim for food or defend it. He found in his study that the agonistic events related with transfer of food are more likely to occur between immature and adults or between immature. However, most of the interactions had a peaceful nature.

Wrangham (1974) also showed in his study, by analyzing behavioural data from a group of wild chimpanzees provisioned with artificial food that the rates of agonistic events increased across the days after the provision, once the food was becoming scarce.

In order to understand what drives agonistic behaviour in the context of the current study, we examined the occurrences of the agonistic events of the individual and tried to relate them with other factors.

We verified that the rate of agonistic events was higher in the sessions in which Ayumu entered during the course of the experiment, suggesting that his entrance in the enclosure broke the stability of the group, by increasing the rate of agonistic events.

In the sessions Ayumu entered when the experiment was ongoing, he showed less tolerance towards Akira performing the task, compared to the sessions when he was in the booth area from the beginning. He took over Akira from the task position in 3 of 4 sessions (session 1, 6 and 9). In the sessions Ayumu was in the area from the beginning and Akira took over first, he showed more tolerance and did not try to replace him on the task (session 2 and session 5). Perhaps, the fact that he was performing cognitive tasks indoors before entering the area, had influence on his takeovers. He could have been more

motivated to perform the task outdoors after leaving the computer task indoors and wanted to keep performing to obtain food.

To support that Ayumu was the main responsible for the increase of the agonistic behaviours, we looked also to the rate of agonistic events, before and after he entered the area. After he entered, the rate of agonistic events was higher compared to the time he was absent from the area, suggesting he is the main responsible for the agonistic behaviour. The fact that we are dealing with a very small sample size, only 4 sessions in which he entered, does not allow us to draw strong conclusions. We needed more sessions to make clearer statements. In a broader scale, in the wild, agonistic events seem to happen when individuals get together after fissioning from the group. In wild spider monkeys and chimpanzees, two species living in fusion-fission society, when individuals meet in the fusion events, aggressive behaviours are more likely to occur than at other situations (Muller, 2002; Aureli and Schnaffer, 2007).

3.5.5. Male dominance and task monopolization

This contest competition situation is different from the real situations of competition for a monopolizable food resource (Wittig and Boesch, 2003). Once, here the “food resource” is continuously providing reward for approximately one hour. In order to understand who monopolized more the task, we considered the individual which spent more time performing it, as an equivalent of the individual that possessed the food after the conflict, as it happens in real situations in contest competition scenarios (Wittig and Boesch, 2003).

Considering only this study, we cannot make strong statements about who is more dominant in the group. According to the background information, Akira is the dominant male in the group, but Ayumu monopolized the current experiment, as showed by the results. His dominance over the task became clear after session 6. When dominants face contest competition with subordinates, they are more likely to get the food after the conflict (Pussey *et al.*, 1997; Wittig and Boesch, 2003).

In the sessions where both males were in the area from the beginning, Ayumu took over more times than Akira and performed the task more. Melis *et al.* (2011b) showed in their study that individuals approaching first to the monopolizable area have advantage towards the others.

Akira probably did not take over Ayumu in the sessions he was the first to approach because he did not want to put so much effort to obtain a reward if he could get free food in other ways.

Why Ayumu is dominant in this study is not clear but, considering the results and the individuals' experience, we can tell that Ayumu has stronger motivations to perform the task and he dares to confront Akira, to reach his goal: monopolize the task and obtain food reward. Akira also showed some tolerance towards Ayumu, more evident in the last sessions, and did not fight back after losing the possession of the task. One of the main reasons might be to avoid conflict with Ai. The presence of Ai in the enclosure during the experiment is a factor to take into consideration. As we mentioned before, Ai stopped a conflict between Ayumu and Akira. If Akira had confronted Ayumu more, or directly, this situation would have happened and would generate tension among the individuals.

Other factor that can explain Akira's tolerance is his less motivation in performing the task, once he has less experience in cognitive experiments mediated by touch panel. Despite of this presence in the area when Ayumu performed the task, Akira rarely stayed in the positions close to the monitor area. Our interpretation of this behaviour is that Akira might have wanted to perform the task, because he stayed in the area around the booth, however, at the same time; he kept some distance to not interfere in with Ayumu's behaviour.

If chimpanzees were tested in similar conditions, but without a touch-panel task, Akira would probably be the one monopolizing it more. We suggest that the experience of the individual on performing the computer tasks might be the factor that is contributing for Ayumu to be the one monopolizing more the task, as well as, the presence of his mother, a dominant female, who can support him. Some mothers are known to support their offspring gaining a better position in the tank (Pusey *et al.*, 2007)

The results regarding the time Akira and Ayumu performed the task are not significant, and this could be due to the fact that we had a small sample size in the number of the sessions. If we kept running more sessions, Ayumu would probably keep monopolizing the task and we could reach significant results, once he monopolized completely the last sessions. However, this would happen if Akira continued to show some tolerance towards Ayumu, but we cannot predict the changes in his behaviour.

Other factor that we have to take into account is that chimpanzees are well fed, and this situation of competition does not mean the survival of the individuals. That might be one consideration we should take in consideration when trying to explain Akira's

tolerance towards Ayumu. In a real situation of competition, we could expect him to win the conflict, if he is the dominant, considering what happens in other studies (Pusey *et al.*, 1995; Wittig and Boesch, 2003).

Taking into account our small sample size, given by the number of individuals (N=6) and number of sessions (N=13) resulting in the lack of interactions among the individuals and non-significant differences between Ayumu and Akira's performance, it is not possible to draw any strong conclusions. However, we tried to explore all the information given by the small number of sessions.

Some behaviours, such as, feeding or foraging, were difficult to follow when the observer was in the experimental booth, and later when observing the videos, once individuals forage and feed in areas out of the camera's range.

3.6. Conclusion

We conducted this experiment to test chimpanzees in a situation of contest competition, introducing a computer touch panel task. We expected the dominants, Ai and Akira, to monopolize more the task. However, the juvenile chimpanzee, son of a dominant female, and one of the most experienced individuals performing computer tasks was the one monopolizing more time the task. Taking that in consideration, we suggest that, besides dominance, there is, in this case, at least, other weighting factors accounting for the current results - the experience in using touch panel and the support of the mother.

Running more sessions would probably allow us to have clearer results: higher rate of anecdotal events that were observed, as well as understanding the evolution of Akira's behaviour towards the monopolization of Ayumu. We could also have changed some variables like separating individuals from the group, e.g. Ayumu. Calling him inside would allow us to verify if less dominant individuals would approach, like they did in the session he was absent would. Other changes could be separate only Ai, to see if Akira changes the behaviour and how it would change, once Ayumu would not have the support of mother. We also could leave in the group only Pendesa, Mari and Reiko, to see if Reiko would learn the task and who understand who is more dominant towards it, Pendesa or Mari.

4. Study 2

**Chimpanzees are Prosocial in a Task
Mediated by a Touch Panel Computer**

4.1. Introduction

Life in social groups, as mentioned before, has costs (van Schaik, 1983). However, animals that live together are known to engage in cooperative and altruistic behaviours (Hamilton, 1964; Trivers, 1971) for the benefit of the group (see: Hamilton, 1963).

In Nature, each individual acts better in their immediate self-interest, although if all the individuals only act according to their own interest, everyone would be worse off. To evolve and to perpetuate in the species, altruistic behaviour has to bring benefits more often than it entails costs to the species: i.e. has to increase their relative fitness (Hamilton, 1963; van Vugt and van Lange, 2006)

Humans are clearly a case in which social exchange acts as a benefit to increase the relative fitness of the individuals that engage in altruistic behaviours, enabling it to spread through the next generations (van Vugt and van Lange, 2006). They frequently engage in a bunch of activities aiming to help others without benefiting themselves from the act and sometimes their acts can entail costs (Fehr and Gaechter, 2002; Fehr and Fischbacher, 2004). They have been described as the unique species that act altruistic towards non-kin related individuals (Fehr and Fischbacher, 2003).

The topic of altruistic behaviour in non-human animals (increasing others fitness by compromising their own), especially in our closest living relatives, generates a lot of controversy. Unlike what once was thought, that humans were the unique altruistic species, altruistic events have been observed in some mammalian *taxa* in many different forms (see: de Waal *et al.*, 2008).

One spread example of altruistic behaviour occurs when an individual loses opportunities to produce their own offspring to help a conspecific raising its own. In this case, the altruistic individual is kin-related to the altruistic target and there is some benefit for the actor once there is some probability of the offspring carrying its alleles (Hamilton, 1974).

There are mainly two ways of looking into altruistic behaviour. Biologists focus on the understanding of the evolution of the behaviour taking into account their ultimate causations, once it can have costs to the author. Meanwhile, psychologists are more interested in the internal motivations, as the proximate mechanisms on the behalf of acting prosocially (de Waal, 2008).

In psychology, altruism is considered to be a motivational concept that can benefit the recipient but at the same time can entail some costs to the actor and in the absence of a direct and obvious reward (Batson and Powell, 2003, de Waal, 2008). This concept is the opposite of egoism which has the ultimate goal of increasing one's own welfare. Prosociality is described as a behaviour that includes actions intended to benefit both the actor and recipient, such as helping, comforting, sharing, and cooperating, but not all the prosocial behaviours have altruistic or egoistic motivations (Batson and Powell, 2003).

In order to understand evolution and the underlying mechanisms of prosocial behaviour, chimpanzees can be a good model for comparative studies due to many reasons (already described in the main introduction): 1) Their shared and recent common ancestry with humans, which makes them the best parsimonious model to study the evolution of human behaviour. 2) Their behaviour in the wild showing evidences of prosocial behaviour, as mentioned in the general introduction. 3) The evidences showing they understand intentions of other individuals, which seems to be crucial to understand others needs in order to help them.

The topic of altruism in non-human primates, especially in chimpanzees has received lately a lot of attention by researchers on social cognition. Chimpanzees have been tested in many different settings regarding cooperative and altruistic behaviour (see: Hirata, 2009).

Some captive studies have reported prosocial tendencies supporting the evidences from their behaviour in the wild (Warneken *et al.*, 2007; Melis *et al.*, 2008; 2011a; 2011b; Horner *et al.*, 2011; Yamamoto *et al.*, 2012), although this question remains controversial, because other studies failed in showing prosocial tendencies (Silk *et al.*, 2005; Jensen *et al.*, 2006; Vonk *et al.*, 2008).

Besides prosociality and cooperation, other topics related to this, such as fairness and economic decision making, are target of interest of many researchers. Results show that chimpanzees, as well as capuchin monkeys, reject to receive a lower quality reward compared to their partner's (Brosnan and de Waal, 2003, Wynne, 2004; Bräuer *et al.*, 2006; Jensen *et al.*, 2007 but see: Brosnan *et al.*, 2005).

Considering captive experimental environments, there are two main paradigms used in social cognition to test prosociality in non-human primates, described by Horner *et al.* (2011) as follows:

- 1) Giving assistant tests (GAT) – requires action or inaction. One can choose between helping, by providing instrumental help, or not helping the other individual. E.g., receptor provides a tool for the actor so he can reach the main goal and obtain the reward.
- 2) Prosocial test choices (PCT) – requires choosing between two actions; contrary to the previous paradigm, in this case, the actor is requested to choose between two actions: prosocial (allowing both of them to be rewarded) or selfish (only the actor receives the reward).

Chimpanzees seem to show better results for prosocial behaviour in GAT paradigms, in which they were requested, for example, to pull a peg in order to allow other individual to get the reward (food or objects), without being themselves rewarded (Melis *et al.*, 2011); to provide a tool to the other individual for him/her to reach the goal (Yamamoto *et al.*, 2012); to help by cooperating with the other individual to pull a rope so that both of them could reach the food reward (Hirata and Fuwa, 2007). They also help their conspecifics and humans in situations that can be costly for the actor, that requires more effort to perform and in situations where no reward was given (Warneken *et al.*, 2007).

Communication seems to have a critical role in this kind of experiments, once under the actors' request chimpanzees tend to cooperate more (Melis *et al.*, 2011a; Yamamoto *et al.*, 2012). However, Horner *et al.* (2011) could not show that under request the prosocial tendencies increase. With regard to PCT, only the study by Horner *et al.* (2011) reported prosociality in chimpanzees when a prosocial and a selfish option are given. The authors claim evidences of prosociality once their results reported that chimpanzees chose the prosocial option above the chance level (58%) compared to a ghost condition (where the recipient was absent), in which the prosocial choices reached 45%. Taking their results in consideration, Skyoles (2011) argues that what Horner *et al.* (2011) have found was not prosociality, arguing that just because chimpanzees chose prosocial above chance level does not mean they are prosocial, once they still chose the selfish option 42% of the trials in the experimental condition. Instead of prosocial behaviour, Skyoles (2011) considers that what they showed should be called *mean-spirited*.

In Horner's *et al.* (2011) experiment, chimpanzees had to exchange the tokens for the food reward. They improved aspects of some of the previous PCT studies. The

experiment was less complex, and probably easier to understand. In order to reduce the position biases, 30 tokens were available for them to make the choices (15 with one color representing one choice and 15 with another color representing another choice) They placed the chimpanzees right next to each other, separated by a grid to allow the communication between the two individuals. Thirty trials were run with each pair of chimpanzees and the role of the actor and the recipient changed across the pairs.

Recognizing some limitations of Horner's and previous studies, our current study on prosocial behaviour tended to improve their paradigm by adding some other important features:

- 1) Using touch panel tasks, allowing us to run more trials in less time, giving more accurate results on statistic tests.
- 2) Changing the housing conditions of the subjects during the task. The chimpanzees in our study were in the same compartment of the experimental booth, to increase the social pressure.
- 3) We added an altruistic option (rewarding only the recipient), in order to see if chimpanzees chose to be altruistic. Instead of having two options chimpanzees had to understand the meaning of three keys.
- 4) We ran 3 different conditions to understand how prosocial behaviour is modulated across the given environments.
- 5) We looked into the distribution of their choices across the trials instead of looking only to the average.

4.2. Subjects

In order to run the prosocial experiment we used three pairs of chimpanzees (mother-offspring) from the same two groups used in the previous study. The subjects were Ai-Ayumu, Pan-Pal, and Chloe-Cleo. Ai and Ayumu belong to Akira's group, previously described in study 1. Besides Akira's group, Primate Research Institute, Kyoto University houses one more chimpanzees' group, where the other 2 dyads are included. Pal, Pan, Chloe and Cleo belong to Gon's (the only male present) group. The group has 7 individuals; Puchi and Popo are the higher ranking females of the group. As Akira's group, Gon's used the outside area from 10 am to 5pm in alternate days to Akira's. When the individuals were not present in the outside enclosure, they spent time in the inside enclosure.

The participants of the current study were requested by the experimenters to enter the inside booth in order to perform the experiment. They are active participants in diverse cognitive tasks performed via touch panel computers and recently engaged also in touch panel experiments in a social context (Martin *et al.*, 2011). Each individual of the dyad played the actor and recipient role in every condition. After one individual has performed all the trials, the experimenters switched the chimpanzees' position in the booth. This was the only time during the experiment that the experiments interacted directly with the chimpanzees. After finishing the task, chimpanzees were brought back to their place.

Despite of having 13 chimpanzees in total, we only used 6 individuals to perform the task. Only mother-offspring pairs were allowed to share the same booth to perform the tasks. Juveniles could not be called to the experimental area without their mothers and vice-versa. Since the juveniles were born they go inside the booth with their mothers so they are used to share the same area of the booth.

4.3. Material and Methods

4.3.1. Housing and Apparatus

The experiment was carried out in an indoor experimental booth (2.5 m x 2.5 m x 2.1 m) delimited by four walls, constituted by acrylic panels and divided in two compartments.

Two identical 17-inch LCD touch panel displays (1280 x 1024 pixels) were embedded into the acrylic panel in a different and perpendicular wall of the same compartment of the booth, where the chimpanzees were located. Chimpanzees were placed in the same compartment of the booth, with an approximate distance of 0.40 m, to increase the social pressure (Figure1). One degree of gaze angle corresponded to approximately 0.7 cm on the screen at a 40 cm viewing distance. Outside of the experimental booth, in front of each touch panel computer, two food trays with their respective universal feeders (Bio Media Co. Ltd.) were set. The function of the feeder is to provide the reward to the chimpanzees once it was activated by their choices, through the coding on the program. The codes to run the program were prepared using Visual

Basic 2010 (Microsoft Corporation, Redmond, Washington, USA), by Professor Ikuma Adachi.

In order to provide the reward to the actor or to the recipient or to both individuals, according to the actor's choice on her/his screen, two feeders were yoked to the main computer, controlled by the experimenters, where the program was running. The actor had total control in providing the food reward to the recipient and to himself/herself. Each feeder, when activated, had different rewarding sounds. When the actor was provided with the reward, the feeder connected to its monitor played a different sound from the situation in which the actor chose to feed the recipient. In case of both individuals being rewarded, their respective sounds played together (actor sound and recipient sound). Playing different sounds for each individual allowed the chimpanzees to discriminate which one was being rewarded.

The reward consisted of pieces of apple with the dimension of 1cm^3 and raisins randomly distributed in the food tray. Each food tray comprised 40 small spaces where the apple pieces and raisins were placed.

The experimenters had no direct contact with the subjects. Their only role was to fill the feeder and to prepare each session on the computer program.

All the sessions were video-recorded with two video digital cameras (Sony HDR-CX560) in two different perspectives, in order to capture any interesting interactions between the individuals.



Figure 1 - Pan and Pal performing the prosocial experiment. Pan as the actor on the left and Pal as the recipient on the right.






















4.3.2. Stimuli

To initiate the task, a circular button was presented as stimuli in the actor’s screen. After pressing the start key, the actor was presented with three (experiment 1) or two (experiments 2, 3) horizontally aligned shapes that served as buttons to indicate the choice of reward: prosocial (reward for both individuals), mean-spirited (reward only for the actor) and altruistic (reward only for the recipient), social, mean spirited and altruistic.

The meaning of each shape (table 1) was randomly assigned to each individual and the horizontal distribution of the shapes also changed across the individuals (see table 1). However, to facilitate the association of the shapes with the choices (prosocial, mean-spirited and altruistic) the shapes were assigned with the same choice meaning for each individual across all the trials and different conditions.

The designation of the mean-spirited key was given according to the definition of Skoyles (2011), by claiming that chimpanzees are mean-spirited when they chose given reward only to themselves. We decided to discriminate altruistic from prosocial. By definition, altruism means any action that benefits other individual, entailing costs to the actor (Vonk *et al.*, 2008). In the current study, once we cannot measure the costs or benefits of the actor’s choice, we designate altruistic the option that benefits only the recipient. Prosocial choice, as the definition states, aims to benefit both the actor and recipient. According to that, we decided to use this term to designate the option that rewards both individuals. The same designation was used by Horner *et al.* (2011). Table 6 indicates the assignment of each key for each individual.

Table 9 – Stimuli assignment across individuals in all three different conditions

Subjects				Order of the presentation of the keys
Ai	Mean-spirited	Altruistic	Prosocial	  
Ayumu	Altruistic	Mean-spirited	Prosocial	  
Chloe	Prosocial	Altruistic	Mean-spirited	  
Cleo	Altruistic	Mean-spirited	Prosocial	  
Pan	Altruistic	Mean-spirited	Prosocial	  
Pal	Prosocial	Selfish	Altruistic	  

4.3.3. Statistical analysis

Statistical analyses were performed using the R software version 2.14.2 (<http://www.r-project.org/>). Microsoft Office Excel 2010 (<http://office.microsoft.com/pt-pt/excel/>) to create the bar plots and Matlab (MATrix LABoratory) version 7.14 (<http://www.mathworks.com/products/matlab/>) for the plots showing the distribution of the cumulative mean of the choices across the trials.

The statistical tests used were non-parametric, chi-square tests according to the assumptions given by Motulsky (1995), in order to compare between to possible outcomes among 2 or 3 groups.

The P-value significance was set as > 0.05 with the confidence interval of 95%, to confirm H0. The error bars present in the plots corresponded to standard error of the mean.

4.3.4. Procedure

4.3.4.1. ***Training phase: associating the different sounds to the reward and introducing the concept of the yoked feeder***

The three dyads were trained to discriminate three different sounds corresponding to the three different options, in order to understand the mechanism of the reward by feeders and to understand that there were two feeders providing food. The sounds used were different from the ones chimpanzees are used to in other tasks and that they associate as a rewarding sound. This concept of the yoked feeders was new to all the chimpanzees, although they are used to share the same compartment to perform tasks in a social context (see: Martin *et al.*, 2011).

In this training phase, the actor was placed in in front of his/her monitor, and the recipient was separated in the other compartment of the booth, so that the actor could easily ear the sound and pick up the reward on the recipient feeder. We chose to separate the individuals in this phase to allow the actor to pick the food in the recipient's place. This way facilitated the actor to understand that both feeders were providing food.

The experimenter, controlling the computer program, randomly chose to deliver food to the actor, or to the recipient (that was not present), or both, by pressing 1, 2 or 3, respectively, in the keyboard of the computer, where the two feeders were connected.

We ran 200 trials for each individual. Chimpanzees showed they were able to recognize that both feeders were being activated. They were picking both rewards: the reward of the recipient's feeder and their own reward.

4.3.4.2. *Learning phase: introducing the stimuli*

In this phase, chimpanzees received their own assignments of the stimuli for the first time (table 1). To assure that individuals were able to associate the shape with the respective function on a later phase, we initially conducted a training phase before starting with the experimental sessions.

Chimpanzees were placed in the same compartment, in front of their respective monitors as it was already the experimental phase. The recipient was introduced to their respective monitor and the actor was trained to understand that their choice would influence the other's reward.

To all the individuals, we ran 3 sessions, in which each stimulus was presented for 24 trials: 24 trials with the presentation of the cube, 24 trials with the sphere and 24 trials with the cylinder. Once the actor finished the 3 sessions, positions were changed, the actor was moved to the recipient position, the recipient took the place of the actor and a new session started.

4.4. Results

4.4.1. Experiment 1: Three button choice

After they showed understanding of the two feeders' yoked condition and the function of each key, we started the experimental phase. The first session was run with the three options: prosocial, mean-spirited, and altruistic, aiming to understand if chimpanzees choose the prosocial option more often giving the other 2 choices: mean spirited and altruistic. The key assignments were the same that were shown in the training phase.

Subjects were placed in their exact locations, in the same compartment. First the actor was shown with the start key, a circular button on the middle button of the screen. After the starting key was touched, the actor was presented with three choices: a prosocial choice, giving reward for both individuals, a mean-spirited choice, giving reward only to the actor, and an altruistic choice, that benefits only the recipient by

providing her/him the reward. Each individual had different assignment for the stimuli and different orders (described in table 1).

We ran 3 sessions of 48 trials (144 trials on total) for each individual (N=6). As it was done on the training phase, after an individual finished the 3rd session chimpanzees changed their places, the actor was moved to the recipient's place and vice-versa. Each pair received the 3 sessions in one day.

In experiment 1, our results indicate that chimpanzees choose to act prosocial above the mean-spirited or altruistic choices in a three-button choice experiment, significantly (Chi-square, $\chi^2 = 554,576$, $df=2$, $P=0.000$).

Taking the mean of the 144 trials (3 sessions) performed by the 6 chimpanzees (N= 864), results show that, on average, subjects chose prosocial in 79% of the trials, mean-spirited in 17% and altruistic in 4% (figure 2).

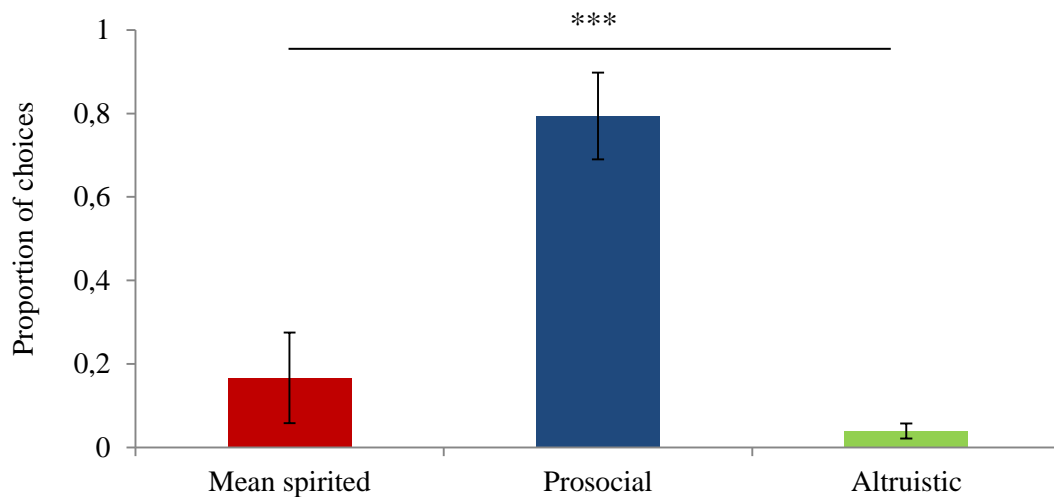


Figure 9 – Mean of the proportion of choices regarding the three different choices with the total of 846 trials. Chimpanzees showed 17% of mean-spirited, 79% of prosocial and 4% of altruistic. *** indicates a P-value <0.001.

By dividing the time course of trials into bins of 8 trials representing the cumulative means of the individuals, we show that, after an initial exploratory phase, all chimpanzees show a predominant tendency towards the prosocial choices (figure 3). Further trial courses reveal an initial phase of ambiguity among the choices, that serves with a purpose to assign the shapes of the button that they learnt in the previous condition to their respective functions (reward options).

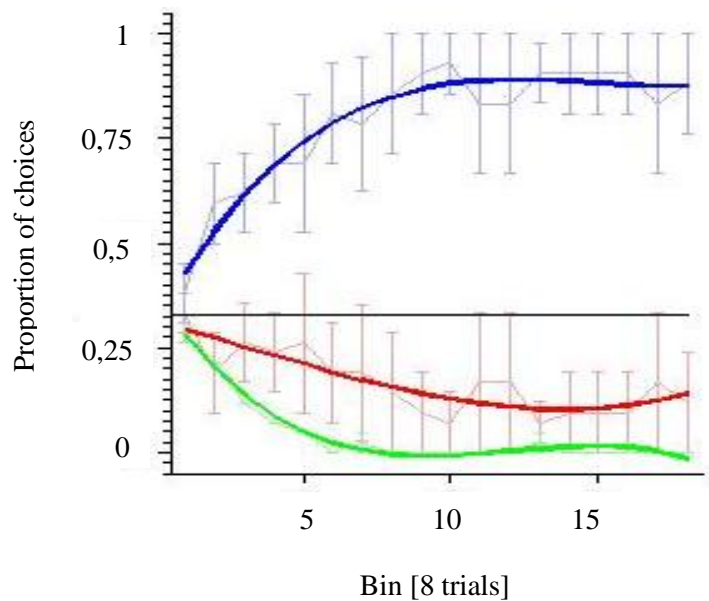


Figure 310 - Distribution of the choices across the trials represented by the cumulative mean: prosocial (blue), mean-spirited (red) and altruistic (green) choices. Trials are grouped in 6 bins of 24 trials.

By looking into the choices of all the individuals in each session (Table 2), we can see that in first session, the one comprising the exploratory phase, the difference between prosocial and mean-spirited is lower than other sessions for all the individuals, excepting Pan.

The trend was clear in the second and third sessions. All the individuals were choosing prosocial key above 90% of the choices (Ai chose prosocial 94% in the third session) with the exception of Pan, which performed 65% as mean-spirited in the second session and 60% in the third session (table 2).

Pan was the only individual that did not follow the general trend. She never chose the altruistic key and in the session 1 only 8% of her choices were prosocial. In the following sessions, she chose prosocial in a higher percentage, although she kept choosing mean-spirited more than prosocial. If we excluded Pan from the sample size, the average of the prosocial choices of all the other five individuals would reach 91%. Although considering that our sample size is already small, we decided not to exclude Pan from the analyses. But it is important to mention that in this experiment she is the

individual who is contributing to the decrease of the prosocial choice's mean. In this experiment Cleo is also an exception once she did not show an exploratory phase. She always chose the prosocial option in all trials. Ayumu and Ai had a very similar performance, by exploring both 3 options in the session 1 and choosing 100% prosocial in the following sessions (except Ai in the third session, with 94%). Chloe also showed the same trend, exploring the three choices in an initial phase, although the rate of prosocial choices was higher compared to Ai and Ayumu, and 100% in the following sessions. Pal did not choose the altruistic key during all the trials, but in the session one she explored both the mean-spirited and the prosocial key.

Table 10 – Mean of the proportion of choices for each individual (P- prosocial, A-altruistic, MS – mean-spirited) in each sessions (S1- session 1, S2- session 2, S3- session 3).

Subjects	S1				S2			S3		
	S	A	MS	P	A	MS	P	A	MS	
Ai	0,52	0,08	0,40	1,00	0,00	0,00	0,94	0,02	0,04	
Ayumu	0,54	0,10	0,35	0,98	0,00	0,02	1,00	0,00	0,00	
Chloe	0,73	0,10	0,17	1,00	0,00	0,00	1,00	0,00	0,00	
Cleo	1,00	0,00	0,00	1,00	0,00	0,00	1,00	0,00	0,00	
Pal	0,94	0,00	0,06	1,00	0,00	0,00	1,00	0,00	0,00	
Pan	0,08	0,00	0,92	0,35	0,00	0,65	0,40	0,00	0,60	
Mean	0,64	0,05	0,32	0,89	0,00	0,11	0,89	0,00	0,11	

4.4.2. Experiment 2: Mixed condition

In this new condition, chimpanzees were kept in their respective locations, and the key assignments were kept as well as their location in the screen.

We reduced the number of choices from three to two and requested the chimpanzees to select between prosocial and mean-spirited (P-MS), mean-spirited and altruistic (MS-A), or prosocial and altruistic (P-A). We ran 96 trials for each subject, in which every 6 trials the two choices were presented randomly, at least 2 times. On the total, 32 of each combination were run. These different types of trials (96 trials) were presented interspersed with three-choice trials at a ratio of 1:5 in random arrangement across 2-choice trial types, to assure that chimpanzees could associate this new condition with the previous one.

In this condition, chimpanzees are forced to explore all the three combinations of the 2 different options aiming to understand if they keep choosing the prosocial key

when the mean-spirited is given, knowing they could be rewarded by both of them. Besides that, we can explore and see their preferences when they are forced to choose between altruistic against any other choice.

Overall, results indicate a prosocial tendency in P-MS as well as in P-A trials, but a mean-spirited preference in M-A trials.

Looking into the average of all the individuals in all of the trials (N=576) we can see a clear tendency to the prosocial choices (71%) compared to mean-spirited (29%, Chi-square, $\chi^2= 35,021$, $df=1$, $P=0.000$, figure 4a).

Looking into to the distribution of the cumulative mean across 32 trials (figure 4a) we can see in the beginning that chimpanzees were choosing prosocial and mean-spirited at the same rate (being prosocial choices slightly higher), however during the course of the trials there is a gradual increase of the prosocial choices (figure 4b)..

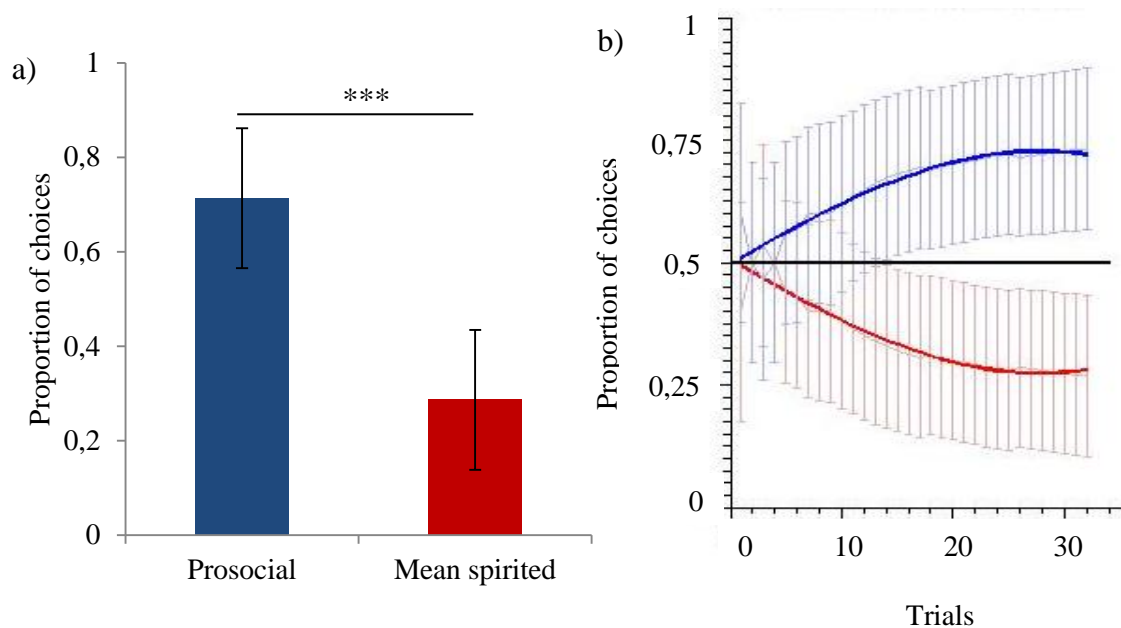


Figure 4 – a) Mean of proportion of mean-spirited versus prosocial choices. b) Distribution of the mean-spirited (red) and prosocial (blue) choices, given by the cumulative mean, across the 32 trials. *** indicates a P-value <0,001.

Considering the trials where they had to choose between mean-spirited and altruistic, there was a clear preference for the mean-spirited key (Chi-square, $\chi^2= 77,521$, $df=1$, $P=0.000$, figure 5a). Across the 32 trials, the choices were kept stable, without an initial exploratory phase as observed in the previous condition (figure 5b).

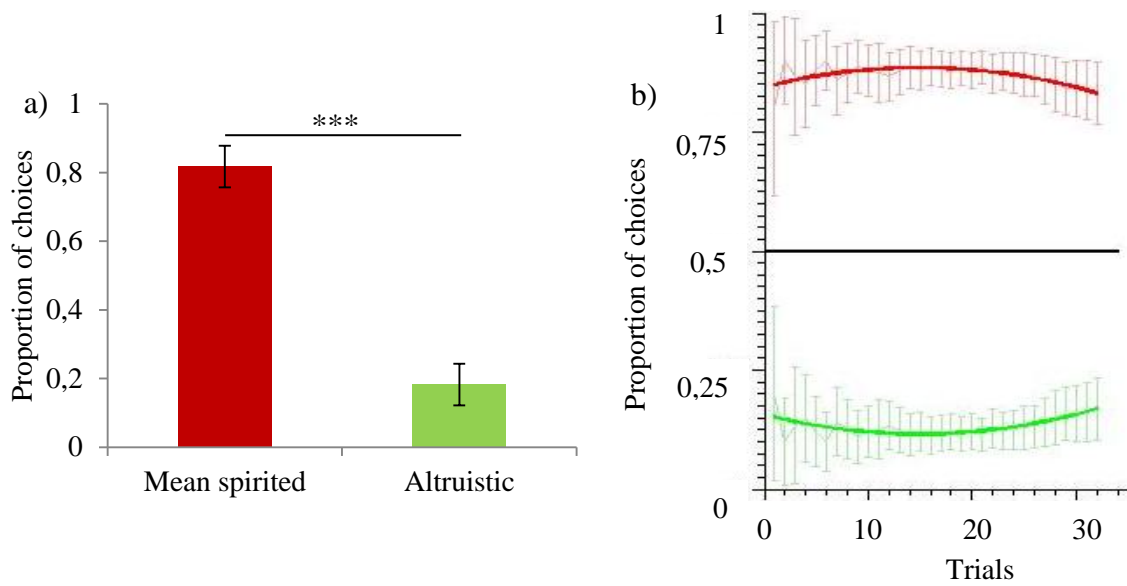


Figure 5 – a) Mean of the proportion of mean-spirited versus altruistic choices. b) Distribution of mean-spirited (red) and altruistic (green) choices, given by the cumulative mean, across the 32 trials. *** indicates P-value <0,000.

In the 32 trials conducted in the condition for the prosocial and altruistic choices, we can see a clear tendency to choose prosocial contrary to altruistic (figure 6a). In the plot representing the cumulative mean of distribution of the choices across the trials, there is an increase of prosocial choices that almost reaches 90% (figure 6b). Again in the first trials there were higher differences in the individuals' performance given by the value of the error bars, larger in the initial trials (Chi-square, $\chi^2=156.688$, $df=1$, $P=0.000$). In this condition chimpanzees chose altruistic less than the previous one, suggesting chimpanzees were choosing altruistic to counterbalance the mean-spirited option in M-A trials.

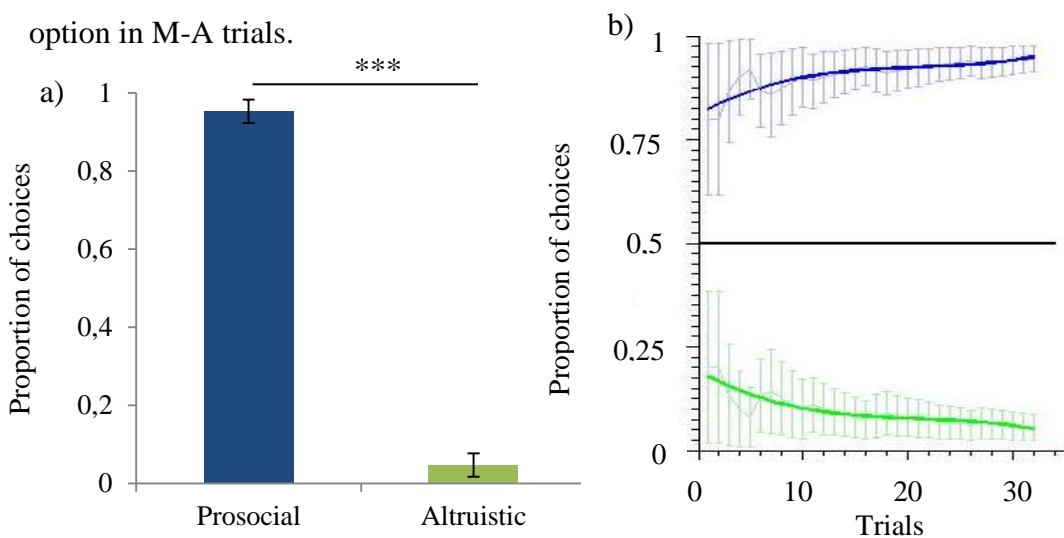


Figure 6 – a) Mean of proportion of prosocial and altruistic choices. b) Distribution of the prosocial (blue) and altruistic (green) choices, given by the cumulative mean, across the 32 trials. *** P-value indicates <0,000.

The performance of each individual showed a clear tendency in choosing to act prosocially instead of altruistically in all of the trials of P-A condition, with the exception of Chloe, that chose altruistic in the initial trials (table 3). Regarding P-MS, there is also a tendency shared by all the individuals on choosing prosocial at a higher rate, with the exception of Pan. Also, Chloe and Ayumu showed less prosocial tendencies in this round, compared to the other individuals, although once again a higher rate of the mean-spirited choice is verified in the initial trials, suggesting a phase where they are trying to understand the key assignments. Compared to the previous condition, we showed here that individuals showed a slightly decrease in the prosocial option in P-MS condition.

Table 11 – Proportion of choices across all the individuals in the three different conditions.

Subjects	Prosocial-Mean-spirited		Prosocial-Altruistic		Mean-spirited-Altruistic	
	P	MS	P	A	MS	A
Ai	0.91	0.09	1	0	0.94	0.06
Am	0.62	0.38	1	0	0.75	0.25
Chloe	0.75	0.25	0.84	0.16	0.87	0.13
Cleo	1	0	1	0	0.59	0.41
Pal	0.97	0.03	1	0	0.75	0.25
Pan	0.03	0.97	1	0	1	0
Mean	0.71	0.29	0.97	0.03	0.82	0.16

4.4.3. Experiment 3: Blocked condition

Finally, we tested chimpanzees in a blocked condition to further explore the dynamics of dyadic preferences. Individuals were in their respective positions and again the same assignments and the location of the keys were kept. In this condition, we requested chimpanzees to choose again between two choices, but this time we blocked the two-choice trials (the same used in condition 2, P-MS, P-A, MP-A), and ran each pair of choices for 96 trials, with a total of 576 trials considering all chimpanzees. Each pair was tested in a different condition of 96 trials (48x2) on different days (table 4).

Table 12 – Distribution of the conditions given to chimpanzees in 3 different days.

Subjects	Day 1	Day 2	Day 3
Ai-Ayumu	MS-O	P-O	P-MS
Chloe-Cleo	P-S	MS-O	P-O
Pal-Pan	P-O	P-MS	MS-O

When looking into the 96 trials corresponding to the prosocial and mean-spirited choices, the results were similar to the previous experiment (mixed condition). Chimpanzees chose acting prosocial in 79% of the trails against 21% mean-spirited (figure 7a, Chi-square, $\chi^2= 196$, $df=1$, $P=0.00$). The proportion of prosocial choices was exactly the same, 79% compared to the experiment 1 (three button choice). The plot with the distribution of the cumulative mean showed that the prosocial tendency increases across trials (figure 7b).

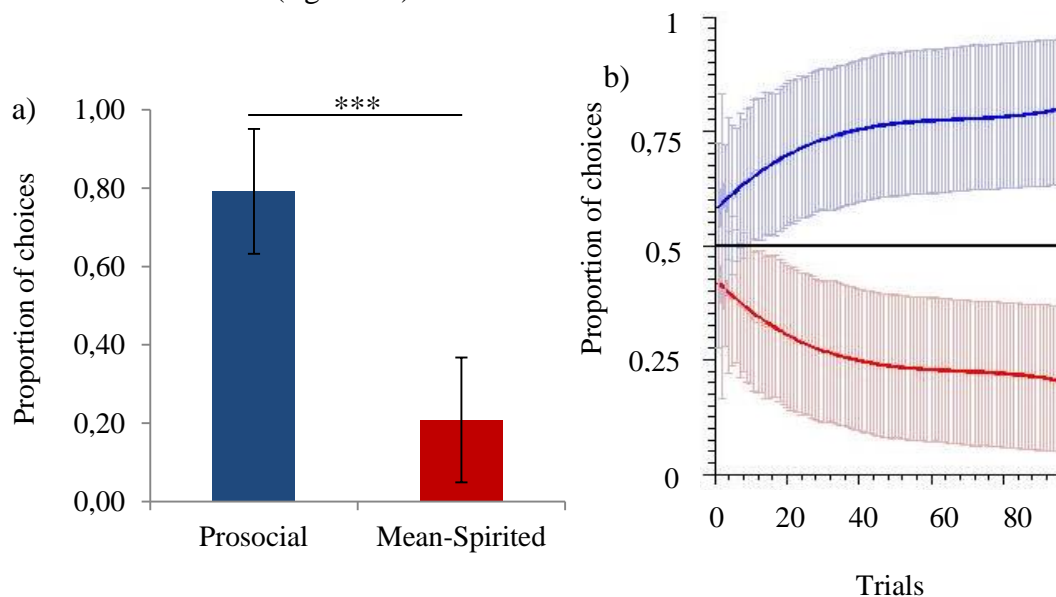


Figure 11 – a) Mean of proportion of prosocial and mean-spirited choices. b) Distribution of the prosocial (blue) and mean-spirited (red) choices, given by the cumulative mean, across the 96 trials. *** indicates P-value <0,000.

Regarding mean-spirited and altruistic choices, the mean of altruistic and mean-spirited choices were similar to what was verified in condition 2 (80% for mean-spirited, 20% for altruistic, figure 8a), however the distribution of the the prosocial choices decreased more along the trials (figure 8b), while in the experiment 2 (figure

5b), the choices were more constant across the trials. Chimpanzees chose on average 80% mean-spirited against 20% (Chi-square, $\chi^2=203,063$, $df=1$, $P=0.000$).

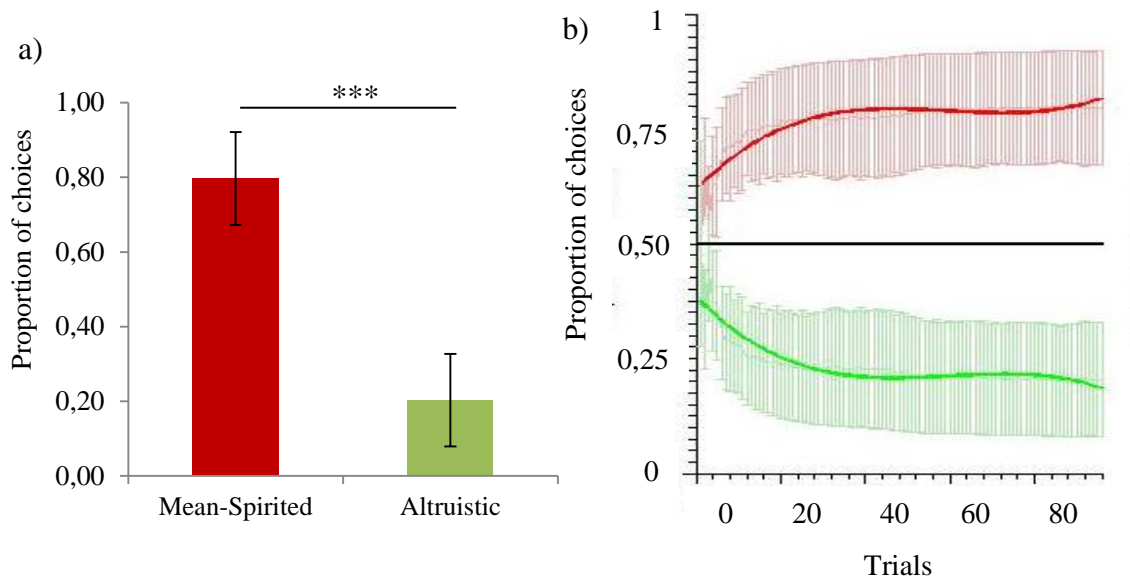


Figure 8 – a) Mean of proportion of prosocial and mean-spirited choices. b) Distribution of the mean-spirited (red) and altruistic (green) choices, given by the cumulative mean, across the 96 trials. *** indicates P -value $>0,000$.

When choosing between prosocial and altruistic choices, chimpanzees chose 99% prosocial on average (Chi-square, $\chi^2=552,250$, $df=1$, $P=0.000$, figure 9a). Regarding the distribution of the choices, the tendency was similar to that observed in condition 2 (figure 6b): in the initial trials, the average was lower and increased during the course of the trials reaching almost 100% (figure 9b).

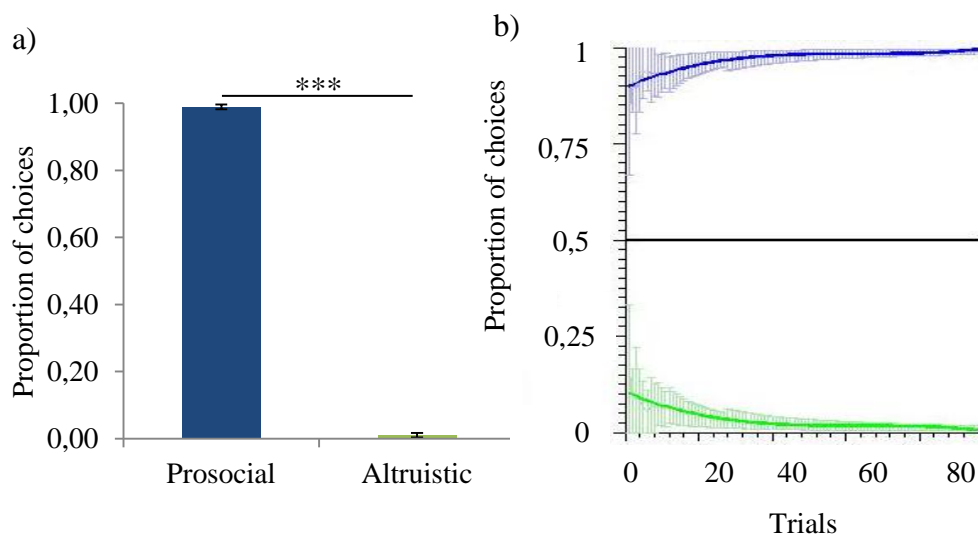


Figure 9 – a) Mean of proportion of prosocial and mean-spirited choices. b) Distribution of the prosocial (blue) and altruistic (green) choices, given by the cumulative mean, across the 96 trials. *** indicates P -value $>0,000$.

For the prosocial and mean-spirited conditions, it is clear the tendency to choose prosocial for all the individuals with the exception of Pan, who never chose to act prosocially (table 5). In trials of the P-A condition, almost all the individuals approached the 100% prosocial and the small exceptions happened in the initial trials.

Cleo was the exception in the MS-A trials, once she chose to act altruistic more often than mean-spirited and Pal distributed equally her choices in the same condition. All the other individuals acted almost 100% mean-spirited.

Table 5 – Mean of choices by each individual in the three different given conditions.

Subjects	Prosocial- Mean-spirited		Prosocial-Altruistic		Mean-spirited- Altruistic	
	P	MS	P	A	MS	A
Ai	0,99	0,01	1	0	1	0
Am	0,93	0,07	1	0	0,98	0,02
Chloe	0,96	0,04	1	0	0,98	0,02
Cleo	1	0	1	0	0,32	0,68
Pan	0	1	0,98	0,02	1	0
Pal	0,87	0,13	0,96	0,04	0,5	0,5
Mean	0,79	0,21	0,99	0,01	0,8	0,2

4.4.3.1. Juveniles versus adults

When we compared the proportion of choices of Mothers and Juveniles separately, the trend observed in the previous conditions was kept. Both groups of chimpanzees chose to act prosocially, significantly in the P-MS and P-A conditions and mean-spirited in MS condition (table 6).

Table 13 – Values of the chi-square test, for juveniles and mothers, comparing the choices in the three different conditions.

Prosocial/ Mean-spirited	P	MS	χ^2	df	P-value
Juveniles	269	19	217,014	1	0.000
Mothers	101	187	25,681	1	0.000
Prosocial/Altruistic	P	A	χ^2	df	P-value
Juveniles	284	4	272,22	1	0.000
Mothers	286	2	280,056	1	0.000
Mean-Spirited/Altruistic	MS	A	χ^2	df	P-value
Juveniles	173	115	11,681	1	0.001
Mothers	286	2	280,056	1	0.000

By comparing the proportion of choices between mothers and juveniles across the three conditions (figure 10), we can see that the condition P-A is the one where the results are almost equivalent, with both mothers and juveniles acting almost 100% prosocial. In MS-A condition, juveniles chose significantly to act more altruistic than their respective mothers (Chi-square, $\chi^2=134,543$, $df = 1$, $P=0.000$), by choosing to act altruistically on average in 40% of the trials, while mothers chose to act altruistically 1% of the trials on average (table 7). Regarding P-MS choices mothers chose to act more mean-spirited compared to the juveniles. The large error bar is due to the results of Pan, which were purely mean-spirited (100%). Table 7 present the results for Chi-square comparing between mothers and juveniles. The differences between prosocial and mean-spirited and mean-spirited and altruistic were significant. Both groups acted similarly in P-A condition.

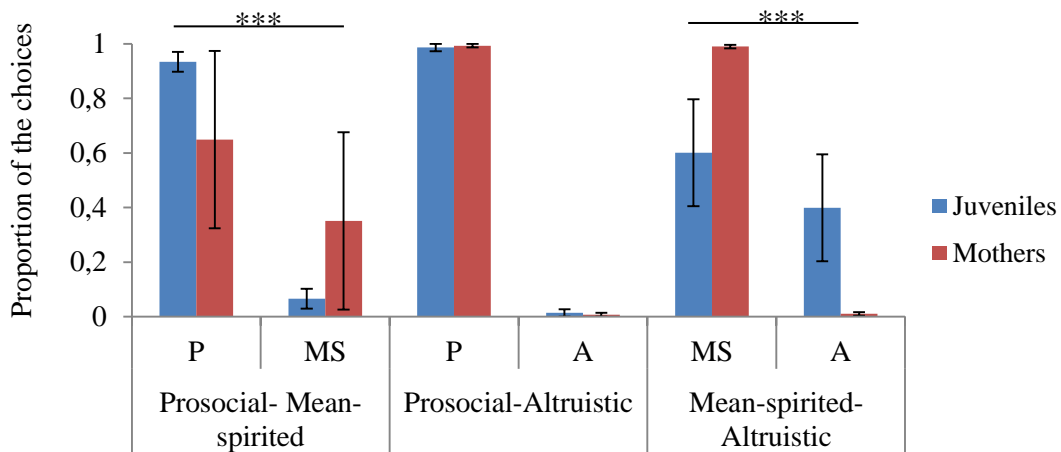


Figure 1012 – Mean of the proportion of the options chose by mothers and juveniles in the three different conditions (P-MS, P-A, MS-A). *** indicates P-value < 0,000.

Table 14 - Chi-square test comparing the choices of the mother with the choices of the juveniles in the three different conditions.

Choices	χ^2	df	P-value
Prosocial/ Mean-spirited	69,063	1	0,000
Prosocial/Altruistic	0,168	1	0.682
Mean-Spirited/Altruistic	134,543	1	0,000

The plots referring the distribution of the choices across trials (Figure11) show that the tendency to choose altruistic in the MS-A condition is more stable in juveniles. While, regarding adults (mothers), it started with 75% and reached almost 100% at the end of the trials (figure 12).

The altruistic choice in P-A decreased across the trials for adults, while juveniles showed a more stable. The large standard error bars in the juveniles plot are due to choices of Ayumu. Contrary to Cleo and Pal, that chose altruistic key above 90% of the trials, Ayumu only chose altruistic in 2% of the trials.

In the case of MS-P, there were also differences between mothers and their respective offspring. Mothers started by choosing mean-spirited above prosocial, although across the session the tendency has inverted and the average of mean-spirited choices was 35%. This value was pulled up due to the choices of Pan, which chose never to act prosocial. Juveniles acted prosocial 93% of the time and the tendency followed as expected in the previous conditions (the rates of prosocial choices increased across trials).

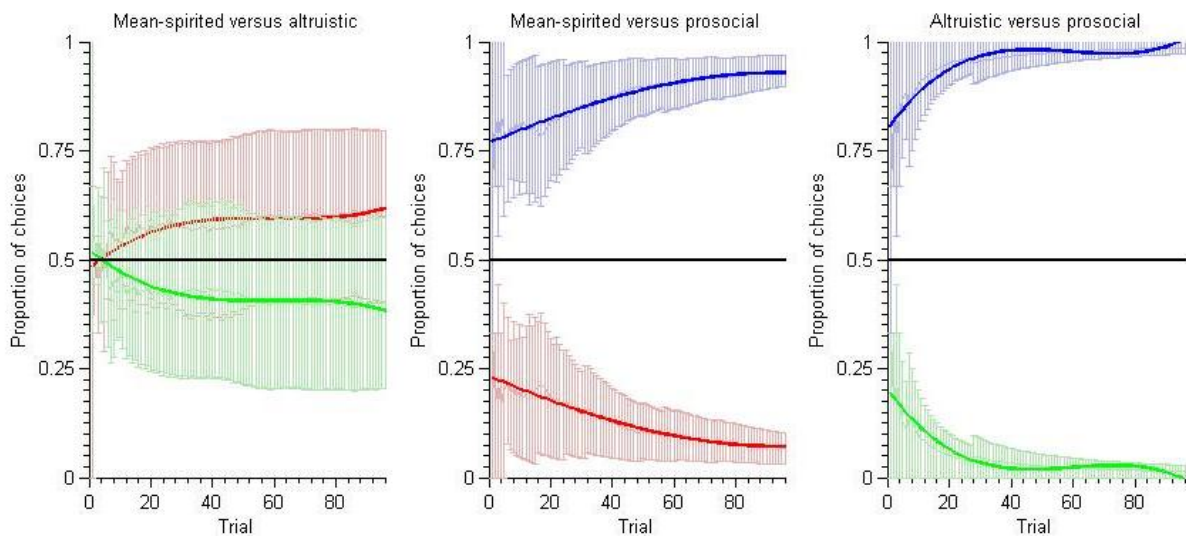


Figure 13 – Distribution of the choices, given by the cumulative mean, across the trials in the three different conditions referred to Juveniles. Red – mean-spirited, blue – prosocial, green – altruistic.

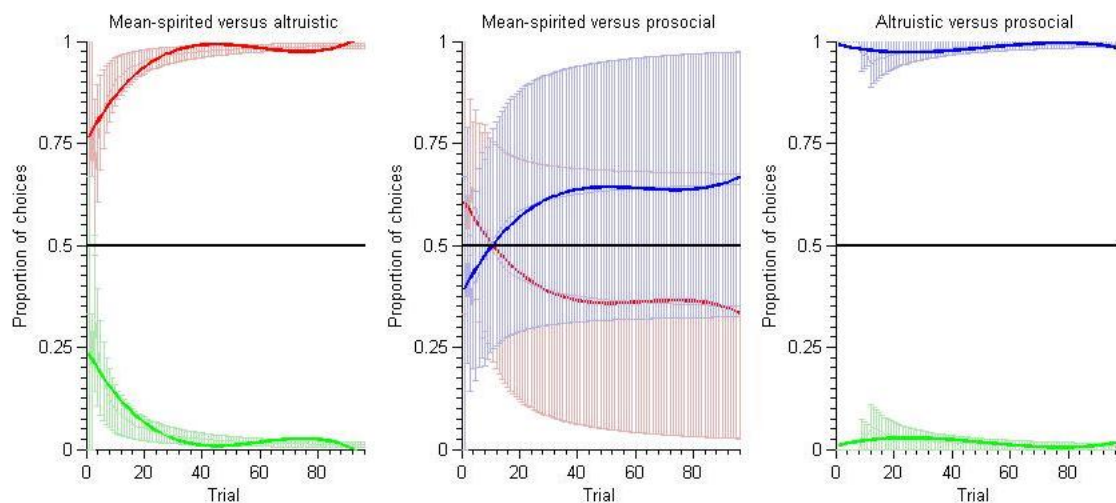


Figure 12 – Distribution of the choices, given by the cumulative mean, across the trials in the three different conditions. On the top the plots are referred to adults (mothers). Red – mean-spirited, blue – prosocial, green – altruistic.

4.5.Discussion

4.5.1. Experiment 1: Three choices button

In the condition 1, we ran trials with the three choices to understand the chimpanzees' preferences regarding act prosocial, mean-spirited or altruistic. Contrary to the previous studies, we decided to add an altruistic choice to explore all the possible options and how they organize them across the time/trials. Also, by adding the altruistic option, we could observe that chimpanzees were not choosing the three options randomly without understanding the meaning of the keys. It would not be advantageous for them to choose the altruistic option at the same proportion than others. Our results suggest an understanding that the altruistic key was not giving reward to them, once they stopped choosing it after a few trials.

The results showed that chimpanzees act prosocial 79% of the trials, and also suggested a presence of an initial phase, denominated by us as exploratory phase, where chimpanzees pressed all the three choices to understand/remember the keys assignment before deciding which key to choose. In this condition, Cleo did not have an exploratory phase, once she kept pressing the prosocial key during all the trials, once she had been rewarded she kept pressing the same button. Pan was the individual that acted less prosocial and she was an exception, because all the other individuals showed a clear increase in their prosocial tendencies after the exploratory phase (more than 90%).

4.5.2. Experiment 2: Mixed condition

In condition 2, mixed condition, we wanted to understand whether chimpanzees associate the assignments of the keys to the respective answers and if they understood that both mean-spirited and prosocial were giving reward to them. This is important for example in the case of Cleo, once she had no opportunity to test other keys. In this condition, as the name suggests, we randomized with the same proportion the two possible combinations of the three different choices across 96. Thus, chimpanzees were presented with the three possible choices in the same session, even though they seemed to discriminate and understand clearly the meaning of each key. They kept choosing prosocial at a higher rate (when this option was presented) and mean-spirited above altruistic after the exploratory phase, as expected and verified in the first condition.

However, the decrease in the proportion of prosocial choices was mainly due to Pan that only chose to act prosocial in 3% of the trials. Other individuals which accounted for the decrease were Chloe and Ayumu, that chose less prosocial in this experiment compared to the first. The fact that this experiment presented randomly the 3 combinations across the 96 could induce the chimpanzees to make mistakes in their choices, but apart from that, they kept showing prosocial tendencies above chance level and in a similar percentage to experiment 1 (experiment 1 - 79%, experiment 2 – 79%) and higher prosocial results compared to PCT of Horner and collaborators (2011).

4.5.3. Experiment 3: Blocked condition

For 96 trials, chimpanzees had to choose between acting prosocial or mean-spirited, mean-spirited or altruistic and prosocial or altruistic. Again, an exploratory phase was verified in P-MS, where the values of mean-spirited and prosocial were closer in the previous trials, and later it became clearer the preference for prosocial tendency. In this experiment, the chimpanzees recovered the same rate of choosing the prosocial key that was observed in experiment 1 (Experiment 1 – 79%; Experiment 3 – 80%). The P-MS condition in this third experiment is the one which resembles more the other prosocial experiments, chimpanzees were presented with 2 option: acting prosocial and mean-spirited/selfish continuously across the trials (Silk *et al.*, 2005; Vonk *et al.*, 2008; Horner *et al.*, 2011).

In the condition MS-A, we wanted to verify how chimpanzees distributed their choices across the trials. If the recipient did not receive the reward across the 96 trials he/she could get frustrated and behave in a way that could change the actor's decision, requesting or behaving in the way of getting attention (Yamamoto *et al.*, 2009; Melis *et al.*, 2011a; Horner *et al.*, 2011). Yet, in this condition subjects did not show any signs of frustration or request. Both juvenile females behaved more altruistically than their respective mothers and the juvenile male, Ayumu. Also, in general, juveniles acted more altruistically than their mothers. This may suggest that mothers are less tolerant than the respective offspring (see the discussion topic about mothers and juveniles).

In P-A condition, the results were similar to those of experiment 2. Chimpanzees kept showing a clear preference for choosing prosocial (almost 100%), and the proportion of altruistic choices was slightly lower in experiment 3. In this condition, both mothers and juveniles behaved similarly.

4.5.4. Comparison with Horner *et al.* (2011)

Considering the PCT paradigm, the study of Horner *et al.*, (2011) was the only one showing prosociality in chimpanzees. However, Skoyles (2011) argued that the results can be interpreted as mean-spirited instead of prosocial because chimpanzees still choose 42% of selfish option. Taking into account Skoyle's statement, we conducted the current experiments following up Horner's *et al.*, (2011) study in order to understand chimpanzee's choices regarding prosociality. By controlling and modifying the choices, we wanted to verify how they organize their choices and if they understand the assignments of the keys.

The results showed to be in accordance with Horner *et al.* (2011). However, improving the paradigm, by enhancing the social pressure and by increasing the number of trials to reduce an initial uncertainty due to button-function assignments, our results increased the overall bias to 80% from an average of 59% in Horner *et al.* (2011). Despite the valid remark by Skoyles (2011), we interpret our results as likely evidence for prosocial behaviour.

Horner *et al.* (2011) placed the actor and recipient in a closer proximity compared to the other studies, and claimed that this change explained their positive results, suggesting communication is very important in this contexts. We conducted the experiments by placing both the actor and recipient in the same compartment of the booth in order to increase the social pressure. Keeping both chimpanzees in the same area, the actor would feel the pressure of having the individual we would chose to reward or not close to him/her and this could be a factor influencing the actor decision. It is also easier for the actor to understand that other individual is involved in the task, if the recipient is positioned close and in the same compartment as the actor.

Individuals are used to share the same booth, compartment for touch panel tasks in a social context (Martin *et al.*, 2011), but not individual context, in which they are used to share different compartments of the same booth (e.g., Inuo and Matsuzwa, 2007). They were also tested in cooperative tasks before (without touch panel) and showed positive results regarding cooperation (Yamamoto *et al.*, 2009; 2012).

They respected their own place and did not interfere directly in the actor's performance. Both individuals stayed in front of their respective computer and the recipient sometimes poked on the glass when they were not being rewarded, especially Ai, although this action did not seem to have any influence on the actor's choice. The

pocking behaviour is also observed in individual tasks, when the chimpanzees finish the session or when feeder runs out of food.

Using computer touch panel tasks to conduct the experiment seemed to be advantageous. We could quickly run the tasks without individuals getting frustrated for not being rewarded and interfering in the other's performance.

Touch panel tasks were also advantageous because we could run more trials in a shorter time. This allowed us to obtain more data and thus more accurate results, given by statistical analyzes.

If we compare the results obtained by Horner *et al.* (2011), in their 30 trials, with our experimental results (considering only the first 30 trials), for the condition 1 or 3, the values obtained on prosociality were very similar. Horner and collaborators obtained in their study, on average, 58% of prosocial choices and 42 % of selfish or mean-spirited. In the current study, if we look into the previous 30 trials, we noticed that chimpanzees choose 55% on average of the prosocial option, in the condition 1 and 73.5% in the condition 3. We obtained similar results, especially in the condition 1, to Horner and collaborators'. We suggest that, if they had run more trials, they would probably have obtained better results regarding the prosocial choice, considering that chimpanzees understood the goal of the experiment.

The fact that Horner *et al.* (2011) did not show in their paper the distribution of chimpanzee's choices across the trials make our assumption harder to support, because we cannot compare the tendency of their choices across the trials with tendency of our results. If chimpanzees have followed a similar tendency to ours, (the increase of prosocial choices after an exploratory phase), instead of choosing randomly the options, it is possible that the number of trials has been a limiting factor in their study. By running more trials, probably they would have obtained a higher difference between prosocial and selfish.

4.5.5. General discussion

Chimpanzees showed prosocial tendencies in diverse experimental contexts (Warneken *et al.*, 2007; Melis *et al.*, 2011; Horner *et al.*, 2011) supporting evidences from the wild and captive observations (de Waal 1982, 1986; Nishida and Hosaka, 1996; Watts, 1998; Duffy *et al.*, 2007).

The current study also reported prosociality in a different and potentially good scenario that is so far not so well explored – touch panel computer tasks. Chimpanzees showed a clear trend to act prosocial and favour the other in all of the three different conditions. Taking together the results obtained in the different conditions in the current study, with the previous ones, reporting altruistic and prosocial behaviours in chimpanzees, the evidences of prosociality in chimpanzees are defying the idea that prosocial behaviour is not unique to humans (Brosnan and de Waal, 2002).

Once humans and chimpanzees show prosocial and cooperative behaviour, we can reason these features may have emerged at least with our common ancestor. However, studies in other apes and monkeys (Mendres and de Waal, 2000; Chalmeau *et al.*, 1997; Lakshminarayanan *et al.*, 2008), reported prosociality and cooperation in these species, suggesting these behaviours have emerged much earlier in our evolutionary course. Some evidences of altruism in a wide range of *taxa* were observed (de Waal, 2008). If the reports are indeed evidences of altruism, evolutionary convergence might be a plausible explanation for the evolution of this behaviour in that species (Yamamoto and Tanka, 2009).

At the date, only Horner *et al.* (2011) showed prosociality in chimpanzees regarding PCT tests, choosing between two options, as opposite of GAT (choosing between helping or not helping). Other PCT studies did not reach the same conclusions (Silk *et al.*, 2005; Jensen *et al.*, 2006; Vonk *et al.*, 2008; Yamamoto and Tanaka, unpublished). This study aided to support the validity of this paradigm.

We agree that the failure in showing prosocial behaviour in the other studies was due to some problems in their methodology. First of all, chimpanzees were housed during the experiments in different compounds, and in some studies they were more than 3 meters apart and separated by barriers (Silk *et al.*, 2005; Jensen *et al.*, 2006; Vonk *et al.*, 2008). Besides, the tasks performed by the chimpanzees in these studies seem to be complex and this could have hindered the understanding of the experiment's main goal.

The previous studies focused on the prosocial behaviour by conducting an experimental phase with a ghost condition phase (where the recipient was absent) and comparing the result of both conditions. Choosing to act prosocial in the experimental condition, significantly more, in comparison with the ghost condition, could be an indicator that they understand what the experiment requires. They only need to provide

food to the other if he/she is present in the area. However, some studies failed in showing that (Silk *et al.*, 2005; Vonk *et al.*, 2008, Yamamoto and Tanaka, unpublished).

Our approach to the topic was different. We decided not to include a ghost condition in our experiments, and instead exploit how they organized their choices. If we had run a ghost condition, we would have had to keep the exact same conditions used in the experimental condition. The only difference would have been the absence of the recipient on the compartment. In case we had run a ghost condition, once chimpanzees were sharing the same area, they would try to maximize their reward by choosing prosocial. That strategy would allow them to obtain twice the reward they would get if they chose mean-spirited or altruistic, and then the results would not be reliable. We can deduce this would be a very plausible scenario, once in the training phase chimpanzees were taking both the rewards provided by both feeders. Other studies showed that chimpanzees act in order to maximize their reward independent of others' presence (Jensen *et al.*, 2007).

In Vonk *et al.* (2008), chimpanzees had to use a stick tool to dislodge two similar food rewards. As soon as they made their decision to dislodge two food rewards, one for each enclosure, or both only for the actor, the food rolled into the respective enclosures. Their trend of the prosocial choices across the trials was the opposite of ours. Chimpanzees started by providing food to the other and across trials the proportion of prosocial choices decreased. The same tendency was verified in the ghost condition (when recipient was absent). The results can be interpreted as they did not understand the goal of the experiment because they behaved similarly either in the presence or the absence of the other. If they, indeed, were selfish, they would not give reward in the ghost condition.

Similar results were obtained in the study performed by Silk *et al.*, (2005) using a bar-pull apparatus, who also compared experimental and ghost conditions in two different populations of unrelated adult chimpanzees. They argued that their results complement observational studies of chimpanzees cooperating with only kin related. However, some experimental studies showed cooperation and prosociality studies showed that chimpanzees act prosocial and cooperate regardless of the nature of the relation with the recipient (Jensen *et al.*, 2006; Warneken *et al.*, 2007; Melis *et al.*, 2011; Horner *et al.*, 2011a). The results obtained do not support Hamilton's (1964) kinship theory, suggesting altruism is more likely to occur among kin-related individuals. In the wild, some studies report that prosocial and cooperative behaviours

are not entirely related to kinship; they seem to occur also among individuals that have non-genetic relatedness (Mitani *et al.*, 2000; Langergraber *et al.*, 2007).

In sum, we interpret these results as an indicator for prosocial, considering each trial as an independent event of decision making, and hence each occurrence (trial n) was not chained from the precedent one (trial $n-1$).

4.5.5.1. Influence of sex, kin and dominance

Taking into account the current results, we cannot support Hamilton's (1964) hypothesis, once we had tested only kin-related individuals: mother-offspring dyads.

In experiments 1 and 2, both mothers and offspring acted prosocially, excepting Pan. She is the individual contributing for the higher proportion of mean-spirited results in mother's group. Cooperative behaviour was previously found in a completely different setting. Using the same pair of chimpanzees, Yamamoto *et al.* (2009) showed that, both mothers and offspring helped the other to obtain the reward by providing a tool he/she needed.

Despite our small sample size, when looking into the experiment 3, we see that females (Pal-Cleo) acted more altruistically than the male (Ayumu). However, these dissimilarities in the choice can be due to inter-individual differences and not to gender differences. It would be interesting to explore sex differences regarding prosociality. We should expect females to act less prosocial than males, since in the wild they are the ones leaving the group (Goodall, 1986; Symington, 1988; Nishida *et al.*, 2003), and males showed are reported to engage in more cooperative behaviours compared to females (Symington, 1990; Mitani *et al.*, 2002). The fact that Ayumu showed less prosociality compared to Pal and Cleo could also be due to his position in the rank and physical strength. Pal and Cleo have no interest in defying their mothers that are more dominant and stronger, by making them frustrated for not providing reward. However, the fact that Ayumu is a male and has a dominant position in the rank, could have influence on their choices.

In the wild, chimpanzees' mothers don't actively share food with their offspring. They are tolerant to the offspring on "stealing" the food from them (Silk, 1978, Hirata, 2009, but see evidence from captive experiment: Ueno and Matsuzawa, 2004). This

behaviour is known as “tolerated theft” (Vonk *et al.*, 2008). Following that reasoning, we would not expect our results to show altruistic behaviour when a mean-spirited option is given, once wild and captive mothers do not share the food with the offspring actively. Ueno and Matsuzawa (2004) reported cases where a mother actively shared food with her offspring, although it happened after the offspring begged. In the current study, mothers chose to provide a reward to their offspring only if they were also rewarded, by choosing prosocial key, when the alternative was mean-spirited.

Besides mother-offspring relation, the individuals have a dominant-subordinate relation, and mothers are dominant to the offspring. In the case of Ai and Ayumu, the situation is less clear, because male and females have different ranks (see: Wittig and Boesch, 2003) and males are often dominant to females (de Wall, 1982; Nishida, 1983; Goodall, 1986; Parish, 1994). Based on background information and the fact that Ayumu is a Juvenile and son of Ai he is probably still less dominant than his mother.

Yamamoto *et al.* (2009) showed in their study that subordinate individuals tend to help more their dominant conspecific than vice-versa. Melis *et al.* (2011b) also verified this trend, although the results were not statistically significant. Horner *et al.* (2011) mentioned in their study that dominance, as well as affiliation, did not have a direct effect on the actor's choice.

In our case, both dominants (mothers) and subordinates (offspring) showed prosocial behaviour, but no altruistic behaviour, with Pan being an exception among the group. Given the results of Pan, we described her behaviour as mean-spirited. Despite of her choices, she seemed to show an understanding of the experiment, once she acted coherently across the three different conditions. Yamamoto *et al.* (2012) also reported that Pan was the only individual to fail in choosing an appropriate tool on first trial when all the individuals chose the correct tool.

4.6. Conclusion

Our study reports evidences of prosocial behaviour mediated by a touch panel task, supporting some previous studies' results. Until now only one study with PCT paradigm revealed prosociality in chimpanzees, although with a smaller difference between the proportion of prosociality and mean-spirited (but significant). We implemented some new changes to the old paradigm and used a different approach

(instead of comparing with a ghost condition) we explored how chimpanzees respond when they have to explore other options, and how their choices change given different conditions.

Despite our results showed prosociality in chimpanzees, it is important to mention that we cannot generalize it to all chimpanzees. Many factors, such as housing conditions, the time they stay together and know each other, their social relationship, personalities, genetics, among others, are factors that might influence every individual's decision. In a sample of 6 individuals, we can clearly say that 5 were prosocial and 1 acted more mean-spirited, according to Skoyles (2011) definition. The results also support that chimpanzees understood the goal of the experiment. In order to the existence of prosociality in chimpanzees, more studies, in different settings, are needed, as well as a combination of observations from the wild.

4.6.1. Further perspectives

In the current study, we obtained positive results about their prosociality when they have to choose among being prosocial, mean-spirited or altruistic. However, there are some improvements that could be done. In the future one should try to clarify and to understand better the underlying mechanisms which lead chimpanzees to act prosocial. The use of touch panel computer tasks revealed to be an efficient way of testing prosociality, once it allows the running of more trials in less time without the direct intervention of the experimenter and also allows keeping both subjects in the same compartment without generating conflict between them.

Our subjects were kin-related, and they represent the strongest bond: mother-offspring (Broad *et al.*, 2006). The idea, which was not possible to test due to logistics, would be to use non-kin pairs, with different positions in the rank, to see if the levels of prosociality would be maintained.

In what concerns prosocial tendencies, it would be interesting to further investigate what are their motivations to engage in this behaviour and their limitations regarding acting prosocially. We could assess that, by testing, for example, if the involvement of the other (recipient) on the task will be considered by the actor and will influence its choice. Both chimpanzees would be involved in the task and the recipient

would have to press a start button to initiate the task. After that action, the actor would be given the keys to choose the option (Prosocial, selfish or altruistic).

In the current studies, chimpanzees had no cost in choosing prosocial. For the actor pressing the button to receive uniquely the reward or pressing the button to reward both individuals required the same efforts. By introducing a task to the actor, before he makes the choice, its choices could be affected, once it had to put more effort in performing the task, instead of just pressing a button on the screen. For example, after pressing the start key, the actor had to perform a task, then, only after he finished the task the choices (prosocial, mean-spirited and altruistic) would be given. It would be advantageous if we used numerical task as the task they had to perform before the choices, once chimpanzees in KUPRI are very familiar with numeral tasks. By using numerical tasks, the difficulty of the task could be easily controlled, if we increased the sequence of numerals, for example. The task difficulty can be related to the effort they must put in the performance: the more difficult the task is, the more effort they have to input. By controlling for these two conditions, we would be able to understand how much the participation of the other and the effort the actor has to input would change or influence their prosociality.

5. Final considerations

We explored two topics on social cognition and behaviour that since an early age have received a lot of attention by the researchers, biologists and also psychologists: competition and prosociality. In spite of the topics being well explored by scientists, some questions remain open, especially with regard to altruism and prosocial behaviour.

The two studies performed and previously described are not directly connected. They were conducted in different compounds and with different environment using distinct targets. However they are somehow related. Both studies were developed in a social context. One study tested mother-offspring dyads in a small compartment indoors. Other, focused on social behaviour competing for a shared food resource, using all the group of chimpanzees in the outside enclosure, enriched with a lot of plants' species, streams, towers, ropes, pretending to simulate the real habitat of chimpanzees.

Both topics explore behaviours that are consequences of living in groups. As mentioned previously in the introduction, competition is a consequence of living in social groups, as well the altruistic and prosocial behaviour. Once individuals live in groups they had to adopt some strategies that allowed them to survive, despite of the costs. Competition and altruistic behaviour can entail cost for the individuals. After a conflict for food there are individuals that win the contest and obtain the reward and others that have been defeated and injured (Smith, 1982). In altruistic behaviour, the altruistic individual is willing to sacrifice their fitness to help another individual (Trivers, 1971). Prosocial behaviours, such as cooperation, are also known to occur in the situations of competition. Male-male alliances are one of the examples where individuals cooperate to compete, for example for a better position in the dominance rank (Goodall, 1986), or against other chimpanzees communities (Watts, 2002). Some authors suggest prosocial behaviours such as: food-sharing and cooperation may have evolved as conflict-avoidance strategies (Wrangham, 1980; de Waal, 1982).

The novelty and innovation of these experiments was the use of touch panel computer to run the tasks. Few chimpanzees in the world received an intensive training on performing cognitive tasks mediated touch panel computers and they are in Primate Research Institute, Kyoto University. For 30 years "Ai Project" developed studies on physical and social cognition in an individual context. Few experiments were done in a social context using touch panel computers. This means the area is only in an initial phase and a lot of studies can be done and paradigms improved by using this method.

6. References

- Albiach-Serrano A, Call J, Barth J. 2010. Great Apes track hidden objects after changes in the objects' position and in subject's orientation. *American Journal of Primatology*, 72:349–35.
- Alexander R D. 1974. The evolution of social behaviour. *Annual Review of ecology and Systematics*, 5: 325–388.
- Allman J, Rosin A, Kumar R., Hasenstaub A. 1998. Parenting and survival in anthropoid primates: Caretakers live longer. *Proceedings of the National Academy of Sciences, USA*, 95:6866–6869.
- Anderson D P, Nordheim EV, Boesch C, Moermond TC. 2002. Factors influencing fissionfusion grouping in chimpanzees in the Tai National Park, Côte d'Ivoire. In: Boesch C, Hohmann G, Marchant L F. (Eds.). *Behavioural Diversity in Chimpanzees and Bonobos*, pp. 90–101. Cambridge, UK: Cambridge University Press.
- Asano T, Kojima T, Matsuzawa T, Kubota K, Murofushi K. 1982. Object and color naming in chimpanzees (*Pan troglodytes*). *Proceedings of Japanese Academy*, 58:118–122.
- Atkinson M H. 1964. Man's Changing Concepts of the Heart and Circulation. *Canadian Medical Association Journal*, 91(11):596–601.
- Aureli F, Schaffner C M. 2007. Aggression and conflict management at fusion in spider monkeys. *Biology Letters*, 3:147–149.
- Bates L A, Lee P C, Njiraini N, Poole J H, Sayialel K, Sayiale S, Moss C J, Byrne R W. 2008. Do elephants show empathy? *Journal of Consciousness Studies*, 15:204–225.
- Batson C D and Powell A A. 1998. Altruism and prosocial behaviour. In: *The Handbook of Social Psychology*. Gilbert D T, Fiske S T, Lindzey G. (Eds.). Boston, McGraw-Hill, pp. 282–316.
- Benett A T D. 1996. Do animals have cognitive maps? *The journal of Experimental biology*, 199:219–224.
- Bermejo M, Illero G. 1999. Tool-set for termite-fishing and honey extraction by wild chimpanzees in the Lossi Forest, Congo. *Primates* 40:619–627.
- Biro D, Inoue-Nakamura N, Tonooka R, Yamakoshi G, Sousa C, Matsuzawa, T. 2003. Cultural innovation and transmission of tool use in wild chimpanzees: evidence from field experiments. *Animal Cognition*, 6:213–223.
- Biro D, Matsuzawa T. 1999. Numerical ordering in a chimpanzee (*Pan troglodytes*): planning, executing, and monitoring. *Journal of Comparative Psychology*, 113(2):178–185.
- Biro D, Matsuzawa T. 2001. Use of numerical symbols by the chimpanzee (*Pan troglodytes*): Cardinals, ordinals, and the introduction of zero. *Animal Cognition* 4:193–199.
- Bjork A, Liu W, Wertheim J O, Hahn, B H, Worobey M. 2011. Evolutionary history of chimpanzees inferred from complete mitochondrial genomes. *Molecular Biology*, 28(1):615–623.
- Boesch C. 1991 Teaching among wild chimpanzees. *International Journal of Primatology*, 41:530–532.
- Boesch C. 1994. Cooperative hunting in wild chimpanzees. *Animal Behaviour*, 48:653–667.

- Boesch C. 1996. Social grouping in Tai chimpanzees. *In: McGrew W C, Marchant L F, Nishida T. (Eds.). Great ape societies.* Cambridge, Cambridge University Press, pp. 101–113.
- Boesch C, Boesch H. 1984. Mental map in wild chimpanzees: an analysis of hammer transports for nut cracking. *Primates*, 25:160–167.
- Boesch C, Boesch H. 1989. Hunting behaviour of wild chimpanzees in the Tai National Park. *American Journal of Physical Anthropology*, 78:547–73.
- Boesch C, Boesch H. 1990. Tool use and tool making in wild chimpanzees. *Folia primatologica*, 54:86–99.
- Boesch C, Boesch H. 1991. Tool Use and Tool Making in Wild Chimpanzees. *Folia Primatologica*, 54:86–99.
- Boesch C, Boesch-Achermann H. 2000. The chimpanzees of the Tai Forest: behavioural ecology and evolution. Oxford, England: Oxford University Press.
- Boesch C, Tomasello M. 1998. Chimpanzee and human culture. *Contemporary Anthropology*, 39:591–611.
- Boesch C, Head J, Robbins M M. 2009. Complex toolsets for honey extraction among chimpanzees in Loango National Park, Gabon. *Journal of Human Evolution*, 56(6):560–569.
- Bräuer J, Call J, Tomasello M. 2005. All great ape species follow gaze to distant locations and around barriers. *Journal of Comparative Psychology*, 119:145–154.
- Bräuer J, Call J, Tomasello M. 2006. Are apes really inequity averse? *Proceedings of the Royal Society, London, B, Biological Science*, 273:3123–3128.
- Broad K D, Curley J P, Keverne E B. 2006. Mother–infant bonding and the evolution of mammalian social relationships. *Philosophical Transactions of Royal Society London B, Biological Sciences*; 361(1476):2199–2214.
- Brosnan S F, de Waal F B M. 2002. A proximate perspective on reciprocal altruism. *Human Nature*, 13:129–152.
- Brosnan S F, de Waal F B. 2003. Monkeys reject unequal pay. *Nature*, 425:297–299.
- Brosnan S F, Schiff HC, de Waal F B M. 2005. Tolerance for inequity may increase with social closeness in chimpanzees. *Proceedings of the Royal Society, London, B, Biological Science*, 272:253–258.
- Byrne R W, Bates L A. 2007. Sociality, evolution and cognition. *Current Biology*, 17:714–723.
- Call J. 2001 Chimpanzee social cognition. *Trends Cognitive Science*, 5:388–393.
- Call J, Tomasello M. 2008. Does the chimpanzee have a theory of mind? 30 years later. *Trends Cognitive Science*, 12:187–19.
- Call J, Carpenter M, Tomasello M. 2005. Copying results and copying actions in the process of social learning: chimpanzees (*Pan troglodytes*) and human children (*Homo sapiens*). *Animal cognition*, 8:151–163.

References

- Call J C, Hare B, Tomasello M. 1998. Chimpanzee gaze following in an object-choice task. *Animal Cognition*, 1:89–99.
- Carvalho S, Cunha E, Sousa C, Matsuzawa T. 2008. Chances and resource-exploitation strategies in chimpanzee (*Pan troglodytes*) nut cracking. *Journal of Human Evolution*, 55:148–163.
- Celli M, Hirata S, Tomonaga M. 2004. Socioecological influences on tool use behaviour of captive chimpanzees. *International Journal of Primatology*, 25:1 267–1281.
- Celli M, Tomonaga M, Udono T, Teramoto M, Nagano K. 2003. Tool use tasks as environmental enrichment for captive chimpanzees. *Applied Animal Behaviour Science*, 81:171–182.
- Chalmeau R, K Lardeux P, Brandibas, Gallo A. 1997 Cooperative Problem Solving by Orangutans (*Pongo pygmaeus*). *International Journal of Primatology*, 18:23–32.
- Chapman C A, Wrangham R W. 1993. Range use of the forest chimpanzees of Kibale: Implications for the understanding of chimpanzee social organization. *American Journal of Primatology*, 31(4):263–273.
- Chapman C A, White F J, Wrangham R W. 1994. Party size in chimpanzees and bonobos: A reevaluation of theory based on two similarly forested sites. In: Wrangham R W, McGrew W C, de Waal FB M. (Eds.). *Chimpanzee cultures*. Cambridge, MA: Harvard University Press, pp. 41–58.
- Charnov E L, Berrigan D. 1993. Why do female primates have such long lifespans and so few babies? Or life in the slow lane. *Evolutionary Anthropology*, 1:191–194.
- Chen F C, Li W H. 2001. Genomic Divergences between Humans and Other Hominoids and the Effective Population Size of the Common Ancestor of Humans and Chimpanzees. *American Journal of Genetics*, 68:444–456.
- Cheng Z, Ventura M, She X, Khaitovich P, Graves T, Osoegawa K, Church D, DeJong P, Wilson R K, 2005. A genomic wide comparison of recent chimpanzee and human segmental duplications. *Nature*, 437:88–93.
- Chevalier-Skolnikoff S, Galdikas B M F, Skolnikoff A. 1982. The adaptive significance of higher intelligence in orangutans: A preliminary report. *Journal of Human Evolution*, 11:639–652.
- Christensen H. 2001. What cognitive changes can be expected with normal aging? *Australian and New Zealand Journal of Psychiatry*, 35:768–775.
- Clutton-Brock T H, Harvey P H. 1978. Mammals, resources and reproductive strategies. *Nature*, 273:191–196.
- Clutton-Brock, T. H. 1974. Primate social organization and ecology. *Nature* 250, p. 539-542.
- Corbey R. 2005. *The Metaphysics of Apes: Negotiating the Animal–Human Boundary*. Cambridge, Cambridge University Press.
- Custance D M, Whiten A, Bard K A. 1995. Can young chimpanzees imitate arbitrary actions? Hayes and Hayes (1952) revisited. *Behaviour*, 132:837–859.
- de Waal F B M. 1982. *Chimpanzee Politics: Power and sex among Apes*. Baltimore: The Johns Hopkins University Press.

- de Waal F. 1986. Deception in the natural communication of the chimpanzees. In: Mitchell R W, Thompson N S. (Eds.). *Deception: Perspectives on Human and Nonhuman Deceit*. Albany, SUNY Press, pp. 221–244.
- de Waal, F. B. M. 1989. Food sharing and reciprocal obligations among chimpanzees. *Journal of Human Evolution*, 18: 433–459.
- de Waal F. 2008. Putting the Altruism Back into Altruism: The Evolution of Empathy, *Annual Review on Psychology*, 59:279 –300.
- de Waal F. 2011. Toshisada Nishida (1941–2011): Chimpanzee Rapport. *PloSBiol*, 9(10): e100118.
- Doran D M. 1997. Influence of seasonality on activity patterns, feeding behaviour, ranging and grouping patterns in Tai chimpanzees. *International Journal of Primatology*, 18:183–206.
- Duffy K G, Wrangham R W, Silk J B. 2007. Male chimpanzees exchange political support for mating opportunities. *Current Biology*, 17(15):R586.
- Dunbar R I M. 2003. The social BraIn: Mind, Language, and Society in Evolutionary Perspective. *Annual Review Anthropology*, 32:163-181.
- Dutton D M, Clark R A, Dickins D V.1997. Personality in Captive Chimpanzees: Use of a Novel Rating Procedure. *International Journal of Primatology*, 18 (4):539–552.
- Eisenberg J F, Muckenhirn N A, Rudran R. 1972. The relation between ecology and social structure in primates. *Science*, 176:863–874.
- Emery N J, Clayton N S. 2004. The mentality of crows: convergent evolution of intelligence in corvids and apes. *Science*, 306:1903–1907.
- Emery Thompson M, Jones J H, Pusey A E, Brewer-Marsden S, Goodall J, Marsden D, Matsuzawa T, Nishida T, Reynolds V, Sugiyama Y, Wrangham R W. 2007. Aging and fertility patterns in wild chimpanzees provide insights into the evolution of menopause. *Current Biology*, 17:2150–2156.
- Fay M P, Proschan M A. 2010. Wilcoxon–Mann–Whitney or ttest? On assumptions for hypothesis tests and multiple interpretations of decision rules. *Statistics Surveys*, 4:1–39.
- Fehr E, Fischbacher U. 2003. The nature of human altruism. *Nature*, 425:785–791.
- Fehr E, Fischbacher U. 2004. Social norm and human cooperation. *TRENDS in Cognitive Sciences*, 8:185–190.
- Fehr E, Gächter S. 2002. Altruistic punishment in humans. *Nature*, 415:137–140.
- Flack J C, de Waal F B M. 2004. Dominance style, social power, and conflict management: a conceptual framework. In: Thierry B, Singh M, Kaumanns W. (Eds.). *Macaque Societies: A Model for the Study of Social Organization*. New York, Cambridge University Press, pp. 157–182
- Fleagle J G. 1999. *Primate Adaptation and Evolution*. New York, Academic Press.
- Fujita K, Matsuzawa T. 1986. A new procedure to study the perceptual world of animals with sensory reinforcement: recognition of humans by a chimpanzee. *Primates*, 27:283–29.
- Gallup G G. 1970. Chimpanzees: self-recognition. *Science*, 167 (3914):86–87.

- Gallup G G. 1982. Self-awareness and the emergence of Mind in Primates. *American Journal of Primatology*, 2: 237–248.
- Gardner R A, Gardner B T. 1969. Teaching sign language to a chimpanzee. *Science*, 165:664–672.
- Gilby I C, Thompson M E, Ruane J D, Wrangham R. 2010. No evidence of short-term exchange of meat for sex among chimpanzees. *Journal of Human Evolution*, 59:44–53.
- Gilby I C. 2006. Meat sharing among the Gombe chimpanzees: harassment and reciprocal exchange. *Animal Behaviour*, 71:953–963.
- Ginn S R, Lorusso L. 2008. Brain, Mind, and Body: Interactions with the Art in Renaissance Italy. *Journal of History of the Neurosciences: Basic and Clinical Perspectives*, 17(3):296–313.
- Goldwyn, R M . 1961. Nicolaas Tulp (1593-1674). *Medical History*, 5:270–276.
- Gomes C M, Mundry R, Boesch C. 2008. Long-term reciprocation of grooming in wild West African chimpanzees. *Proceedings of Royal Society London B*, 276(1657):699–706.
- Gomes C, Boesch C. 2009. Wild chimpanzees exchange meat for sex on a long-term basis. *PLoSone*, 4:e5116.
- Gonder M K, Disotell TR, Oates JF. 2006. New genetic evidence on the evolution of chimpanzee populations and implications for taxonomy. *International Journal of Primatology*, 27:1103–1127.
- Goodall J. 1986. *The Chimpanzees of Gombe: Patterns of Behaviour*. Cambridge, MA: Harvard University Press.
- Goodman M, Tagle D A, Fitch D H A, Bailey W, Czelusniak J, Koop B F, Benson Philip, Slightom J L. 1990. *Journal of Molecular Evolution*, 30:260–266.
- Gross C G. 1997. Neuroscience, early history of. *Encyclopedia of Neuroscience*: 1444–1447.
- Hamilton W D. 1963. The Evolution of Altruistic Behaviour. *The American Naturalist*, 97(896):354–356.
- Hamilton W D. 1964. The genetical evolution of social behaviour. I. *J Theoretical Biology*, 7:1–16.
- Hare B, Tomasello, M. 2004. Chimpanzees are more skilful in competitive than in cooperative cognitive tasks. *Animal Behaviour*, 68:571–81.
- Hare B, Call J, Tomasello M. 2001. Do chimpanzees know what conspecifics know? *Animal Behaviour*, 61:139–151.
- Hare B, Call J, Tomasello M. 2006. Chimpanzees deceive a human competitor by hiding. *Cognition*, 101:495–514.
- Hare B, Call J, Agnetta B, Tomasello M. 2000. Chimpanzees know what conspecifics do and do not see. *Animal Behaviour*, 59:771–85.
- Heyes C M. 1998. Theory of mind in nonhuman primates. *Behavioural Brain Sciences*, 21:101–148.
- Hill K, Boesch C, Goodall J, Pusey A, Williams J, Wrangham R. 2001. Mortality rates among wild chimpanzees. *Journal of Human Evolution*, 40:437–450.

- Hirata S, Celli M L. 2003. Role of mothers in the acquisition of tool use behaviours by captive infant chimpanzees. *Animal Cognition*, 6(4):235–244.
- Hirata S, Fuwa, K. 2007. Chimpanzees learn to act with other individuals in a cooperative task. *Primates*, 48:13–21.
- Hirata S, Matsuzawa T. 2001. Tactics to obtain a hidden food item in chimpanzee pairs (*Pan troglodytes*). *Animal cognition*, 4:285 – 295.
- Hirata S. 2009. Chimpanzee social intelligence: selfishness, altruism, and the mother-infant bond. *Primates*, 50:3–11.
- Horner V, Carter D, Suchak M, de Waal F B M. 2011. Spontaneous prosocial choice by chimpanzees. *Proceedings of the National Academy of Sciences USA*, 108: 13847-13851.
- Horner V, Whiten A. 2005. Casual knowledge and imitation/emulation switching in chimpanzees (*Pan troglodytes*) and children (*Homo sapiens*). *Animal cognition*, 8:164–181.
- Humle T, Matsuzawa T. 2002. Ant dipping among the chimpanzees of Bousou, Guinea and some comparisons with other sites. *American Journal of Primatology*, 58:133–148.
- Inoue S, Matsuzawa T. 2009. Acquisition and memory of sequence order in young and adult chimpanzee (*Pan troglodytes*). *Animal Cognition*, 12:S59–S69.
- Inoue S, Matsuzawa T. 2007. Working memory of numerals in chimpanzees. *Current Biology*, 17:1004–1005.
- Isbell L A .1991. Contest and scramble competition: patterns of female aggression and ranging behaviour among primates. *Behavioural Ecology*, 2:143–155.
- Itakura S, Tanaka M. Use of experimenter-given cues during object-choice tasks by chimpanzees (*Pan troglodytes*), an orangutan (*Pongo pygmaeus*), and human infants (*Homo sapiens*). *Journal of Comparative Psychology*, 112:119–126.
- Jensen K, Call J, Tomasello M. 2007. Chimpanzees are rational maximizers in an Ultimatum Game. *Science*, 318:107–109.
- Jensen K, Hare B, Call J, Tomasello M. 2006. What's in it for me? Self-regard precludes altruism and spite in chimpanzees. *Proceedings of Royal Society B*, 273:1013–1021.
- Kawai M, Matsuzawa T. 2000. Numerical memory span in a chimpanzee. *Nature*, 403:39–40.
- Kawai M. 1965. Newly-acquired Pre-cultural Behaviour of the Natural Troop of Japanese Monkeys on Koshima Islet. *Primates*, 6(1):1–28.
- Kawamura S. 1956. The Process of Sub-culture Propagation among Japanese Macaques. *Primates*, 2(1):43–54.
- Klein R G. 2009. *The human career: human biological and cultural origins*. Chicago, University of Chicago Press.
- Koops K. 2011. Chimpanzees in the Seringbara Region of Nimba Mountains. In: Matsuzawa T, Humle T, Sugiya Y. (Eds.). *The Chimpanzee of Bossou and Nimba*. Tokyo, Springer, pp. 277–288.

- Lakshminarayanan V R, Santos L R. 2008. Capuchin monkeys are sensitive to others' welfare. *Current Biology*, 18:R999–R1000.
- Langergraber K E, Mitani J C, Vigilant L. 2007. The limited impact of kinship on cooperation in wild chimpanzees. *Proceedings of the National Academy of Sciences*, 104:7786–7790.
- Langergraber K E, Boesch C, Inoue E, Inoue-Murayama M, Mitani JC, Nishida T, Pusey A, Reynolds V, Schubert G, Wrangham RW, Wroblewski E, Vigilant L. 2010. Genetic and 'cultural' similarity in wild chimpanzees. *Proceedings of Royal Society London B*, 278:408–416.
- Lehmann J, Boesch C. 2004. To fission or to fusion: effects of community size on wild chimpanzee (*Pan troglodytes verus*) social organization. *Behavioural Ecology and Sociobiology*, 56:207–216.
- Lonsdorf E V. 2005. Sex differences in the development of termitefishing skills in the wild chimpanzees, *Pan troglodytes schweinfurthii*, of Gombe National Park, Tanzania. *Animal behaviour*, 70:673–683.
- Lonsdorf E V. 2006. What is the role of mothers in the acquisition of termite-fishing behaviours in wild chimpanzees (*Pan troglodytes schweinfurthii*)? *Animal Cognition*, 9:36–4.
- Martin C L, Biro D, Matsuzawa T. 2011. Chimpanzees' use of conspecific cues in matching-to-sample tasks: public information use in a fully automated testing environment. *Animal Cognition*, 14(6):893–902.
- Martin P, Bateson P. 1993. *Measuring behaviour: An introductory guide*. Cambridge, Cambridge Press.
- Matsumoto-Oda A, Hosaka K, Huffman MA, Kawanaka K. 1998. Factors affecting party size in chimpanzees of the Mahale mountains. *International Journal of Primatology*, 19:999–1011.
- Matsuzawa T, Biro D, Humle T, Inoue-Nakamura N, Tonooka R, Yamakoshi G. 2001. Emergence of culture in wild chimpanzees: education by master-apprenticeship. In: Matsuzawa T. (Ed.). *Primate origins of human cognition and behaviour*. Tokyo Berlin Heidelberg, Springer, pp. 557–574.
- Matsuzawa T. 1985. Use of numbers by a chimpanzee. *Nature*, 315:57–59.
- Matsuzawa T. 1994. Field experiments on use of stone tools by chimpanzees in the wild. In: Wrangham R, McGrew W, de Waal F, Heltne P. (Eds.). *Chimpanzee cultures*. Cambridge, Harvard University Press, pp. 351–370.
- Matsuzawa T. 2001. Primate Foundations of human intelligence: a view of tool use in onhuman primates and fossil hominids. In: Matsuzawa T. (Ed.). *Primate origins of human cognition and behaviour*. Tokyo Berlin Heidelberg, Springer, pp. 557–574.
- Matsuzawa, T. 2003. The "Ai Project": historical and ecological contexts. *Animal Cognition*, 6:199–211.
- Matsuzawa, T. 2008. *Primate Origins of Human Cognition and Behaviour*. Tokyo Berlin Heidelberg, Springer.
- Matsuzawa T. 2009. Symbolic representation of number in chimpanzees. *Current Opinion in Neurobiology*, 19:92–98.
- Matsuzawa T, McGrew W C. 2008. Kinji Imanishi and 60 years of Japanese primatology. *Current Biology*, 18:587–591.

- Matsuzawa, T., Tomonaga, M., Tanaka, M. (2006). *Cognitive Development in Chimpanzees*. Tokyo, Springer.
- McGrew W. 1974. Tool use by Wild Chimpanzees in Feeding upon Driver Ants. *Journal of Human Evolution*, 3:501–508.
- McGrew W C. 1992. *Chimpanzee Material Culture: Implications for Human Evolution*. Cambridge University Press, Cambridge.
- McGrew W C. 1998. Culture in Nonhuman primates? *Annual Review of Anthropology*, 27:301-228.
- McGrew W C. 2004. *The Cultured Chimpanzee: Reflections on Cultural Primatology*. Cambridge Univ. Press, Cambridge.
- McGrew. 2010. Chimpanzee Technology. *Science*, 328:579-580.
- McGrew W C, Ham R M, White L J T, Tutin C E G, Fernandez M. 1997. Why don't chimpanzees in Gabon crack nuts? *International Journal of Primatology*, 18:353–374.
- Melis A P, Hare B, Tomasello M. 2008. Do chimpanzees reciprocate received favours? *Animal Behaviour*, 76: 951–96.
- Melis A, Warneken F, Jensen K, Schneider A, Call J, Tomasello M. 2010. Chimpanzees help conspecifics obtain food and non-food items. *Proceedings of Royal Society, Biological Sciences*. doi: 10.1098/rspb.2010.1735.
- Melis A P, Warneken F, Jensen K, Schneider A C, Call J, Tomasello M. 2011a. Chimpanzees help conspecifics obtain food and non-food items. *Proceedings of Biological Sciences*, 278:1405–1413.
- Melis A P, Schneider A C, Tomasello M. 2011b. *Pan troglodytes*, share food in the same way after collaborative and individual food acquisition. *Animal cognition*, in press.
- Mendres K A, de Waal F B M. 2000. Capuchins do cooperate: The advantage of an intuitive task. *Animal Behaviour*, 60:523–529.
- Menzel E W. 1973. Chimpanzee spatial memory organization. *Science*, 182:943–945.
- Menzel E W. 1971. Communication about the environment in a group of young chimpanzees. *Folia Primatologica*, 15:220–23.
- Milton K. 1981. Distribution Patterns of Tropical Plant foods as an evolutionary stimulus to Primate Mental Development. *American Anthropological association*, 83(3):534–548.
- Mitani J C, Watts D P. 2001. Why do chimpanzees hunt and share meat? *Animal Behaviour*, 61:915–924.
- Mitani J C, Watts D P, Lwanga J S. 2002. Ecological and social correlates of chimpanzee party size and composition. In: Boesch C, Hohmann G, Marchant L F. (Eds.). *Behavioural diversity in chimpanzees and bonobos*. Cambridge, England: Cambridge University Press, pp. 102-111.
- Mitani J C, Merriwether D A, Zhang C. 2000. Male affiliation, cooperation, and kinship in wild chimpanzees. *Animal Behaviour*, 59:885–893.
- Motulsky H. 1995. *Intuitive Biostatistics*. Oxford, Oxford University Press.

References

- Muller M N, Mitani J C. 2005. Conflict and cooperation in Wild chimpanzees. *Advances in the study of Behaviour*, 39:275–331.
- Muehlenbein M P, Watts D P, Whitten P L. 2004. Dominance rank and fecal testosterone levels in adult male chimpanzees (*Pan troglodytes schweinfurthii*) at Ngogo, Kibale National Park, Uganda. *American Journal of Primatology*, 64:71–82.
- Muller M N. 2002. Agonistic relations among Kanyawara chimpanzees. In: *Behavioural Diversity in Chimpanzees and Bonobos*. Boesch C, Hohmann G, Marchant L F. (Eds.). Cambridge, UK, Cambridge University Press, pp. 112–123.
- Muncer S J. 1983. “Conversations” with a chimpanzee. *Developmental Psychology*, 16:1–11.
- Mundry R, Fisher J. 1998. Use of statistical programs for nonparametric tests of small samples often leads to incorrect P values: examples from Animal Behaviour. *Animal Behaviour*, 56:256–259.
- Murofushi K. 1997. Numerical matching behaviour by a chimpanzee (*Pan troglodytes*): Subitizing and analogue magnitude estimation. *Japanese Psychological Research*, 39:140–153.
- Murray C M, Mane S V, Pusey A E. 2007. Dominance rank influences female space use in wild chimpanzees. *Animal Behaviour*, 74:1795–1804.
- Newton-Fisher N. 2003. The home range of the Sonso community of chimpanzees from the Budongo Forest, Uganda. *African Journal of Ecology*, 41:150–156.
- Nishida T, Corp N, Hamai M, Hasegawa T, Hiraiwa-Hasegawa M, Hosaka K, Hunt KD, Itoh N, Kawanaka K, Matsumoto-Oda A, Mitani JC, Nakamura M, Norikoshi K, Sakamaki T, Turner L, Uehara S, Zamma K. 2003. Demography, female life history, and reproductive profiles among the chimpanzees of Mahale. *American Journal of Primatology*, 59:99–121.
- Nishida T, Hosaka K. 1996. Coalition strategies among adult male chimpanzees of the Mahale Mountains, Tanzania. In: McGrew W, Marchant L, Nishida T. (Eds.). *Great Ape Societies*. Cambridge, Cambridge University Press, pp. 114–134.
- Nishida T, Matsusaka T, McGrew W C. 2009. Emergence, propagation or disappearance of novel behavioural pattern in the habituated chimpanzees of Mahale: a review. *Primates*, 50:23–36.
- Nishida T, Takasaki H, Takahata Y. 1990. Demography and reproductive profiles. In: Nishida T. (Ed.). *The Chimpanzees of the Mahale Mountains*. Tokyo, University of Tokyo Press, pp. 63–97.
- Nishida T, Zamma K, Matsusaka T, Inaba A, McGrew W. 2011. *Chimpanzee Behaviour in the Wild: An Audio-Visual Encyclopedia*. Tokyo, Springer.
- Nishida T. 1990. Deceptive behaviour in young chimpanzees: An essay. In: Nishida T. (Ed.). *The Chimpanzees of the Mahale Mountains*. Tokyo, The University of Tokyo Press, pp. 285–290.
- Nishida T. 1983. Alpha status and agonistic alliance in wild chimpanzees (*Pan troglodytes schweinfurthii*). *Primates*, 24:318–336.
- Nishida, 1996. Deceptive Tactic by an Adult Male Chimpanzee to Snatch a Dead Infant from its mother. *Pan Arica News*, 5(2):13–15.
- Normand E, Boesch C. 2009 Sophisticated Euclidean maps in forest chimpanzees. *Animal Behaviour*, 77:1195–120.

- Normand E. 2009. Spatial abilities of Wild Chimpanzees (*Pan troglodytes verus*) [PHD dissertation] Leipzig University.
- Oates J F, Dunn A, Greengrass E, Morgan B J. 2008. *Pan troglodytes ssp. ellioti*. In: IUCN 2011. IUCN Red List of Threatened Species. Version 2011.2. <www.iucnredlist.org>. Downloaded on 04 January 2012.
- Osvath M. 2009. Spontaneous planning for future stone throwing by a male chimpanzee. *Current Biology*, 19:R190–R191.
- Parish A R. 1994. Sex and food control in the “uncommon chimpanzee”: How bonobo females overcome a phylogenetic legacy of male dominance. *Ethology and Sociobiology*, 15:157–79.
- Patterson N, Richter D J, Gnerre S, Lander E S, Reich D. 2006. Genetic evidence for complex speciation of humans and chimpanzees. *Nature*, 441:1103–1108.
- Povinelli D J, Vonk J. 2003: Chimpanzee minds: suspiciously human? *Trends in Cognitive Science*, 7:157–160.
- Povinelli D J, Vonk J. 2004. We don't need a microscope to explore the chimpanzee mind. *Mind and Language*, 19:1–28.
- Premack, D. and Woodruff, G. 1978. Does the chimpanzee have a theory of mind? *Behavioural Brain Science*, 1:515–52.
- Pruetz J, Bertolani P. 2007. Savanna chimpanzees (*Pan troglodytes verus*) hunt with tools. *Current Biology*, 17:412–417.
- Pusey A E, Pintea L, Wilson M L, Kamenya S, Goodall J. 2007. The contribution of long-term research at Gombe National Park to chimpanzee conservation. *Conservation Biology*, 21:623–634.
- Pusey A E, Williams J M, Goodall J. 1997. The influence of dominance rank on the reproductive success of female chimpanzees. *Science*, 277:828–31.
- Reiss D, Marino L. 2001. Mirror self-recognition in the bottlenose dolphin: A case of cognitive convergence. *Proceedings of the National Academy of Sciences, USA*, 98:5937–5942.
- Rumbaugh D M, Gill T V, von Glasersfeld E C. 1973. Reading and Sentence Completion by a Chimpanzee (*Pan*). *Science*, 182(4113):731–733.
- Sakura O. 1994. Factors affecting party size and composition of chimpanzees (*Pan troglodytes verus*) at Bossou, Guinea. *International Journal of Primatology*, 15:167–183.
- Sibley C G, Ahlquist J E. 1984. The phylogeny of the Hominoid Primates, as Indicated by DNA-DNA hybridization. *Journal of Molecular Evolution*, 20(2):2–15.
- Silk J B. 1978. Patterns of food sharing among mother and infant chimpanzees at Gombe Stream National Park, Tanzania. *Folia Primatologica*. 29:129 – 141.
- Silk J B, Brosnan S F, Vonk J, Henrich J, Povinelli D J, Richardson A S, Lambeth S, Mascaró J, Schapiro S. 2005. Chimpanzees are indifferent to the welfare of unrelated group members. *Nature*, 437:1357–1359.

- Singer C. 1949. Section of History of Medicine. *Proceedings of the Royal Society of Medicine*, 32:563–568.
- Skoyles J R. 2011. Chimpanzees make mean-spirited, not_prosocial, choices. *Proceedings of the National Academy of Sciences*, 108(42):E835.
- Smith J M. 1982. *Evolution and the Theory of Games*. Cambridge, Cambridge University Press.
- Sousa C, Biro B, Matsuzawa T. 2009. Leaf-tool use for drinking water by wild chimpanzees (*Pan troglodytes*): acquisition patterns and handedness, *Animal cognition*, 12:115–125.
- Sousa C, Matsuzawa T. 2001. The use of tokens as rewards and tools by chimpanzees. *Animal Cognition*, 4:213–221.
- Stanford C B, Wallis J, Matama H, Goodall J. 1994. Patterns of Predation by Chimpanzees on Red Colobus Monkeys in Gombe National Park, 1982-1991. *American Journal of Physical Anthropology*, 94:213–228.
- Sterck E H M, Watts D P, van Schaik C P. 1997. The evolution of female social relationships in nonhuman primates. *Behavioural Ecology and Sociobiology*. 41:291–309.
- Stumpf R. 2007. Chimpanzees and bonobos. In: Campbell C J, Fuentes A, MacKinnon K C, Panger N, Bearder S K. (Eds.). *Primates in perspective*. Oxford, Oxford University Press, pp. 321–344.
- Suda C, Call J. 2004. Piagetian liquid conservation in the great apes (*Pan paniscus*, *Pan troglodytes*, and *Pongo pygmaeus*). *Journal of Comparative Psychology*, 118:265–27.
- Suda C, Call J. 2005. Piagetian conservation of discrete quantities in bonobos (*Pan paniscus*), chimpanzees (*Pan troglodytes*), and orangutans (*Pongo pygmaeus*). *Animal Cognition*, 8:220–235.
- Sugiyama Y. 1965. Social organization of hanuman langurs. In: Altmann S. (Ed.). *Social Communication among Primates*, Chicago, University of Chicago Press, pp. 221–236.
- Sugiyama Y, Koman J. 1979. Social structure and Dynamics of Wild chimpanzees at Bossou, Guinea. *Primates*, 20(3):323–339.
- Sugiyama Y. 1981. Observations on the Population Dynamics and Behaviour of Wilde Chimpanzees at Bossou, Guinea, in 1979-1980. *Primates*, 22(4):435–444.
- Sugiyama Y. 1984. Population dynamics of wild chimpanzees at Bossou, Guinea, between 1976–1983. *Primates*, 25:391–400.
- Sugiyama Y. 1995. Tool-use for catching ants by chimps at Bossou and Monts Nimba. *Primates*, 36:193–205.
- Sugiyama, Y. 1988. Grooming interactions among adult chimpanzees at Bossou, Guinea, with special reference to social structure. *International Journal of Primatology*, 9:393–407.
- Sugiyama Y, Fujita S. 2011. Demography and Reproductive Parameters of Bossou Chimpanzees. In: Matsuzawa T, Humle T, Sugiyama Y. (Eds.). *The Chimpanzee of Bossou and Nimba*. Toky, Springer, pp. 23–34.
- Suzuki A. 1969. An ecological Study of chimpanzees in a Savanna Woodland. *Primates*, 10:103–148 .

- Symington M M. 1990. Fission-fusion social organization in *Ateles* and *Pan*. *International Journal of Primatology*, 11:47–53.
- Tanaka M. 2001. Discrimination and categorization of photographs of natural objects by chimpanzees (*Pan troglodytes*). *Animal Cognition*, 4:201–211.
- Taylor A H, Hunt G R, Holzhaider C, Gray R D. 2007. Spontaneous Metatool Use By New Caledonia Crows. *Current Biology*, 17:1504–1507.
- Tennie C, Call J, Tomasello J. 2005. Push or Pull: Imitation vs. Emulation in Great Apes and Human Children. *Ethology*, 112:1159–1169.
- Tennie C, Call J, Tomasello J. 2010. Evidence for Emulation in Chimpanzees in social settings using the Floating Peanut Task. *PLoS one*, 5(5):e10544.
- Tomasello M. 1994. The question of chimpanzee culture. In: Wrangham R, McGrew W, de Waal F, Heltne P. (Eds.). *Chimpanzee cultures*. Harvard University Press, Cambridge, pp. 301–317.
- Tomasello M. 1996. Do apes ape? In: Heyes C M, Galef B G. (Eds.). *Do apes ape?* London, Academic, pp. 319–346.
- Tomasello M, Call J. 1997. *Primate cognition*. New York, Oxford University Press.
- Tomasello M, Call J, Hare B. 1998. Five primate species follow the visual gaze of conspecifics. *Animal Behaviour*, 55:1063–1069.
- Tomasello M, Call J, Hare B. 2003. Chimpanzees understand psychological states—the question is which ones and to what extent. *Trends of Cognitive Science*, 7:153–156.
- Tomasello M, Hare B, Agnetta B. 1999. Chimpanzees (*Pan troglodytes*) follow gaze direction geometrically. *Animal Behaviour*, 58:769–777
- Tomasello M, Carpenter M, Call J, Behne T, Moll H. 2005. Understanding and sharing intentions: The origins of cultural cognition. *Behavioural and Brain Sciences*, 28: 675–735.
- Tomasello M, Call J, Nagell K, Olguin R, Carpenter M. 1994. The Learning and Use of Gestural Signals by Young Chimpanzees: A Trans-generational Study. *Primates*, 35(2):137–154.
- Tomonaga M. 1998. Perception of shape from shading in chimpanzees (*Pan troglodytes*) and humans (*Homo sapiens*). *Animal Cognition*, 1:25–35.
- Tomonaga M, Matsuzawa T. 2000. Sequential responding to Arabic numerals with wild cards by the chimpanzee (*Pan troglodytes*). *Animal Cognition*, 3:1–11.
- Tomonaga M, Matsuzawa T. 2002. Enumeration of briefly presented items by the chimpanzee (*Pan troglodytes*) and humans (*Homo sapiens*). *Animal Learning and Behaviour*, 30:143–157.
- Tonooka R, Tomonaga M, Matsuzawa T. 1997. Acquisition and transmission of tool making and use for drinking juice in a group of captive chimpanzees. *Japanese Psychological Research*, 39: 253–265.
- Trivers R L. 1971. The Evolution of Reciprocal Altruism. *The Quarterly Review of Biology*, 46(1):35–57.
- Ueno A, Matsuzawa T. 2004. Food transfer between chimpanzee mothers and their infants. *Primates*, 45:231–239.

References

- van Schaik C P, Deaner R O, Merrill M Y. 1999. The conditions for tool-use in primates: Implications for the evolution of material culture. *Journal of Human Evolution*, 36:719–741.
- van Schaik C P, Pradhan G R. 2003 A model for tool-use traditions in primates: implications for the coevolution of culture and cognition. *Journal of Human Evolution*, 44:645–664.
- van Schaik. 1983. Why are diurnal primates living in groups? *Behaviour*, 88:120–144 .
- Van Vugt M, Van Lange P A M. 2006. The altruism puzzle: Psychological adaptations for prosocial behaviour. In: Schaller M, Simpson J A, Kenrick D T. (Eds.) *Evolution and Social Psychology*. New York: Psychology Press, pp. 237-261.
- Visalberghi E, Fragaszy D M. 2002. Do monkeys ape? Ten years later. In: Dautenhahn K, Nehaniv C. (Eds.). *Imitation in animals and artifacts*. Cambridge, MA: MIT Press, pp. 471–479.
- Visalberghi E, Fragaszy D. 1990 Do monkeys ape? In: Parker S, Gibson K. (Eds.). *“Language” and intelligence in monkeys and apes*. Cambridge: Cambridge University Press, 247–273.
- Visalberghi E, Tomasello M. 1998. Primate causal understanding in the physical and psychological domains, *Behavioural processes*, 42: 189–203.
- Vonk J, Brosnan S F, Silk J B, Henrich J, Richardson A S, Lambeth S, Schapiro S, Povinelli D J. 2008. Chimpanzees do not take advantage of very low cost opportunities to deliver food to unrelated group members. *Animal Behaviour*, 75:1757–177016.
- Warneken F, Hare B, Melis A P, Hanus D, Tomasello M. 2007. Spontaneous altruism by chimpanzees and young children. *PLoS Biology*, 5(7):e184.
- Warneken F, Tomasello M. 2006. Altruistic helping in human infants and young chimpanzees *Science*, 311:1301–1303.
- Watts D P. 1998. Coalitionary mate-guarding by male chimpanzees at Ngogo, Kibale National Park, Uganda. *Behavioural Ecology and Sociobiology*, 44:43–55.
- Watts D P. 2002. Reciprocity and interchange in the social relationships of wild male chimpanzees. *Behaviour*, 139:343–370.
- Watts D P, Mitani J C. 2002. Hunting behaviour of chimpanzees at Ngogo, Kibale National Park, Uganda. *International Journal of Primatology*, 23:1–28.
- Whiten A, Custance DM, Gomez J C., Teixidor P, Bard K A. 1996. Imitative learning of artificial fruit processing in children (*Homo sapiens*) and chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, 110:3–14.
- Whiten A, Goodall J, McGrew W C, Nishida T, Reynolds V, Sugiyama Y, Tutin C E G,
- Whiten A, Horner V, de Waal F B M. 2005. Conformity to cultural norms of tool use in chimpanzees. *Nature*, 437:737–740.
- Whiten A. 1998. Imitation of the sequential structure of actions by chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, 112:270–281.

- Whiten A, McGuigan N, Marshall-Pescini S, Hopper LM. 2009. Emulation, imitation, over-imitation and the scope of culture for child and chimpanzee. *Philosophical Transactions of the Royal Society B, Biological Sciences*, 364:2417–2428.
- Whitley E, Ball J. 2002. Statistics review 6: Nonparametric methods. *Critical Care*, 6:509–513.
- Wiley R H, Rabenold K N. 1984. The evolution of cooperative breeding by delayed reciprocity and queuing for favorable social positions. *Evolution*, 38:609–621.
- Wittig R M, Boesch C. 2003. Food competition and Linear Dominance Hierarchy among female chimpanzees of the Tai National Park. *International Journal of Primatology*, 24(4):847–867.
- Won Y J, Hey J. 2005. Divergence Population Genetics of Chimpanzees. *Molecular Biology and Evolution*, 22:297–307.
- Woodruff G, Premack D. 1979. Intentional communication in the chimpanzee: The development of deception. *Cognition*, 7:333–62.
- Wrangham R W. 1980. An ecological model of female-bonded primate groups. *Behaviour*, 75:262-299.
- Wrangham R W, Boesch C B. 1999. Culture in chimpanzees. *Nature* 399(6737):682–685.
- Wrangham R W, Chapman C A, Clark-Arcadi A P, Isabirye-Basuta G. 1996. Social ecology to Kanyawara chimpanzees: implications for understanding the costs of great ape groups. In: McGrew W, Marchant L, Nishida T. (Eds.). *Great ape societies*. Cambridge: Cambridge University Press, pp. 45–57.
- Wrangham R W, McGrew W C, de Waal F B M, Heltne P G. 1994. *Chimpanzee Cultures*. Cambridge MA: Harvard University Press.
- Wrangham R W, Nishida T. 1983. *Aspilla* spp. Leaves: A puzzle in the feeding behaviour of wild chimpanzees. *Primates*, 24:276–282.
- Wrangham R W. 1974. Artificial feeding of chimpanzees and baboons in their natural habitat. *Animal Behaviour*, 22:83–9.
- Wynne C DL. 2004. Fair refusal by capuchin monkeys. *Nature*, 428(6979):140.
- Yamamoto S, Humle T, Tanaka M. 2009. Chimpanzees help each other upon request. *PLoS one*, 4:e7416.
- Yamamoto S, Humle T, Tanka M. 2012. Chimpanzees' flexible targeted helping based on an understanding of conspecifics' goals. *Proceedings of National Academy of sciences*, 109(9):3588–3592.
- Yamamoto S, Tanaka M. 2009. How did altruism and reciprocity evolve in humans? Perspectives from experiments on chimpanzees (*Pan troglodytes*). *Journal of Interaction Studies*, 10:150–182.

7. Appendixes