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EMOTIONAL CONTEXTS AND EMPATHIC RESPONSES – WHAT CAN WE EXPECT FROM THE CHIMPANZEE?

Ana Rita de Oliveira de Castro

MESTRADO EM BIOLOGIA EVOLUTIVA E DO DESENVOLVIMENTO

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Resumo

Os avanços nas áreas de etologia, psicologia e neurociências obrigam à revisão de conhecimento depauperado pela ideia da existência de emoções ser exclusivamente humana. Hoje em dia já se aceita pacificamente que muitos outros animais revelam um leque complexo de emoções nas suas actividades sociais, e que tais emoções promovem o fitness inclusivo, garantido a coesão do grupo e uma comunicação célere e eficaz.

Apesar da contribuição das áreas acima referidas, nenhuma foi tão pioneira na defesa da existência de empatia enquanto fenómeno biológico e, como tal, abrindo as portas à possibilidade de se revelar em outras espécies, como a área das neurociências. Há cerca de dez anos, Rizzolatti e colegas descobriram o Mirror Neuron System (Sistema de Neurónios Espelho), um grupo de neurónios que é activado pela realização de uma acção motora e pela observação da mesma sendo realizada por outro indivíduo. Apesar de a descoberta ter sido inicialmente realizada em macacos rhesus, este sistema já se tornou conhecido em humanos e estudos apontam para que exista igualmente em chimpanzés. Foi recentemente descoberto que certas áreas do cérebro, tais como a amígdala e a ínsula, estão envolvidas na interpretação de emoções de outros indivíduos, bem como a existência de um sistema de espelhamento de emoções observadas à semelhança do Sistema de Neurónios Espelho. Empatia, interpretada como a capacidade de um indivíduo experimentar uma situação do ponto de vista de outrém, é tida como um mecanismo de coesão social que facilita a comunicação emocional e motiva o comportamento pro-social e altruísta. Muitos autores reforçam a ideia de empatia enquanto uma supra categoria que possui dois mecanismos distintos, que se modelam entre si: empatia cognitiva e empatia emocional. Empatia cognitiva refere-se à capacidade de entender o que outro indivíduo sabe, enquanto que empatia emocional se prende com o entender do que outro indivíduo sente. Estes dois mecanismos modelam-se entre si e dados sugerem que algumas disfunções sociais podem ser devidas ao mau funcionamento de um destes mecanismos, tais como o autismo ou a psicopatia. A empatia é igualmente tida como uma categoria complexa construída sob fenómenos emocionais mais simples tais como o contágio emocional e a simpatia.

Os novos dados fornecidos pelas neurociências sustentam a ideia de um mecanismo neuronal para interpretação de pistas emocionais e fornecem a base biológica que permite a defesa de empatia emocional como o que aparenta ser uma habilidade comum aos grandes primatas e outros animais, tais como golfinhos e elefantes. A existência de empatia não se dá ao acaso, como um *byproduct* da evolução, mas sim enquanto mecanismo seleccionado pela vantagem evolutiva que confere, tanto como sistema motivacional de respostas altruísticas que asseguram a coesão do grupo, como um poderoso mecanismo de recolha de informação relevante sobre o ambiente circundante, sociedade e experiência individual, através da observação da experiência de outros.

O presente trabalho foi desenvolvido no quadro referencial da etologia para o estudo de empatia emocional e apresenta dados que corroboram a existência de empatia emocional em chimpanzés. Este projecto foi desenvolvido entre Março e Junho de 2008, no santuário Chimp Eden do Instituto Jane Goodall, África do Sul. Com os objectivos de estudar evidências de empatia emocional em chimpanzés, e em particular testar a eficácia de um método de recolha de dados, foram observados dois grupos de chimpanzés, um de 10 indivíduos constituído maioritariamente por juvenis e outro por 7 adultos, todos os indivíduos foram resgatados da “Bushmeat Trade” ou transferidos de Zoos que já não recolhiam as condições necessárias à manutenção sustentável de todos os seus indivíduos. Mesmo sabendo que ambos os grupos não constituem exemplos “saudáveis” da espécie pela história individual de cada um, os dados obtidos sugerem a existência de uma relação significativa entre alguns comportamentos emocionais e respectivas respostas empáticas. Após observações *ad libitum* iniciais e recorrendo a pesquisa bibliográfica, estabeleceu-se que os comportamentos Raiva (Anger), Medo (Fear) e Stress Social (Social Distress) seriam comportamentos *trigger*, ou comportamentos emocionais que incitam resposta empática; as respostas emocionais a estes *triggers* foram registadas e foram analisados comportamentos que revelassem entendimento do estado emocional de outrém e proporcionassem a suspeita de uma resposta complementar, tais como Consolação a Medo ou Medo a Raiva.

Procurou-se igualmente cruzar os dados de evidências empáticas com dois factores que poderão influenciar as respostas: a qualidade de uma relação e a proximidade física de um indivíduo ao *performer* (o indivíduo que realiza o *trigger*). De modo a estudar a qualidade de uma relação, *scans* de grupo foram conduzidos a cada 15 minutos de observação, e todas as interacções entre indivíduos foram registadas de modo a permitir o cálculo de índices de Qualidade de Relação para inferir o incremento que a relação entre dois indivíduos confere à resposta empática. Os *triggers* foram procurados com scans comportamentais (*behavioural scanning*), e a cada *trigger* exibido foram registadas as respostas de todos os indivíduos presentes. Para inferir sobre o incremento do factor Proximidade, o indivíduo mais próximo do displayer (indivíduo que realiza o *trigger*), numa distância aproximada de quatro braços, era registado.

Realizaram-se testes de qui-quadrado para analisar a independência dos dados. Os resultados obtidos corroboram a existência de todos os níveis de empatia emocional em chimpanzés; contágio emocional, simpatia, e tomada de perspectiva empática. No grupo dos juvenis, foram encontradas cinco relações fortemente significativas entre *trigger* e resposta, sendo estas, Medo a Raiva, Imitação a Raiva, Não-Resposta a Raiva, Consolação a Stress Social e Consolação a Medo. Medo a Raiva pode ser interpretado como evidência de empatia dado que assume o reconhecimento do estado emocional de outro indivíduo, pelo reconhecimento da agressividade exibida e pela antecipação da consequência desse mesmo estado, gerando a resposta Medo. Imitação a Raiva observou-se no grupo juvenil mas não nos adultos de acordo com os conhecimentos teóricos; a maior incidência de imitação dá-se na juventude, dando depois lugar a comportamentos mais adequados, ou pro-sociais. A observação de Raiva gerava a imitação enquanto comportamento “vazio”, ou seja, não dirigido a ninguém e sem objectivo aparente. Não-Resposta a Raiva pode ser justificado tendo em atenção que 65,45% dos *triggers* de Raiva foram realizados por Cozy, um chimpanzé que apresenta comportamentos aberrantes frequentes, e que aparentemente recebe um tratamento diferencial por parte dos restantes indivíduos. Consolação a Medo e Consolação a Stress Social são por excelência os indicadores de empatia emocional. Consolar uma vítima implica o reconhecimento do estado emocional da mesma e ajustar o comportamento para acalmar e reconfortar, comportamentos aparentemente “altruístas”. Foi salvaguardado que Consolação seria apenas cotada se fosse prestada de forma voluntária.

No grupo dos adultos, foram encontradas três relações significativas: Consolação a Stress Social, Socorro a Stress Social e Imitação a Excitação. Consolo a Medo e Consolo a Stress Social estão de acordo com os resultados obtidos nos juvenis. A novidade no grupo dos adultos prende-se com a resposta Socorro a Stress Social, na qual o observador interfere na acção observada procurando remover o objecto ou indivíduo causador de Stress Social, revelando uma apreciação pelo estado emocional de outro e apresentando uma resposta pro-social.

As maiores limitações estruturais prenderam-se com a visibilidade limitada às duas áreas, dado que não era possível contorná-las por inteiro, bem como a existência de uma floresta no interior de cada uma das áreas, que impossibilitava as observações. No grupo de adultos, o fraco número de interacções entre indivíduos incapacitou a colheita de um número de *triggers* elevado e comprometeu o estudo da Qualidade de

Relação dado que as relações eram virtualmente inexistentes. Vários factores poderão ter contribuído para este resultado, tais como o isolamento prolongado de muitos indivíduos (sendo que alguns nunca tinham sido expostos à presença de conspecíficos até ao momento de integração no santuário) e o facto de o grupo ser relativamente recente, tendo pouco mais de um ano na altura de realização do estudo.

Algumas questões ficaram em aberto, tais como a importância da Proximidade e da Qualidade de Relação, bem como a possível correlação entre estas duas medidas. Para futuros estudos, sugerimos um ajuste das medidas de Qualidade de Relação, através da inclusão de mais comportamentos afiliativos tais como *allogrooming*, brincar, beijar, abraçar, em vez de utilizar apenas o comportamento social mais frequente do grupo. Quanto ao método de recolha de *triggers*, *behavioural scanning* é o método mais satisfatório já que se adequa à colheita de dados raros e de curta duração, pelo que sugerimos que se mantenha este método.

Em suma, os objectivos desta tese prendem-se com a exposição do conhecimento contemporâneo do fenómeno empático, bem como a tentativa de superar algumas limitações na abordagem científica ao estudo de empatia emocional, desenhando um modelo que permita o estudo do fenómeno em *designs* naturalistas e de laboratório. Igualmente, utilizando medidas comportamentais que forneçam uma recolha sistemática de episódios de empatia emocional em chimpanzés, prentende-se estabelecer que medidas comportamentais formam as melhores hipóteses para evidências de empatia, de uma lista de possíveis candidatos.

Palavras-chave: empatia emocional, consolação, qualidade de relação.

Summary:

As social species, mechanisms of social cohesion must exist to secure the harmony within the group and defence of the survival of the kind. Empathy could have emerged to answer just that: an internal mechanism allowing the embodiement of emotions that ensures the efficient contagion of emotional states for the synchrony of individuals within the group. Even though understanding the actions and emotions of others is a pragmatic need of social animals, the study of empathy remained crippled through many years due to the erroneous idea of human exclusivity. The new tools brought by psychological, behavioural and neural sciences not only make it possible, but urge the redefinition of many abilities we thought until now to be exclusive to man. The present study reviews what we know so far regarding the study of empathy, and presents behavioural work towards the systematic approach to the phenomenon.

With the purpose of inferring on the existence of emotional empathy in chimpanzees, presenting a method of systematic data collection and investigating further into the empathic process, the present study was carried out for the course of four months in South Africa, at Jane Goodall's Institute sanctuary, Chimp Eden. *Behavioural sampling* was carried out to register empathy *triggers* and *group scans* were conducted in order to obtain measures of Relationship Quality and Proximity and ascertain their possible relation to the empathic response.

The present study presents results that support the existence of empathy in chimpanzees and proposes the next steps in the systematic study of the phenomenon, either in laboratory or wild conditions.

Keywords: emotional empathy; behaviour evolution; chimpanzee; relationship quality

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Chapter 1

General Introduction

Sociality, particularly in Primates, greatly depends on behavioural measures that ensure the co-operation between individuals and the sensitivity to the emotions of others (Bekoff et al. 2002; de Waal 2008). Sympathy, empathy and community concern create a solid bond between individuals that ensures the circulation of emotional information with efficiency and celerity (Flack and de Waal 2000). However, some authors are still debating the *succorant* nature and function of altruism and empathy; Dawkins wrote “be warned that if you wish, as I do, to build a society in which individuals cooperate generously and unselfishly towards a common good, you can expect little help from biological nature. Let us try to teach generosity and altruism, because we are born selfish” (Dawkins 1976, p.3). Another evolutionary biologist, George C. Williams, also claims that the biological processes are usually against generosity and helping behaviours, and goes as far as claiming that altruism and morality are accidental capabilities “produced, in its boundless stupidity, by a biological process that is normally opposed to the expression of such a capability” (1988, p.438). However, Trivers (1971) proposed that by engaging in helping behaviours and creating an assisting network, individuals achieve greater benefits in the long term than the short term ones obtained through competing with their conspecifics. Altruism, as opposed to situations such as mutualism or simultaneous co-operation, implies that an action is costly to the benefactor, which conflicts with the “survival of the fittest” competition-like view of several authors (Trivers 1971; Flack and de Waal 2000). Being the fittest means being the best adjusted to the surrounding environment and maximizing the potentials of survival through various techniques. In complex societies such as primate societies, being the fittest is can also be synonym with being the “most social”.

Since emotions translate very often into the behavioural cues that sign intent, possessing a mechanism that allows the automatic understanding of observed emotions serves as a crucial tool in the assurance of survival (Panksepp 2004; Rizzolatti et al. 2006). Current developments in neural sciences acknowledged the relevance of neural pathways in the understanding and management of emotional information (Rizzolatti et al. 2003; Rizzolatti et al. 2004; Iacoboni et al. 2005; Rizzolatti et al. 2006). The discovery of the Mirror Neuron System (Rizzolatti et al. 1996) made it clear that the brain does simulate observed motor actions and, to an extent, observing allows for an unconscious simulation of the action, which benefits the individual through the collection of relevant environmental, social and personal information. Since then, a similar system has been discovered in humans regarding the simulation of observed emotions, and studies seem to establish a similar system in chimpanzees (Parr and Hopkins 2000; Parr 2001; de Vignemont and Singer 2006; Rizzolatti et al. 2006).

Empathy, which study had been neglected outside the human species, has finally found support from fields of knowledge other than Psychology. Probably because empathy was postulated, for many years, as the ability to consciously simulate another individual's emotional state or point of view, attempts to study the phenomenon in other animals would even be looked at as "bad" science (de Waal 2008). Nowadays, evidence seems to confirm that no effortful processing or cognitive perspective taking is required for empathy to be engaged (e.g. Dimberg and Thunberg 1998; Preston and de Waal 2001; Rizzolatti et al. 2004; de Vignemont and Singer 2006).

When conducting behavioural field work in semi-wild or wild conditions, due to the limitations in manipulating the environment or social contexts, to look for evidence of empathy we must look at *trigger* behaviours, or emotional behaviours that require by nature an emotional response. Evidence of empathy will be found in the behaviours that suggest the adjustment to such observed emotional behaviour, depicting an adequate response to the emotional problem exposed by the *trigger*.

The present dissertation aims to present a review on the subject of empathy, the evolution of the concept and how the many fields of knowledge have contributed to the investigation of the phenomenon and what are the predictable next steps. Also, the present dissertation aims to propose a method that allows for the systematic study of empathy, as well as to define which empathic behaviours are most likely to occur in given emotional contexts.

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Chapter 2

How far back does Emotional Empathy go? Recent evidence making the case for the remote evolutionary origins of human Empathy and for Empathic non-human animals.

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Abstract

Empathy has always been a concept of difficult definition. A communication gap between psychologists and neurobiologists crippled the study of the empathic processes for long, but that has been changing in recent years. With the discovery of mirror neurons (Rizzolatti et al. 1996), we witnessed a revolution in the way we understand how the mind works; neurological evidence of the much discussed “embodiement of observed behaviours”, envisaged by Psychophisiologists, was finally found and neuroscientists are coming ever closer to social psychologists in finding the substrate for the proposed relations between gender, mimicry, emotional contagion and empathy, and they are stumping on evidence of empathy in non-human animals. In this review we define the different degrees of empathy, explain the empathic process with special insight on the Perception-Action model (Preston and de Waal 2001), review the discovery of the mirror neurons and their implication to empathy, and discuss the possible evolutionary advantages of the empathic process.

Keywords: emotional empathy; behaviour evolution; altruism; mirror neurons

What is Empathy

Empathy is a complex concept to define, as it involves the domains of the emotional and the cognitive, and is conditioned by the inherent variability inside species, sex and age groups, as well as environmental context (de Waal 2008). Its overall meaning is accepted as the sharing of the emotional experience of another individual, but throughout the years many authors published their own distinct definitions of empathy, some of which are presented in Table 1.

The word “empathy” derives from the Greek *ἐμπάθεια* (*empatheia*), meaning passion or affection - *ἐν* (*en*), "in, at" + *πάθος (pathos)*, "feeling” (Liddell and Scott 1940). The word was then adapted into Einfühlong (“feeling into”), a German word used to describe the human ability to symbolize inanimate objects of nature and art (Preston and de Waal 2001; Gallese 2007). Theodore Lipps extended the concept of Einfühlong to the domain of intersubjectivity, which he characterized in terms of inner inhibited imitation of the perceived movement of others, without any intervening labelling, associative or cognitive perspective-taking processes (Preston and de Waal 2001; Gallese 2007).

In Psychology, the dominant view up until very recently has been that Empathy is the mental ability to understand the emotional and mental states of others, a concept deeply connected with self-awareness, i.e., the ability to have a *Theory of Mind* – a view that, despite its popularity, restricted the empathic process to cognition (Gallup 1977; Preston and de Waal 2001; Bekoff et al. 2002). Assessment of these processes is a difficult task, since researchers have to infer from observable behaviours, emotions and mental states that are not directly observable (de Waal 2008). It is much easier to elaborate paradigms to assess those processes in humans than in non-human animals. Thus, not surprisingly, the most widely accepted view has been quite resilient and roughly corresponds to Clark’s (1980) statement: *it is my considered judgment that empathy, like language, humour, and the rituals surrounding sex and death, is uniquely human. It is my belief that the capacity for empathy is a consequence of the most recent developed portion of the human brain, the anterior frontal lobes*.

In this paper we review evidence that this view has been overtaken. First and foremost, there is ample and ever-growing evidence that understanding the emotions of others involves automatic and unconscious *embodying* mechanisms that occur with no effortful processing or cognitive perspective-taking (Dimberg and Thunberg 1998; Preston and de Waal 2001; Rizzolatti et al. 2004; de Vignemont and Singer 2006).

Activation of brain areas such as the insula, amygdala and premotor cortex in response to emotional stimuli, and resulting emotion congruent visceral-motor responses reveal that the brain is equipped to deal with the understanding of emotions in oneself and in others (Rizzolatti et al. 2004; de Vignemont and Singer 2006). We shall elaborate on these structures in detail further ahead in this paper.

Table 1. The definition of empathy according to various authors.

Author	Year	Definition
Hogan	1969	The act of constructing for oneself another person's mental state.
Clark	1980	That unique capacity of the human being to feel the experiences, needs, aspirations, frustrations, sorrows, joys, anxieties, hurt, or hunger of others as if they were his or her own.
Hoffman	1978	An affective response more appropriate to someone else's situation than to one's own.
Eisenberg & Strayer	1987	An emotional response that stems from another's emotional state or condition and that is congruent with other's emotional state or situation.
Hollin	1994	The ability to see the world, including one's own behaviour, from another person's point of view is to display empathy.
Parr	2001	The ability to understand emotion in others; emotional awareness
Preston & de Waal	2001	Understanding of another person's feelings, affect sharing.
Schino et al.	2004	Empathic processes range from emotional contagion to cognitive empathy, that is, the capacity to understand the emotional, visual, or cognitive perspective of another individual.
Adam	2006	Refers to sensitivity to, and understanding of, the mental states of others.
Vignemont & Singer	2006	There is empathy if: (i) one is in an affective state; (ii) this state is isomorphic to another person's affective state; (iii) this state is elicited by the observation or imagination of another person's affective state; (iv) one knows that the other person is the source of one's affective state.
de Waal	2008	The capacity to (a) be affected by and share the emotional state of another, (b) assess the reasons for the other's state, and (c) identify with other, adopting his or her perspective.

We are witnessing a shift in perspective and are now aware of the relevance of empathy as a socially facilitating tool, which might have had important advantages throughout the evolution of pre-human societies and even more ancient primate societies. Empathy is no longer looked at as an obstacle to the biological urges of power and personal satisfaction, as Clark (1980) saw it, but as a vital component in the coordination of an individual´s social life, incidentally benefiting the entire community. Emotions are often the contextual element that signs the intent of an action, which animals are required to understand in order to lead a successful social life (Rizzolatti et al. 2006). Although non-human animals may not be able to express or understand such a vast array of emotions as humans do, it is widely accepted that basic emotions, those that organize behaviour crucial to survival – anger, joy, sadness, fear and disgust (for more information see Panksepp 2004) – are common in the animal world, and thought to be easier to empathize with than secondary emotions such as jealousy (de Vignemont and Singer 2006; Grandjean et al. 2008; Jabbi and Keysers 2008). Emotions are known to be social facilitators and allow the formation of social bonds, since being in an emotional state serves as a form of communication, as it reflects the position of the individual within a specific social context (Gallese 2007).

Empathy has been accepted as an “umbrella term” for affective phenomena such as emotional contagion, sympathy and empathic perspective taking, which can co-occur in a species or manifest separately in different animals (Preston and de Waal 2001; de Waal 2008). We begin by defining each one:

Emotional Contagion

Also known as *the neighbour effect*, *emotional transference, self-centered vicarious arousal* or *affective resonance* (Parr 2001; Videan et al. 2005; de Waal 2008), it is the process by which the observer (the *subject*) is affected by another individual’s emotional or arousal state (the *object*) and does not perceive it to affect or influence his own (Videan et al. 2005; de Waal 2008). Behaviour syncing is advantageable especially in social animals, as it works as a survival facilitating tool (Bekoff et al. 2002; de Waal 2008). Emotional contagion is the most basic form of affective communication, and one of the primary ways of learning and experiencing the emotional states of others (Bekoff et al. 2002; de Waal 2008). De Waal (2008) considered emotional contagion the *lowest common denominator of all empathic processes*, presenting continuity between humans and other animals. The principle of emotional contagion, by comparison with empathic mechanisms of higher complexity, has been proposed quite simply as the “trying on” of emotional expressions and vocalizations that can lead to physiological changes which initiate a matching emotional state in the subject and observer, thus allowing a shared emotional experience, non-dependent of conscious processing (de Waal 2008). In support of this idea, voluntary facial activity replicating prototypical emotional facial expressions was reported to generate emotion specific patterns of autonomic activity (Jabbi and Keysers 2008) Observable examples of emotional contagion have long been reported and include the reflex-like spread of fear and distress, such as the take-off of a flock of birds because one is startled, or the contagion of cry in a room full of newborns when one starts crying (Bekoff et al. 2002;

de Vignemont and Singer 2006; de Waal 2008). Emotional contagion can also result from intentional communication, such as the loud temper tantrums of infants, with the purpose of distressing the mother into changing her behaviour and providing more attention to the juvenile. This mother-infant bond facilitation is observed in human and non-human animals (Preston and de Waal 2001; Panksepp 2005; de Waal 2008).

Sympathy or Sympathetic Concern

An evolutionary landmark of empathy takes place when emotional contagion is associated with appraisal off the affective state of others and their emotional context (Gruen and Mendelsohn 1986; de Vignemont and Singer 2006; Gallese 2007; de Waal 2008). Data on rats and monkeys show that individuals will inhibit their behaviour if they perceive it to be responsible for a conspecific’s distress (for reviews see Bekoff 2007 and de Waal 2008). Sympathy is not to be confused with personal distress, where one seeks to alleviate his/her own suffering, with no regard for the suffering of the other (de Waal 2008). Sympathetic individuals do not exhibit any reproduction of a perceived emotion in other, but will rather react with concern to the sight of a distressed individual (Gruen and Mendelsohn 1986; Boesch and Boesch-Acherman 2000; de Waal 2008). This occurs both in human and other animals. For example, some experiments revealed that not only children will react with concern for a family member, but pets such as cats and dogs also exhibit signs of concern (Clutton-Brock 1999; de Waal 2008) Rhesus monkeys are known to embrace, mount or even pile on top of a screaming conspecific in an attempt to reduce their own negative arousal (de Waal 2008).

Consolation has been pointed as the most significant behaviour outcome of sympathetic concern (de Waal 2008): an individual initiates contact with a distressed peer, even without being solicited, with reassuring behaviour in (Preston and de Waal 2001; Koski et al. 2007). It has been observed in captive apes, wild chimpanzees, large-brained birds and human children (Preston and de Waal 2001; Schino et al. 2004; de Waal 2008). Despite intensive observations, it has never been observed in monkeys (Boesch and Boesch-Acherman 2000; Schino et al. 2004; de Waal 2008). Macaque mothers fail to console their offspring after a fight, ignoring the bodily cues of distress presented by the infants (Schino et al. 2004; Plotnik et al. 2006; de Waal 2008). Monkeys, when compared with chimpanzees, seem to lack significantly important mental skills. Even regarding mirror self-recognition, while chimpanzees appear to be aware of the reflection as an image of themselves, monkeys do not behave in such way, independently of how many hours they are exposed to the mirror

(Gallup 1977). Neurophysiologically, processing emotional states and overall interoceptive awareness is deeply connected with the anterior insula and frontal operculum (IFO), an area with no homologue in the monkey's insula (Jabbi and Keysers 2008). This stage of emotional awareness is probably made possible by this phylogenically new region, yet another evidence of the evolutionary gap between monkeys and Hominoidea (Schino et al. 2004; de Waal 2008; Jabbi and Keysers 2008).

Empathic Perspective-Taking

From a psychological point of view, empathy undertakes emotional perspective-taking, as the subject is required to understand and adopt the object's point of view and emotions, engaging in imagination and mental state attribution (de Waal 2008). Such requirements constitute the main reason why empathy in non-humans has been very hard to accept. Some authors still argue to this day that our closest cousins do not possess the ability to understand mental or emotional states in others (Povinelli and Giambrone 2001). Accumulated data contradicts this opinion: apes (although not monkeys) show some level of perspective-taking both in their spontaneous social behaviour and under experimental conditions (Boesch and Boesch-Acherman 2000; de Waal 2008). de Waal (2008) referred targeted helping as proof of empathy; in his words, *for an individual to move beyond being sensitive to others toward an explicit other-orientation requires a shift in perspective*, becoming sensitive to the specific needs of others and behaving accordingly (Plotnik et al. 2006; de Waal 2008). Mere perspective-taking is not enough for the display of empathy; emotional engagement needs to occur as well (de Waal 2008). Tree bridging in an orangutan female is one example of empathic perspective taking, in which the mother anticipated the offspring need to move from one tree to another (de Waal 2008). Boesch and Boesch-Acherman (2000) reported chimpanzees hiding from a displaying dominant male if they perceived themselves to be the target of aggression, and moving accordingly as not to be seen. The dominant male showed some levels of awareness for such escapist behaviours, as he would go look for the hidden individuals, engaging in perspective-taking as well. Chimpanzees are also known to cater to the needs of an injured individual, assessing the adequate care required by the wound, adjusting their behaviour accordingly and displaying different emotions depending on the nature or severity of it (Boesch and Boesch-Acherman 2000). This behaviour is not limited to kin, but extended to all group members (Boesch and Boesch-Acherman 2000). Other examples of empathic behaviours in chimpanzees include the removal of a foreign body from a companion's eye (Miles 1963), helping an elder chimpanzee climb a tree (Goodall 1986; de Waal

2007), consoling a defeated male after a power struggle (de Waal and van Roosmalen 1979; Aureli et al. 2008; de Waal 2008), and helping a trapped bird escape (de Waal 2006). Elephants reassure distressed companions and help injured ones by supporting or lifting them if they're too weak to stand; dolphins support sick companions near the surface to keep them from drowning, stay close to females in labour and help release companions trapped in fishing nets (de Waal 2008).

Empathic perspective-taking assumes the understanding that the new emotional state derives from an external source (the object's emotional state), an awareness absent in emotional contagion (Boesch and Boesch-Acherman 2000; Gallese 2007; de Waal 2008). Such concept comprises the notion of *self*, as self knowledge is used in the reproduction of the observed emotion and on the inferring of other's mental states and intentions (Preston and de Waal 2001; Oberman and Ramachandran 2007). Gallup proposed that mirror self-recognition appears together in both development and phylogeny with the ability to sympathize, empathize and attribute intent and emotions to others – the Coemergence Hypothesis – which seems to be supported by the substantially different results between monkeys and apes when it comes to mirror self-recognition, consolation and targeted help (Gallup 1977; 1998; Plotnik et al. 2006; de Waal 2008). Monkeys do not exhibit any behaviours that suggest mirror self-recognition, independently of how many hours that are exposed to the mirror (Gallup 1977). Besides the great apes, only elephants and dolphins exhibit mirror self-recognition (Reiss and Marino 2001; Bekoff et al. 2002; Plotnik et al. 2006; de Waal 2008). And indeed it is in regard to these two animal species that we find the most compelling reports on consolation and targeted helping (de Waal 2008). Both possess a high level of encephalization and an impressive cognitive and behavioural complexity (Reiss and Marino 2001; Plotnik et al. 2006). Plotnik et al. (2006) also suggested that the elephant and dolphin's mirror self-recognition could be related with a convergent evolution most likely related to complex sociality and cooperation. Reiss and Marino (2001) suggest different neurological substrates of mirror self-recognition for dolphins and primates, as both lines have diverged about 65-70 million years ago.

Empathy, although automatic by nature, can be modulated by several factors – empathic responses are thought to be heightened by similarity, familiarity, social closeness, and positive experience with the object (Preston and de Waal 2001; de Waal 2008). Morphology and biomechanics seem to play an important role in the triggering of empathy; monkeys do not display empathic reactions to the sight of albino rats being shocked, nor to the sight of a puppet monkey in distress (Preston and de Waal 2001). However, monkeys will starve themselves if getting food implies shocking a conspecific, and that response is heightened if the individual has been shocked before and is familiar with the other individual (Masserman et al. 1964). Humans respond very differently depending on the perceived nature of a relationship or situation; tests showed that an individual would empathize with another individual's pleasure or distress if they perceived their relationship as cooperative, and show an antipathic response (distress to perceived pleasure or pleasure to perceived distress) if the relationship was perceived as competitive (de Waal 2008). With functional imagining resonance (fMRI), it is possible to register activation of the anterior cingulated cortex (ACC) and the anterior insula (AI) at the sight of a likeable character in pain, and no activation if the character is reported to be unlikeable; also, activation of pain related areas in the brain is smaller if the pain observed is perceived as necessary (e.g.: to cure the observed individual) (de Vignemont and Singer 2006). It appears that empathy can be biased into activation with positive relationships and suppressed (or turned into *Schadenfreude*) with negative relationships (de Waal 2008). Such as humans, chimpanzees can engage in aggressive behaviours, and "warfare" tactics towards individuals of rival groups are fairly common (Wrangham 1986; de Waal 2005; 2008). Intragroup tensions tend to be less serious due to the adaptive value of group life, and are usually resolved with reconciliatory approaches such as kissing and embracing (de Waal 2005; 2008).

Cognitive and emotional empathy

Some authors choose to acknowledge empathy as a concept with two separable, complementary systems: *cognitive empathy* (mental perspective taking) and *emotional empathy* (the vicarious sharing of emotion) (Smith 2006). Cognitive empathy relates to the understanding and predicting of behaviour in others, particularly in terms of attributed mental states (Smith 2006). It can be used in manipulating others to our benefit (Smith 2006), or helping with simple task-solving problems (Call 2001). Empathic processes do not require conscious awareness, but can be augmented by cognitive capacities in evolution and development, so that empathy is possible even in the absence of the object of distress, recurring to imitation or effortful processing (Preston and de Waal 2001). In the words of Smith (2006), t*he demands of the complex social environment in human evolution have selected for cognitive empathy because it enhances social functioning* (Smith 2006). Emotional empathy promotes inclusive fitness, acting as an inhibitor for violent behaviour, and helping with group cohesion through intrinsic rewards (de Vignemont and Singer 2006; Smith 2006; de

Waal 2008). It also helps distributing basic emotions and facilitates behavioural synchronization and group cohesion (de Vignemont and Singer 2006; Smith 2006). The heightened sense of other's emotions could contribute to quicken helping behaviour (Smith 2006). Emotional empathy is predominant over cognitive empathy situations such as violence inhibition, or in the cases of automatic response to an emotional vocalization from an out-of-sight offspring (Smith 2006). The combination of the two brings balance to social interactions, as emotional empathy facilitates prosocial motivation and cognitive empathy provides prosocial insight; cognitive empathy buffers the urge to help given by emotional empathy, and selects what kind of help is most appropriate in a given situation, and vice-versa: emotional empathy buffers the violent and manipulative impulses, as well as the Machiavellian uses of cognitive empathy (Smith 2006).

The purpose of empathy

The ability to understand the inner state of another, i.e., to recognize emotional states in conspecifics and act on them, is one of the most important skills in social life, as it gives rise to pro-social motivation and altruistic behaviour, and its absence to sociopathic behaviour (Iacoboni et al. 2005; Maibom 2008). Not only it allows the individual to learn from others and their experience, but it also allows the active learning of the surrounding environment through behavioural cues. Primates in particular are known to learn much about their surroundings by observing conspecifics (Scherer 1984; Quiatt and Reynolds 1993; Cunningham and Janson 2007; van der Gaag et al. 2007). Animals capable of predicting the behaviour of their peers, especially in novel situations, possess clear advantage over those who do not possess this ability and, consequently, higher fitness over them (Quiatt and Reynolds 1993; Call 2001). This emotional awareness serves in the formation of long-lasting relationships, and facilitates the pursuit of shared interests and coordination of group activity (Parr 2001). This interpretation tears with the old school of thought, where empathy was considered a liability to the animalistic impulses of personal satisfaction and search for power (Clark 1980). Although the evidence on non-human empathy is still scant, mostly because no one was looking for it outside the human species, there is a growing body of data showing that at least some non-human primates possess the neural basis that allows for the display of empathic behaviour (Brothers 1990; Rizzolatti et al. 1996).

In 2001, Preston and de Waal proposed the Perception-Action Mechanism model to explain why some animals are so inclined to help others. According to this model, the observer (or *subject*), through his own neural and bodily representations, accesses the emotional state of the individual experiencing the situation (the *object*), because perception and action share a common code of representation in the brain (Preston and de Waal 2001). The familiarity or proximity between the two individuals will result in a much more detailed representation of the situation by the subject, which will in turn translate into a richer and more accurate pattern of response (Preston and de Waal 2001). The Perception Action mechanism supports behaviours such as mother-infant responsiveness, alarm, social facilitation, amongst others, as it underpins sympathetic concern and perspective-taking, and motivates behavioural outcomes (Preston and de Waal 2001; de Waal 2008). In the words of Preston and de Waal (2001), *having a nervous system that responds automatically with empathy to situations where they must respond creates the appearance of reciprocity and maximizes inclusive fitness.* In order to relate the different affective phenomena, de Waal (2008) proposed the Russian Doll model, which also links imitation to the empathic process. Imitation is *the spontaneous reproduction of novel acts yielding disparate sensory inputs when observed and executed* (Heyes 1998). Data gathered on children (25-64 months) suggests that friendly relationships are characterized by imitative or reciprocal behaviour, as children who were friends had the highest rates of imitation, parallel play and requesting, as well as a greater concordance in baseline heart rate and other concordance measures (de Waal 2008). Examples of imitation in primates ("aping") include contagious yawning in chimpanzees, eating at the sight of others eating, contagious scratching in monkeys, as well as neo-natal imitation in similarity with human children (Anderson et al. 2004; Nakayama 2004; de Waal 2008). Several monkey species, although exhibiting social facilitative behaviours, show no evidence of imitation (Bekoff et al. 2002). It appears that the tendency to imitate is as spontaneous at the empathic response but tends to decrease with age, as pro-social behaviours such as helping increase (Preston and de Waal 2001; de Waal 2008). Refined mental segregation of self and others, increased pre-frontal functioning and learned display rules also contribute to the inhibition of the automatic imitation response (Preston and de Waal 2001). Imitation is an important socially facilitating tool – the chameleon effect of imitation is found to create affiliation and fondness (de Vignemont and Singer 2006; Trivers 2006). Imitation undertakes the mental ability to understand a situation from a novel point of view (Bekoff et al. 2002). The relation between observation and imitation is supported by neurophysiological data regarding facial expression of emotion: both activate the same group of brain structures, including the ventral premotor cortex, the insula and the amygdala (Gallese 2007). According to de Waal (2008), empathy and imitation share the same motivational structure, which includes shared representations, identification through physical similarity, automaticity and spontaneity.

The Mirror Neuron System

Lingering scepticism around the idea of emotional empathy in non-human primates, as well as other animals, has been mitigated by the neurosciences. And despite the valuable contributions of the most various fields of science, no discovery was as significant in the enlightening of empathy in primates as the shared circuitry organization of the brain, a discovery made possible through the discovery of the *Mirror Neuron System* (Rizzolatti et al. 1996). Empathy switched from being interpreted as a psychological phenomenon, where one was required to consciously *deal with abstract ideas and to create and function in terms of abstract realities* (Clark 1980) to being recognized as a bodily or mechanical phenomena. The core argument is that, through its own neural and bodily representations, it is possible for the observer to experience the subjective state of another individual, given that the neural representations of that particular state are activated in the observer (Rizzolatti et al. 2004; de Vignemont and Singer 2006; Rizzolatti et al. 2006; van der Gaag et al. 2007). This mechanism removes conceptual reasoning from the equation, allowing the individual to understand the observed action through direct simulation using a mirror mechanism, creating a subpersonally instantiated, *we-centric common space* (Rizzolatti et al. 2004). The similarity between individuals allows the enhancement of the observer's matching motor and autonomic responses (de Waal 2008).

The discovery of mirror neurons took place in the early 1990s, when Rizzolatti, Gallese, Fadiga, and Fogassi were investigating neuron controlled responses concerning hand control in macaque monkeys (Rizzolatti et al. 2006). Rizzolatti and his team observed that some neurons in the monkey's brain not only fire at the performance of certain motor actions (eg: grasping), but also fire at the perception of the same actions being performed by other individuals, the first evidence of the brain's involvement in processing first and third person perspectives (Keysers and Perrett 2004; Keysers and Gazzola 2006; Rizzolatti et al. 2006). Three areas in the monkey brain become active at the performance of motor actions by other individuals: the superior temporal sulcus (STS), the anterior inferior parietal lobule (area 7b or PF) and the ventral premotor cortex (area F5) (Keysers and Perrett 2004; Keysers and Gazzola 2006; Rizzolatti et al. 2006). The superior temporal sulcus connects reciprocally with area PF, which also connects reciprocally with area F5; there are no direct connections between the superior temporal sulcus and area PF (Keysers and Perrett 2004; Keysers and Gazzola 2006). The singularity of area F5 lies in the fact that virtually all neurons that fire when the monkey observes an action being performed by someone else, also fire when the action is performed by the monkey, whether it can see its own action or not (Keysers and Perrett 2004; Keysers and Gazzola 2006; Rizzolatti et al. 2006). These neurons were hence named mirror neurons (Keysers and Perrett 2004; Keysers and Gazzola 2006; Rizzolatti et al. 2006). About two thirds of the neurons in area PF and half of the neurons in the STS area also exhibit mirroring properties, working on a excitatory way, contrasting with the other half of the neurons in STS, who clearly distinct between self- and other- performed actions (Keysers and Perrett 2004; Keysers and Gazzola 2006). Studies using functional imaging resonance (fMRI), positron emission tomography (PET) and magnetoencephalography (MEG) have located three areas in the human brain which become active with observation of actions: the caudal inferior and frontal gyrus and adjacent premotor cortex (Broadman areas (BAs) 44 and 6) corresponding to the monkey's area F5, the rostral inferior parietal lobule (IPL) corresponding to the monkey's area PF, and caudal sectors of the temporal lobe, in particular the posterior superior temporal sulcus (pSTS) and adjacent MTG corresponding to the monkey's STS (Keysers and Perrett 2004; Keysers and Gazzola 2006; Rizzolatti et al. 2006). The IPL and BA44/6 have important roles in the observation and execution of motor actions and, like in the monkey's PF and F5, some neurons behave in a mirroring fashion (Keysers and Gazzola 2006). These mirror neurons fire during the performance of simple goal-directed actions (e.g.: grasping), during the sight of the performed action or an audio stimulus of a perceived action, with no need for external reward (Rizzolatti et al. 2004; 2006; Iacoboni et al. 2005; de Waal 2008). Mirror neurons are thought to encode templates for specific actions, thus eliminating the necessity for explicit reasoning about basic observed actions and facilitating the learning process by imitation (Rizzolatti et al. 2006). After establishing that the brain uses the same hardwired connections to code observed and performed actions, investigators tried to understand if the mirror neuron system was capable of coding the *intention* of an observed action. Iacoboni and colleagues found that, in humans, actions embedded in context yielded a greater signal response in the parieto-cortical circuit for grasping than activities with absence of context. In monkeys, experiences with placing food in a container or in the mouth fired different sets of neurons, evidencing the final goal of the action matters and is understood by the brain

(Rizzolatti et al. 2004; 2006; Iacoboni et al. 2005). Regarding coding of intention, data suggests a set of “logically related” mirror neurons acts complementarily to the neuronal chain of mirror neurons that codes the motor acts (Iacoboni et al. 2005). In humans, it appears that the motor system codes both the goal of the observed action and the way the action is performed, reacting to a wider range of actions than the monkey’s system (Rizzolatti et al. 2004). To the contrary of what happens in the monkey’s neuron system, no physical object is required for the mirror neurons in the human brain to fire – mimed actions can trigger the neuron system (Rizzolatti et al. 2004).

The empathic machinery

Rizzolatti established that the patterns of neuron activity associated with observed actions were true representations in the brain of the act itself, regardless of who was performing it, working as an “offline simulation” of an observed situation through the embodiment of the observed individual’s behaviours and emotions (Rizzolatti et al. 2006; Oberman and Ramachandran 2007). After the discovery of mirror neurons, it became obvious that the brain – monkey or human – is organized in circuits that overlap observed and performed information (Keysers and Gazzola 2006). These “shared-circuits for motor actions” constitute an efficient mechanism for the unconscious understanding of actions in others (Keysers and Gazzola 2006). Shared-circuits are now known to be applicable to actions, sensations and emotions (Rizzolatti et al. 2003; 2004; 2006; de Vignemont and Singer 2006; Keysers and Gazzola 2006; Gallese 2007). The connection between shared-circuits and sensations was proved by Keysers and Gazzola; they found that touching someone’s own legs or face activates the primary and secondary somatosensory cortex, and that the secondary somatosensory cortex was also active at the sight of someone else’s legs or face being touched (Keysers and Gazzola 2006). The somatosensory cortices deal with experiencing touch in oneself and viewing human beings or objects being touched (Keysers and Gazzola 2006). The activation of somatosensory areas when we are touched overlaps in time with visual cues of an object moving towards us and touching our body; through Hebbian associations, the sight of someone else being touched will trigger the same somatosensory activation (Keysers and Gazzola 2006). Hebbian associations can be related to the emergence of associations between first and third person perspective of actions, sensations and emotions (Keysers and Gazzola 2006).

Pain also seems to be interpreted through such a shared circuit (Decety et al. 2006; Keysers and Gazzola 2006; Moriguchi et al. 2007). The experiencing of pain or the perception of pain in someone else activates a common circuitry which includes the anterior cingulated cortex (ACC) and the anterior insula (Keysers and Gazzola 2006). This shared circuit cross-talks with shared-circuits of actions, as the observation of pain influences motor responses in the subject (Keysers and Gazzola 2006). The insula appears to be linked with most of the brain, specifically with regions associated with gustation (basal ganglia, amygdala, ACC, orbitocortical cortex), somatosensation (SI, SII and posterior insula), high level vision (STS), memory and semantics (temporal pole and hippocampus, and the motor cortices (IFG-premotor, SMA/preSMA, M1 and cingulated motor cortex) (Rizzolatti et al. 2006; Gallese 2007; Jabbi et al. 2008). Electrical stimulation of the monkey's insula produces movement in several body parts (Rizzolatti et al. 2004). In humans, electrical stimulation of the anterior insula produces unpleasant sensations in the throat and mouth, as well as the sensation of nausea (Rizzolatti et al. 2003; Keysers and Gazzola 2006). Although the human's insula is larger than the monkey's, cytoarchitectonically the both are strikingly similar (Keysers and Gazzola 2006). Rizzolatti, Wicker, Keysers, Plailly, Royett and Gallese found that human volunteers would experience the activation of overlapping neuron populations in the left anterior insula and adjacent frontal operculum (IFO) when smelling a disgusting odour or watching a video of someone else smelling something and displaying a disgusted face, suggesting a mirroring of the observed emotion (Rizzolatti et al. 2003; 2006; Keysers and Gazzola 2006; Keysers et al. 2006). Audio clues of disgust are also processed in the insula (Keysers and Gazzola 2006). Lesion data supports the importance of the insula in the processing of disgust: damage in the insula area can result in the inability to experience disgust and an impaired recognition of disgust in others (Keysers and Gazzola 2006). The area of the brain with higher activation at the sight of disgust when compared with neutral faces was the ipslateral right BA45, located in the inferior frontal gyrus (IFG), known to be involved in the execution, imitation and observation of facial expressions (Jabbi et al. 2008; Jabbi and Keysers 2008).

The amygdala seems to work in a similar way regarding the regulation and the processing of fear (Keysers and Gazzola 2006). Fear conditioning experiments in rats have led to the discovery of a direct subcortical pathway from the thalamus to the amygdala (Preston and de Waal 2001; Grandjean et al. 2008). The amygdala appears to possess a dual route architecture, consisting of a direct subcortical pathway and an indirect cortical pathway (Preston and de Waal 2001; Grandjean et al. 2008). Several results obtain in humans suggest that the emotional value of visual stimuli could be detected by a collico-pulvinar-amygdala pathway (Grandjean et al. 2008). The indirect cortical pathway is composed by the vast connections the amygdala is able to establish with the thalamus and different sensory cortices (Grandjean et al. 2008). Damage in the human's amygdala causes impaired recognition of facial cues of fear and anger in others, although such impairment only seems to affect about half of the subjects (Keysers and Gazzola 2006). Damage in the monkey's insula causes disinhibition for general accepted fearful activities and behaviours (Keysers and Gazzola 2006). Controversy still exists on whether the amygdala is responsible for the processing of fear; the amygdala is known to activate during the observation of facial expressions, whether emotional or not, and individuals with early set lesions in the amygdala are still able to experience fear, even though in unusual social circumstances (Keysers and Gazzola 2006). The role of the amygdala in the processing of fear might be indirect, as part of a circuit, by coordinating information regarding facial stimuli with other areas that are responsible for the experience of fear (Keysers and Gazzola 2006).

Such knowledge provided empathy with a physiological dimension that did not exist before – and by steering the concept away from a purely psychological definition, it allowed empathy to be established as a phenomenon that occurs in children, whom may not possess the tools necessary for a “online-simulation” of the emotions of others (Hallenbeck 1981; de Vignemont and Singer 2006) and also in animals equipped with a nervous system developed enough to allow for these complex processes to exist (de Waal 2008). Although some authors are concerned with applying “evolutionary plausibility”, evidence points to some sort of connection among species (Povinelli and Bering 2002). Areas of the brain previously identified in the perception and production of facial emotional expressions are activated by the sight of a facial expression of the same emotion (Singer et al. 2004; Gallese 2007). In primates, studies seem to suggest that some neurons respond selectively to facial expressions, also supporting the theory that emotional reactions are controlled by a innate biological affect mechanism (Dimberg and Thunberg 1998). Chimpanzees subjected to emotionally charged images react with changes in the brain and peripheral skin temperature in a strikingly familiar fashion to humans (Parr 2001; de Waal 2008). Humans and chimpanzees share a very imilar structure of communication and emotional recognition (Bard and Gardner 1996; Leavens et al. 2005; Gaspar 2006; Hirata 2009), and chimpanzees seem to be able to differentiate emotional expressions very similar to human ones. Chimpanzees also exhibit anatomical asymmetries in areas of the brain that are thought to be homologous with language related areas in humans (Parr and Hopkins 2000). As mentioned before, the insula receives information from olfactory and gustatory receptors, as well as from the anterior sectors of the ventral bank of the superior temporal sulcus, the same zone that shows activation in the monkey regarding the sight of faces (Rizzolatti et al. 2003; 2004; Gallese 2007).

Damage to the nervous system and impairment of empathy

Gazzola, Azziz-Zadeh and Keysers (2006) found that people who are more empathic (based on a self-report questionnaire) have stronger activations both in the mirror system for hand actions and the mirror system for emotions providing more direct support to the idea that the mirror system is linked to empathy via the reactivation of emotion circuits in the brain that are active during self experience of those emotions (e.g., anterior insula, amygdala, secondary sensory cortices) (Keysers and Gazzola 2006; Keysers et al. 2006; Jabbi et al. 2008; Jabbi and Keysers 2008). Damage in the frontal brain also reinforces the connection between neural processes and empathy. Adjacent frontal operculum (IFO) lesions cripple the recognition of disgust (Rizzolatti et al. 2003; Jabbi et al. 2008). The IFO area is related to the recognition of disgust, pleasure and pain, and is also activated during autobiographical recall and the attribution of taste to images of food. Most likely, IFO is related with interoceptive awareness (Rizzolatti et al. 2003; Jabbi et al. 2008). Individuals with early onset damage to the prefrontal cortex exhibit standard behaviours of sociopathy, impaired empathy, autism, Asperger's syndrome and schizophrenia (Preston and de Waal 2001; Shamay-Tsoory et al. 2005). Although, because autistic individuals have difficulty in the production, imitation and recognition of expressions – an overall defective embodied simulation – this disorder is likely to be characterized by an early on impairment in the perception-action pathway (Preston and de Waal 2001) or altered regulation of the Mirror Neuron System (de Vignemont and Frith 2007; Gallese 2007). The deficit in imitation and empathic responses by autistic children agrees with de Waal's Russian doll model (Preston and de Waal 2001; de Waal 2008). Autistic children also show delayed or absent responses in the mirror self-recognition test (Gallup 1998).

Why has empathy evolved?

Through empathic perspective-taking, an individual has a faster access route to another individual's emotions, and the reproduction of the observed emotion through its own neural system allows the individual to predict future behaviours from the arousal of its own motivational and action systems (de Vignemont and Singer 2006; Keysers and

Gazzola 2006). The activation of shared-circuits allow for an unconscious connectedness of all individuals within a social group through a neural basis (Gallese 2007). According to Gallese (2007) *such connectedness finds its phylogenetic and ontogenetic roots in the social sharing of affect*.

As noted before, the ability to understand behaviours and to predict them can prove to be a huge fitness advantage (Call 2001). Empathy can serve as a great tool to acquire information about the surrounding environment – for example, seeing a conspecific eating food and looking disgusted will allow the individual to infer that the food is bad and should not be eaten; watching an individual get burnt and observing his pain will trigger the mirror neurons related with coding pain in the observer, generating a state of "intentional atunement" (Rizzolatti et al. 2003; Gallese 2007). This pain the observer feels is a result of his own stored memories and the emotion he observes in the other individual that is reproduced by his own system through Hebbian associations, allowing him to make the connection between fire and pain, and preserving him from the actual experience to understand how it feels like (de Vignemont and Singer 2006; Keysers and Gazzola 2006; Gallese 2007). Singer and colleagues (2004) proposed that the re-representations form the basis for our ability to form subjective representation of feelings that allow us to predict the effects of emotional stimuli with respect to the self; they serve as a neural basis for our ability to understand the emotional importance of a particular stimulus for another person and to predict its likely associated consequences. From a functional perspective, fully detailed representations of stimulus are only useful when concerning one's own body, where information such as intensity and location play important aspects when dealing with a possible unpleasant stimulus (Singer et al. 2004). When assessing another individual's reaction to pain, the relevance is not as much of a sensory-discriminative kind, but rather the balance between the relevance of the stimulus reproduced and its observable unpleasantness (Singer et al. 2004).

The mirror neuron system could have evolved to simplify the comprehension of other's behaviour – in a mechanic and direct way without recurring to a complex cognitive machinery (Rizzolatti et al. 1996; 2006). Such system would be a stepping stone in efficiency regarding time and energy consumption, since coding templates for simple behaviours would remove the explicit reflective mediation and allow more complex cognitive process to develop through the simple coded ones (Rizzolatti et al. 2004). An individual develops a generalization from his own behaviour and observing the same behaviour in others triggers the stored memory (Rizzolatti et al. 1996; Holton and Langton 1998). The observer understands the observed action because he knows the expected outcome from his previous experiences, since the visual cues allow the access of the experiential motor knowledge (Keysers and Gazzola 2006; Rizzolatti et al. 2006). Translating the actions, feelings and emotions of others into our own neural language, allows for a connection through primary representations of the states of others and, in such reality, when someone is asked to elaborate on someone else's actions, feelings, and emotions, it's not that different from elaborating about oneself (Keysers and Gazzola 2006).

Empathy may lead to cooperative and altruistic behaviour, although not always, but it certainly seems to set the motivation to do so even if the beneficiary of the altruistic behaviour is not a close kin or a potential reciprocator of altruism. Research is still needed to explore whether an absence of control of these non-conscious emotional reactions increases the likelihood of acting upon them with manifestations of sympathy, such as altruistic acts or consolation. Based on the reviewed evidence, there is no doubt that human empathy related behaviour has been primed by evolution and that it largely depends on both emotional and cognitive processes.

And, although we see reflections of empathy in other animals, some could have evolved independently of our own. Do we know how far back do our sympathy, consolation and altruistic behaviours go back in time? The species *Homo sapiens sapiens* is ca. 200.000 years old and descends from a long lineage of 7-5 million years of Hominins (Sibly and Ahlquist 1984; Kumar et al. 2005). Our 5 MA ancestors were physically and genetically very much like chimpanzee's ancestors, and we know from paleoanthropological evidence that our estimated 300.000 year old relatives, the Neanderthals, took care of their elderly and ill fellows, who crippled by serious bone disease such as bone cancer, osteoarthritis or damaged and even absent teeth (Stringer and Gamble 1993; Tappen 2005), couldn't have survived without extensive assistance from other members of their clans. The Mirror Neuron System similarities and the empathic behaviour in other primates suggests it has its roots in a far more distant past. From its advantages in both human and non-human primates we can certainly envisage its advantages in the lives and survival of other social mammals, of whom we have only heard anecdotal reports of empathic behaviour (for a review see Bekoff, 2007) and so far no knowledge of a MNS.

The new path to follow; no longer will Psychology attend to prejudice about our biological selves and remain isolated from Physiology or Neuroscience in its quest to understand brain and behaviour, human or non-human, for these are inextricable realities.

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Chapter 3

Can we grasp Emotional Empathy in the behaviour of the chimpanzee (*Pan troglodytes*)?

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Abstract:

The lack of a systematic approach to the study of empathy allowed critics to remain dismissive to the existence of the phenomenon outside the human species. Nowadays, the first scientific studies are steering empathy away from an anecdotal realm and stirring some controversy by urging a review on what was once considered an exclusivity of the human mind. According to Preston and de Waal (2001), empathy serves as an umbrella term for affective phenomena such as emotional contagion, sympathy and empathic perspective-taking, and each phenomenon builds on top of the other with increasing complexity. In this study we observed emotional contexts and evidence of being affected by emotions of others. Observations obeyed a systematic design and were carried out in a naturalist setting: two semi-free ranging chimpanzee colonies composed by 7-10 individuals were observed for a period of four months and all relevant emotional events (*triggers* and responses) were counted. Relationship Quality and Proximity between individuals were tested as influential categories in empathy related behaviours, and so every empathic interaction was characterized for both measures. The results underplayed the role of these two factors, which with the current data seem unimportant. Significant associations between *triggers* and emotional responses were found using a χ^2 of Independence test and these are generally supportive of the existence of empathic responses in chimpanzees.

Keywords: emotional empathy, emotional contagion, sympathy, empathic perspective-taking, relationship quality

Introduction

The concept of empathy has been, for many years, raising interest in various fields of knowledge. Philosophers, psychologists, ethologists and neuroscientists have looked at empathy through different lenses, and the lack of common ground crippled our understanding of the phenomenon for a very long time. The predominant view postulated empathy as a conscious simulation of the observed emotions in others, and therefore an ability exclusive to man (Clark 1980). For many decades such definition did not impose a problem as emotional phenomena were regarded as exclusive human traits, and so a huge barrier stood in the way of acknowledging the evolutionary benefits of empathy outside of the human species. Empathy was considered the exact opposite of egocentricity, an impediment to the urges of power and survival, and even a *liability to animalistic efficiency* (Clark 1980). Probably because research relied almost exclusively on verbal reports of subjective experience, any attempt to study these subjects in non-human animals would be castaway. Today, though, emotions are studied recurring to behavioural, neuroanatomical and physiological sciences, and the paradigm of animals possessing emotional lives is accepted (Rizzolatti et al. 2006; Gallese 2007; Grandjean et al. 2008; Jabbi and Keysers 2008). It is widely recognized that many animals display emotions as part of their complex array of social behaviours, and some behaviours exhibit amazing similarity between humans, rats and other mammals (for examples see Panksepp 2004; 2005). Such knowledge makes similarities between the pairs emotion-behaviour in humans and those pairs in chimpanzees expected to be similar and, in accordance, similarities between humans and chimpanzees have been reported, among others, for emotional facial expressions (van Hooff 1972; Dimberg and Thunberg 1998; Parr 2001; Waller and Dunbar 2005; Gaspar 2006), for attachment (Bard and Gardner 1996; Leavens et al. 2005; Gaspar 2006; Hirata 2009) and for physiological responses to emotion (Parr and Hopkins 2000).

Empathy can be defined as the ability to understand the mental state of others (Smith 2006) or to identify with a situation, be it a mental state or a particular emotion (Rizzolatti et al. 2004). As proposed by some authors, empathy can be interpreted as a shell that encases two separate but complementary phenomena: cognitive and emotional empathy. Cognitive empathy is directly linked with the understanding of what the other *knows*, while emotional empathy relates to the knowledge of how the other *feels* (Call 2001; Smith 2006; de Waal 2008). Cognitive empathy comes in use in situations such as the joint effort of solving problems, where the individual is required to understand a situation from his own perspective, but also acknowledging and recurring to the perspective of others. Manipulation, relatively common in primates (Hirata 2009), is a practical example where an individual uses cognitive empathy to his advantage, such as hiding food from a dominant male (Call 2001; Smith 2006) or hiding from an aggressive individual (Boesch and Boesch-Acherman 2000). Emotional empathy, in turn, helps an individual relate and understand the emotional state of others, as is thought to have been selected to motivate cooperative and prosocial behaviour, facilitate group cohesion and behaviour synchronization, and distribute quickly and effectively basic emotions, promoting inclusive fitness through intrinsic rewards (de Vignemont and Singer 2006; Smith 2006).

Over ten years ago, Rizzolatti and colleagues discovered the Mirror Neuron System, a group of neurons that fire at the performance of an action and to the perception of the same action being performed by someone else (Rizzolatti et al. 1996; Rizzolatti et al. 2004; Rizzolatti et al. 2006). This mirroring property is now found to be applicable to emotions as well, as studies in humans reported the activation of the amygdala and insula in the processing of emotions such as fear as disgust (Rizzolatti et al. 2004; de Vignemont and Singer 2006; Keysers and Gazzola 2006; Keysers et al. 2006). For the brain to be hardwired in such fashion, evolutionary benefits must arise, and mother–child bonding is one of the fitness outcomes thought to be facilitated by empathy (de Waal 2008). In social animals such as chimpanzees, the ability to understand and predict the behaviour of conspecifics can translate into gathering relevant information about the surrounding environment and the consequent increase in survival aptitude (Call 2001; Iacoboni et al. 2005; de Vignemont and Singer 2006; Hirata 2009). Empathy also allows the regulation of social interactions, establishment of long-lasting individual relationships, and the pursuit of shared interests, among others (Parr 2001; Iacoboni et al. 2005). Although cognitive empathy is of major importance in facilitating social life and constitutes a topic of high interest to the study of mental processes and intelligence, we will focus on emotional empathy from now on in this study. de Waal (2008) defined empathy as the ability to be affected by and share the emotional states of others. Emotional empathy serves as an umbrella term for affective phenomena such as emotional contagion, sympathy and empathic perspective-taking (Preston and de Waal 2001; de Waal 2008). Emotional contagion, thought to be the most primary form of emotional communication, is the phenomenon by which an individual is affected by the emotional state of another but does not perceive this transference of emotional information (Bekoff et al. 2002; de Vignemont and Singer 2006; de Waal 2008). Another evolutionary step takes place with sympathy which, as defined by de Waal, is the *succorant* behaviour that translates into being sensitive and showing concern for the emotional welfare of another individual (de Waal 1997).

The most complex display of empathic behaviours, empathic perspective-taking, requires the ability to understand and adopt the other individual's emotional state and to engage in imagination and mental state attribution (de Waal 2008).

The empathic response, although automatic by principle, is known to be modulated by factors such as kin, proximity, social closeness or positive experience with the other individual (Masserman et al. 1964; Preston and de Waal 2001; de Waal 2008). Chimpanzee behaviour comprises actions that suggest that they may experience empathy, such the removal of a foreign body from a companion's eye (Miles 1963), assisting a sic fellow (Goodall 1986), helping an elder climb a tree (de Waal 2007), and the consolation of a defeated male after a power struggle (de Waal 2008), because these actions require understanding of an emotional state and being emotionally affected by it. Or so would be the interpretation of the same actions performed by humans. The similarity of emotional responses led some authors to suggest that emotional empathy might have been selected during hominid evolution (Smith 2006). Therein we shall adopt de Waal's definition (2008) presented above, which goes in line with the recent evidence on the Mirror Neuron system. One considerable gap in the study of emotional empathy in chimpanzees is that the support for such ability comes from anecdotal evidence of cooperation and altruistic behaviour and not from systematic work (for a review see de Waal 2008). An exception is the experimental work by Parr (2001), which shows that the passive viewing of negative emotional stimuli in chimpanzees can produce the same physiological responses as in humans, with decreases in skin temperature resulting from sympathetic activity initiated by the noradrenergic vasoconstriction, typically associated with negative emotional arousal in humans. Parr (2001) has also exhibited evidence that chimpanzees match spontaneously emotional videos to conspecific facial expression, using emotional valence as an emotional cue, in similarity with humans.

Since empathy is the result of a process - a response to specific sets of behavioural stimuli - to look for it one must begin by searching for the *triggers*. We refer to *trigger* as a combination of emotional and behavioural cues that elicit a complementary empathic response. After bibliographic research and initial *ad libitum* observations of both groups, we considered Anger, Fear, Social Helplessness and Excitement as emotional *triggers*. Accordingly, we expected Fear to anger, Fear to Social Helplessness, Consolation to Fear and Consolation to Helplessness to be the appropriate complementary responses that would reveal acknowledgment of the emotional state of the displayer and some sort of complementary emotional response. We also considered Excitement to be the best emotional *trigger* to test for emotional contagion. Operational definitions are presented in Tables 2 and 3. In order to measure empathy we must be able to predict the occurrence of what usually is an empathy associate behaviour from a *trigger* that is usually present when empathy occurs. Thus, the underlying assumption in the current study was that in the contexts of witnessing aggression or displays of helplessness or fear related behaviours such as fleeing, empathy can occur, at least in some individuals. Also, that Excitement, as a highly volatile emotional behavior, will illicit contagion in other group members.

In an attempt to deepen the study of empathy, we considered factors that could potentially affect the empathic response. Individuals with high Relationship Quality levels will, in theory, exhibit higher rates of empathy than individuals who have a low measure of Relationship Quality. We established Relationship Quality as a comparative measure of the time spent engaging in affiliative or positive social behavior within a particular dyad. We also tried to infer on the importance of proximity in the responsiveness to a *trigger*. In order to do so, the closest individual to the performer (individual performing the *trigger*) was identified every time a *trigger* was displayed. Although the tendency is for individuals with a high relationship value to remain closer, that condition was not always verified, which made Proximity a relevant factor to observe. The closest individual will have, in theory, a better view of the displayer and of the *trigger*, and therefore will mirror internally better than any other individual. Like Relationship Quality, we expect Proximity to have a positive increment on the empathic response. This hypothesis was drawn after initial *ad libitum* observations and has no bibliographical support.

Empathy can serve as the most adequate explanation for certain behaviours observed in chimpanzees, as it is the most parsimonious solution: humans in the same context, subjected to the same environmental and social laws, produce the same behavioural outcomes. We are not building a model to advocate the existence of emotional empathy, but merely trying to fill the gap of the creation of a systematic model that allows for the scientific study of the phenomenon. In sum, and based on bibliographic research, we expect significant associations between the pairs Fear to Anger, Fear to Social Helplessness, Consolation to Fear and Consolation to Helplessness. We expect Excitement *triggers* to be significantly associated with Excitement responses, and Relationship Quality and Proximity to positively increment the probability of an empathic response.

Methodology

Study Groups

We studied two groups of chimpanzees in the Jane Goodall Institute's Chimp Eden, with composition described in Table 1. Both groups were kept in 2-3 hectares savannah areas with large forest patches within. Although the night quarters were joined and individuals could see each other, no significant amount of interaction between groups was observed. For practical reasons we shall refer to them as *juvenile group* and *adult group*. The three males in the adult group were transferred from the Johannesburg Zoo, and the elder male in the juvenile group was transferred from the Maputo Zoo. All other individuals were rescued from illegal ownerships and placed in the sanctuary for possible reintegration in the wild. None were related by blood and, for the exception of the three males in the adult group, none shared long relationship bonds (the males shared a 7 year stay at the Johannesburg Zoo). The four youngest individuals were rescued together, but all remaining individuals were stranger to each other until the moment of integration in the groups. No individuals shared a blood connection which excluded kin as an increment measure for this present study.

Table 1: Composition of both study groups. Legend: M – male, F – female.

	Name	Sex	Age
Juvenile Group	Jao	M	43
	Zac	M	16
	Cozy	M	10
	Sally	F	9
	Thomas	M	3
	Zeena	F	2,5
	Nina	F	3
	Charlie	M	1,5
	Dinka	M	1,5
	Zee	F	1
Adult Group	Abu	M	15
	Amadeus	M	15
	Nikki	M	11
	Lika	F	13
	Jinga	F	10+
	Mimi	F	8
	Guida	F	7

Procedures

Approximately 100 hours of data were collected in order to construct a social network so Relationship Quality levels could be assessed. We measured the relationship quality of all dyads for both groups.

The first author observed both groups during March – July 2008, assisted by a volunteer colleague, J.H., for 50% of the observation samples. Interobserver reliability was ensured by an index of concordance of ≈ 96,75% similarity in the group scans and

≈ 93,25% in the behavioural scans, using the formula Agreements / (Agreements + Disagreements) (Martin and Bateson 1986). Social interactions were recorded by scan sampling with instantaneous samples carried out every 15 minutes (Martin and Bateson 1986), and interactions between individuals scored in a matrix. We initially considered grooming, playing and contact-sitting as indicators of proximity, from bibliographic research (Koski et al. 2007). However, contact-sitting could not be used as a measure of Relationship Quality as initial observations led to the conclusion that there was not a general measure of proximity that could be used.

Behavioural sampling (Martin and Bateson 1986) was used to optimize the collection of empathy *triggers*. For every *trigger* (Anger, Fear, Social Helplessness or Excitement), the response of every individual in the group was registered. Individuals who were not present at the performing time of the *trigger* were labelled as “Not Present”. Individuals who did not appear to respond to the *trigger* were categorized as “Non-Responsive”. The closest individual to the performer was also identified, so that we could infer on the “weight” of proximity in the empathic response.

The data collection period ranged between 8:00 and 15:30 every day, the time window when the individuals were outside their night quarters (where observations were not possible). The influence of human presence was a factor impossible to correct, as humans were present at every time around both enclosures, as keepers or tourists. Another obstacle for the observations was the forest patch located inside each enclosure. The forest patch was created so that individuals could experience a habitat as close as possible to their native one. The density of such forests made it impossible to observe individuals. Only the area around the forest was stripped enough to allow a 100% positive identification and observation of the individuals. Since it was not possible to circulate around the enclosures as they were jointed, many observations were limited to the visibility.

Measures:

Empathy

Emotional Behaviour measures (*triggers* and responses) were coded according to operational definitions in Tables 2 and 3.

Table 2: Operational definitions of *triggers*.

Behaviour patterns signalling context: Aggressive Display / Attack

Coded Empathy *Trigger*: Anger

Description:

The individual displays conspicuous movements such as rocking to the sides or front to back, while standing bipedally, tripedally or quadrupedally (King et al. 1991). Arms are usually swayed and objects can be used in aid of the display as weapons of intimidation. The individual can stand in one place, run next to another individual, or charge towards him (King et al. 1991). Certain facial expressions are usually associated with displaying, such as the *tense-mouth face* (Van Hoof 1973), *bulging-lips face* (Van Hoof 1973), *hoot-Face* (Goodall 1968), and *stretched lips face* (Gaspar 2001). An *horizontal head-shake* (Van Hoof 1973) can also be performed in the early stages of the display. Attacks include the behaviours: hitting, punching, slapping, stamping, charging and chasing (King et al. 1991), object-throwing (Goodall 1986), trampling (Koski et al. 2007) and biting (Van Hoof 1973). Characteristic vocalizations include loud pant-hoots (King et al. 1991).

Behaviour patterns signalling context: Avoid / Withdraw

Coded Empathy *Trigger*: Fear

Description:

The individual moves to escape another individual or a frightful event, such as a fall or a loud noise. It is common to see a progression from creeping, where the individual slowly starts to walk away, to a full flight. This escaping behaviour can also be known as *Avoidance* (King et al. 1991). Display patterns of fear include: avoidance movements (Gaspar 2001; King et al. 1991), piloerection, *full-closed grin* (Gaspar 2001), *low-open grin* (Goodall 1988). Although fear is usually a silent behaviour, huu hoots (King et al. 1991) and waaa-barks (King et al. 1991) can occasionally be vocalized.

Behaviour patterns signalling context: Social Helplessness

Coded Empathy *Trigger*: Helplessness

Description:

It is performed exclusively in social contexts. The individual stands bipedally and scans its surroundings while performing loud vocalizations such as barks, hoots and screams, in a “call for attention” fashion. Running is common, although the individual can also stand still while vocalizing. This behaviour is observed after aggressions or thefts (eg: food, toy). Vocalizations associated include *whimpering* (Goodall 1986, King et al. 1991) and *hooing* (Goodall 1986) in the initial stages, *pant-bark* (Goodall 1986), *pant-scream* (Goodall 1986, King et al. 1991), *squeak* (Goodall 1986), *bark* (Goodall 1986), *bared-teeth scream* (Van Hoof 1973), *bared-teeth yelp* (Van Hoof 1973), *shrill- bark* (Van Hoof 1973), *rising-hoot* (Van Hoof 1973).

Intensity of vocalization can increase if consolation is not provided rapidly.

Behaviour patterns signalling context: Excitement

Coded Empathy *Trigger*: Excitement

Description:

Characterized by non-aggressive vocalizations. Usually associated with food or human presence. A particular kind of hoot was used in these situations, what we designated by Amadeus’s hoot. A loud rising-hoot with a musical tone to it, particular of that group, introduced by Amadeus.

Table 3: Operational definitions of responses.

Behaviour patterns signalling context:	**Coded Empathy *Trigger*:**	**Description:**
Consolation	Consolation	Consolation works as a complementary behaviour, i.e., it only exists as a response to another behaviour, not existing by itself. Consolation can be solicited or offered without any kind of solicitation from the distressed individual (e.g.: hands stretched, reaching out to another individual, full-grin, whimpering). Empathy was considered only in the second case, where consolation was provided without solicitation from the distressed individual. Consolation provided upon solicitation was labelled as Other. Both individuals (the consoler and the consoled) embrace (King et al. 1991) each other ventrally, or side-ways, with arms wrapped around one another. Kissing can also be observed during the embrace. Behaviours include: kiss (King et al. 1991), touch (King et al. 1991), embrace (King et al. 1991) and patting (King et al. 1991).
Imitation	Imitation	Replication of behaviour. Imitation was only considered if the behaviour was replicated by an individual in the following 5 seconds after it was displayed by another individual. In the case of Anger, imitation was considered only in the cases where the imitating individual was not the target of the aggression.
Rescue	Rescue	The individual tries to remove the object of Distress or Fear, usually another individual, either by chasing it or by displaying against it. Consolation can also be given upon request, otherwise quoted Rescue as Consolation.
Non-Responsive	Non-Responsive	Lack of response. The individual is present while an empathy *trigger* (i.e., Aggressiveness, Fear or Helplessness) is being displayed, but presents no observable physical reaction to it. There are no typical vocalizations associated.
Avoid / Withdraw	Fear	The operation definition of Fear in Table 2 applies.
Aggressive Display / Attack	Anger	The operation definition of Anger in Table 2 applies.

Relationship Quality

The Relationship Quality (RQ) index used represented the relative frequency an individual engaged in affiliative behaviours within a particular dyad by comparison with all his affiliative interactions. We adjusted the index in both groups, as initial observations led to the conclusion that while grooming was the most common behaviour in the adults, playing was the most common activity in juveniles. Therefore, two different formulas were used.

In the Adult Group, relationship quality was measured by the formula RQ = $\frac{number\ of\ grooming\ counts\ in\ dyad}{total\ number\ of\ grooming\ counts\ by\ the\ individual}$, which only quoted the times an individual engaged in grooming another and not being groomed by in order to avoid scoring an interaction more than once.

In the Juvenile Group, the Relationship Quality index was calculated using the following formula: RQ = $\frac{number\ of\ play\ counts\ in\ dyad}{total\ number\ of\ play\ counts\ by\ the\ individual}$.

Table 4: Operational definitions of Relationship Quality behaviours.

Behaviour patterns signalling context: Play

Coded Behaviour: Play

Description:

Non-aggressive but energetic physical interaction between two of more individuals. Behaviours coded as Play include: gnawing (Van Hoof 1973), gnaw-wrestle (Van Hoof 1973), tickling, haring toy, swinging together, play bow, floor slapping, trampling (Van Hoof 1973), cling/hold, wrestling, poking, biting, chasing, butting, kicking, dragging, rubbing, rolling (King et al. 1991). Individuals engaged in play can exhibit a *play-fac*e (Gaspar 2001), *relaxed open-mouth face* (Gaspar 2001) or *laughing-mouth face* (Chevalier-Skolnikoff 1982). *Laughter* (King et al. 1991) and pan**t** (Goodall 1986) are typical vocalizations of Play.

Behaviour patterns signalling context: Grooming

Coded Behaviour: Grooming

Description:

Picking through the fur of another individual, with fingers and mouth (Van Hoof 1973, King et al. 1991). Individuals engaged in Grooming often present a *relaxed open-mouth face* (Van Hoof 1973) or a *lip-smacking fac*e (Van Hoof 1973).

Proximity

Proximity was determined as being the *closest neighbour/not being the closest neighbour* when the empathic behaviour occurs. When recording the responses of all present individuals at the performing time of the *trigger*, the closest individual to the displayer was registered. Closest neighbour was only considered when within a range of approximately 4 arms length of the performer.

Data analysis procedures

To explore whether *trigger* variables associated with empathic response variables, and whether these occurred preferentially in certain dyads and not randomly, we performed χ^2 analyses of independence on the respective contingency tables: *Trigger* x Response and Performer x Witness. When independence was rejected (at the alpha level $p<.001$), we considered significant cell associations those that presented counts equal or above 5 with adjusted standard residuals equal or above 2 (after Everitt 1977). The Relationship quality index was determined for both groups and for each possible dyad. The relation between Relation Quality and Proximity was tested using a Spearman two tailed analysis of correlation.

Results

Relationship Quality

Table 5. Relative frequencies of play counts between individuals of the juvenile group. Note: In the main diagonal (in bold squares), the values represent the comparative amount of counts the individual spent playing alone.

	Jao	**Zac**	**Cozy**	**Sally**	**Thomas**	**Zeena**	**Nina**	**Charlie**	**Dinka**	**Zee**
Jao	0	0	0	0,06	0,16	0,05	0,11	0,26	0,10	0,26
Zac	0	0	0	0	0,30	0,10	0	0,20	0,20	0,20
Cozy	0	0	0,07	0,29	0,07	0	0,07	0	0	0,5
Sally	0,02	0	0,08	0,02	0,08	0,14	0,20	0,14	0,06	0,12
Thomas	0,04	0,04	0,01	0,05	0,13	0,08	0,15	0,18	0,21	0,11
Zeena	0,01	0,01	0	0,1	0,08	0,05	0,17	0,18	0,17	0,23
Nina	0,02	0	0,01	0,11	0,13	0,16	0,09	0,22	0,16	0,1
Charlie	0,1	0,01	0	0,05	0,11	0,1	0,15	0,06	0,29	0,18
Dinka	0,01	0,02	0	0,02	0,12	0,1	0,11	0,29	0,05	0,28
Zee	0,04	0,02	0,05	0,05	0,07	0,14	0,07	0,19	0,29	0,07

Table 6. Relative frequencies of grooming counts between individuals of the adult group. Note: In the main diagonal (in bold squares), the values represent the comparative amount of counts the individual spent grooming himself.

	Abu	**Amadeus**	**Nikki**	**Lika**	**Jinga**	**Mimi**	**Guida**
Abu	0	0	0	0	0	0	1,00
Amadeus	0	0	0,13	0	0	0,87	0
Nikki	0,62	0	0	0	0,25	0	0,13
Lika	0	0	0	0	0,67	0	0,33
Jinga	0,20	0,14	0,09	0,24	0	0	0,33
Mimi	0	1,00	0	0	0	0	0
Guida	0,17	0	0,17	0,33	0,33	0	0

Empathic responses

A total of 142 *triggers* and 609 emotional responses for the juvenile group, and 36 *triggers* and 88 emotional responses for the adult group were recorded (Tables 7 and 8). As can be seen in the tables, the observed *triggers* are not all the same and the most frequent types of responses are also different in the two groups; Social Helplessness triggered Consolation alone in the juvenile group, but also triggered Rescue in the adult group. Excitement was observed in the adult group but not in the juvenile. Detailed responses are presented below:

Table 7. Frequency results for emotional responses in the juvenile group.

		Response			
		Consolation	**Fear**	**Imitation**	**Non-Responsive**
Trigger	**Anger**	0	34	25	462
	Social Helplessness	46	0	0	0
	Fear	42	0	0	0

Table 8. Frequency results for emotional responses in the adult group.

		Response				
		Anger	**Consolation**	**Fear**	**Imitation**	**Rescue**
Trigger	**Anger**	1	0	1	0	0
	Social Helplessness	0	7	0	0	7
	Excitement	0	0	0	72	0

The χ^2 test of independence showed that where were significant associations between emotional *triggers* and empathic responses in the juvenile group ($\chi^2_{(6)}$ = 609,000; N=609; p=0), and in the adult group ($\chi^2_{(6)}$ = 176,000; N=88; p=0).Tables 9 and 10 present the adjusted residuals of the emotional responses rendered significant for both groups.

Table 9. Significant associations between empathic *triggers* and emotional responses, with according adjusted residuals, for the juvenile group.

Trigger	Response	Adjusted residuals
Anger	Fear	2,466247
Anger	Imitation	2,09431
Anger	Non-Responsive	17,98016
Social Helplessness	Consolation	17,1637
Fear	Consolation	16,34253

Table 10. Significant associations between empathic *triggers* and emotional responses, with according adjusted residuals, for the adult group.

Trigger	Response	Adjusted residuals
Social Helplessness	Consolation	6,340152
Social Helplessness	Rescue	6,340152
Excitement	Imitation	9,380832

Empathic responses and Relationship Quality

The Analysis of association between performer and witness performed for both groups revealed that Relationship Quality plays little of no effect at all in the display of emotional responses to the empathic *triggers*; only one relationship was considered significant in the juvenile group – between the dyad Zac-Cozy (adjusted residual =4,963893) ($\chi^2_{(81)}$=118,183; N= 609; p<0,005), which presents an RQ index of zero.

Also, only one relationship could have been considered significant in the adult group – in the dyad Nikki-Amadeus (adjusted residual = 3,308364) but this association is dismissed as the overall performer x witness association was rendered non-significant ($\chi^2_{(30)}$= 36,359; N= 88; *NS*).

Proximity

From the significant associations between empathic *triggers* and emotional responses, we counted the number of times the emotional response was performed by the closest neighbour to the *trigger* (Tables 11 and 12). Also, we estimated the strength of the *trigger* by removing the Non-Responsive answers to the *triggers*.

Table 11. Counts of proximity for the emotional responses in the juvenile group.

Trigger	**Response**	**Strenght of *trigger***	**Count of Closest**	**Not Closest**
Anger	Fear	11,32%	20	14
Anger	Imitation	11,32%	1	24
Anger	Non-Responsive	-	0	462
Social Helplessness	Consolation	100%	29	17
Fear	Consolation	100%	28	14

Table 12. Counts of proximity for the emotional responses in the juvenile group.

Trigger	**Response**	**Strenght of *trigger***	**Count of Closest**	**Not Closest**
Social Helplessness	Consolation	100%	2	5
Social Helplessness	Rescue	100%	0	7
Excitement	Imitation	100%	8	64

Relationship Quality and Proximity

The Spearman test run between Relationship Quality and Proximity revealed no correlation between the two measures in the juvenile group (r=0,08; p=0,456). The test was not repeated for the adult group since Proximity almost never occurred.

Discussion

The main purpose of the present study was to investigate the occurrence of possible empathic behaviours in naturally occurring emotional events, using a systematic data collection approach. Another goal was to explore the usefulness and limits of the emotional measures chosen as *triggers* and responses as well as the relevance of proximity and relationship quality in empathic responses.

Emotional *triggers* and Empathic responses

The Juvenile group

Five significant associations were found in the juvenile group: Fear to Anger, Imitation to Anger, Non-Responsive to Anger, Consolation to Social Helplessness and Consolation to Fear. For humans, it's almost intuitive to expect Fear when exposed to Anger, and chimpanzee reactions suggest they follow the same rule. Displaying Fear when witnessing Anger could be translating the ability to understand the emotional state of the angry individual and the likely outcome of his/her behaviour. Imitation to Anger was only considered when Anger was observed to be an "empty behaviour", i.e., a behaviour with no apparent motive. Individuals engaged in Imitation would often imitate a segment of the Anger display instead of the full behavioural palette of the *trigger*. When imitating, individuals can experience the emotional state and bodily adaptation to a specific situation, almost like a test-run of an emotional state (Bekoff et al. 2002). Imitation to Anger did not occur in the adult group, which corroborates the theory that imitation is more frequent in juveniles and thought to decrease with age and social experience, being replaced by more socially beneficial behaviours, such as helping (Preston and de Waal 2001; de Waal 2008). The same motivational structure is also thought to exist behind empathy and imitation, including shared representations, identification through physical similarity, automaticity and spontaneity (de Waal 2008). Such idea seems to be supported by neural data, as the observation and imitation of facial expressions activate the same brain structures - yet another evidence of the "test-run" (Gallese 2007).

The high frequency of Non-Responsive to Anger can be explained by the fact that 65,45% of Anger *triggers* came from the same individual, the 10 year old male Cozy. Cozy is a castrated male who is known to have suffered regular beatings while in the care of humans, which resulted in frequent abnormal behaviours. All the other individuals of the group seemed to be aware of this difference, and treated Cozy differentially, almost like the case of Knuckles, the chimpanzee with cerebral palsy reported by de Waal (de Waal 2008). Knuckles would receive differential treatment from all individuals in his group, who showed more patience and sympathy towards him than towards the remaining individuals. Cozy would display with no apparent reason so the other individuals would, most of the time, choose to ignore him. To account for the remaining percentage of Non-Responsive, an "attention structure" (Quiatt and Reynolds 1993) could have been engaged ensuring the cohesion of the group, i.e. when an emotional stimulus occurs, a few individuals deal with it while others remain fairly dismissive.

Consolation to Fear is probably the flag behaviour of empathy in non-human animals. In the classical definition of sympathy, an uninvolved third party engages in succorant behaviour towards the distressed individual. Being aware of the distress of a peer and acting to appease him shines a light in the possibility of animals being aware of the emotional states of others, being emotionally affected by them, and acting in a pro-social fashion. Although we don't know what motivates altruistic behaviour, the nature of the Mirror Neuron System suggests that the mirroring of an emotion propels an individual to act towards others as to appease his own new mirrored emotional state. Consolation to Social Helplessness occurring in a significant way is interesting because the context "injustice", associated with "cry for help" understanding of Social Helplessness, is a secondary emotion, and therefore harder to empathize with (de Vignemont and Singer 2006; Grandjean et al. 2008; Jabbi and Keysers 2008). Panksepp (2004) defended that primary emotions – the ones that are crucial to survival, such as anger, joy, sadness, fear and disgust, are easier to empathize with than secondary emotions such as jealousy.

The Adult group

Three associations were rendered significant: Consolation to Social Helplessness Rescue to Social Helplessness and Imitation to Excitement Consolation to Helplessness occurred in a significant way in accordance with the data collected in the juvenile group. What is new in the adult group is the association between Social Helplessness and Rescue, an interaction not observed in the juvenile group. This result can also be interpreted as evidence of empathy, in particular the "higher-order" empathic phenomenon of *empathic perspective-taking*, since the removing the object causing distress, will be followed by the return of the distressed individual to his/her anterior emotional condition (de Waal 2008). In the current study, this *trigger* happened more frequently during feeding times when, being robbed by another individual would set an individual into Social Helplessness. A third individual would then chase the robber away from the feeding group and, very commonly, sit next to the distressed individual until the *trigger* behaviour ceased, then carry on eating. The rest of the group would remain fairly unresponsive, another fact corroborating the “attention structure” proposed by Quiatt and Reynolds (1993). Finally, Imitation to Excitement is also in accordance with emotional contagion. Imitation in the adult group was particularly easy to categorize, as the displayer was usually Amadeus, with a very particular hoot that other individuals would immediately imitate at particular occasions, such as feeding times.

Relationship Quality

Regarding Relationship Quality, only one relationship was rendered significant in the juvenile group, between Zac and Cozy. In the adult group, the lack of interaction between individuals translated into extremely poor relationship quality indexes. The majority of time spent by the adults was alone, either foraging, walking, or sitting in the grass by themselves. Due to the social value of emotions, when an individual is by himself there is a strong tendency to not display emotions, and so almost no *triggers* were collected. Finally, the use of grooming to obtain a Relationship Quality index proved to be insufficient as it measured only one direction of the relation. Individuals who did not engage in grooming but were frequently groomed would be represented by poor Relationship Quality indexes which are an inaccurate characterization of the strength of the dyad relationship.

Proximity does not exhibit a clear importance in the display of emotional responses. The tendency of empathic responses tends to concentrate around the closest individual in the juvenile group, while the opposite occurs in the adult group.

Also, this study suggests no correlation between Relationship Quality and Proximity. However, such situation needs to be approached with caution as the Relationship Quality indexes, once adjusted to fit more affiliative behaviours, can offer more reliable results and allow for more stable conclusions.

Final considerations

Overall, the method of data collection proved to be satisfactory. Behaviour scanning (Martin and Bateson 1986) is the best way of sampling rare or short behaviours as are emotional *triggers*, and registering the emotional responses of all present individuals is also the best way of securing a "photograph" of the moment, retaining information on all the emotional responses. We did encounter some problems regarding Relationship Quality, and we would recommend adjusting the collection model for future studies: instead of using just the most common affiliative social interaction, Relationship Quality is measure by quoting every affiliative social interaction, such as grooming, playing, mounting, kissing, all in accordance with Koski (2007).

Even though the classically used method of data collection in behavioural studies is focal sampling (Martin and Bateson 1986), the time span did not allow the use of this technique - the chosen sampling methods were the ones that allowed for maximum data collection. Also, focal sampling would require intensive observation of a single individual, losing the information of the group as a whole and its dynamic social interactions, which can change over time (if the future study is conducted through an extensive time period, as it should, fluctuations in social structure or dynamics do not impose a problem regarding later relating emotional response with the Relationship Quality of any given two individuals, which can be calculated and adjusted to a desired time period).

Also, it is fundamental to understand that the majority of the individuals sheltered by the sanctuary were rescued from situations of abuse and most of them were not exposed to a normal environment for chimpanzees, therefore do not exhibit the normal reactions expected to some situations. None share a blood bond and Relation Quality was a difficult factor to attest because both groups were relatively new (formed about 1 year before the study). Additionally, almost half the individuals, prior to the integration in the sanctuary, had never even been exposed to a conspecific. In the adult group, males appeared to ignore females for most of the time and showed ostensive segregation in their everyday activities (Phillip Crönje, personal communication). The Relationship Quality indexes we obtained were extremely poor for the fact that social interactions only occurred in very few moments of the day. In the juvenile group, the array of behaviours seemed to approximate more to the expected normal behaviour of a chimpanzee. Wrongful upbringing may lead to deficits in empathic processing of behaviours and emotions, thus reinforcing the importance of early rearing and socialization. However, even with all of the above, the data collected supports the existence of empathy in chimpanzees, either by evidence of engaged emotional contagion, sympathy or empathic perspective-taking.

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Chapter 4

General Comments and Final Remarks

So far, the systematic study of empathy is still at its beginning; behavioural, psychological and neural sciences must converge to create a common definition of empathy and assist in the systematic study of the phenomenon. The benefits of empathy are recognized beyond the human sphere and the future entails the discovery of which animals display empathy through the integration of behavioural and neural investigation.

The need for cohesion and effective cognitive and emotional communication inside social groups is likely to have resulted in the selection of empathy as a mechanism that motivates pro-social and altruistic behaviour. A breakthrough discovery regarding the concept of empathy is the discovery of the source of this impulse coming from internal body imaging of observed behaviours and emotions, rather than by rationalizing or consciously simulating, which opens the doors to empathy being discussed outside of the human species. The major contribution to this knowledge was the discovery of the Mirror Neuron System, which revealed that the brain fires the same groups of neurons to the perception and to the execution of motor actions. Such system translates into enormous fitness advantages in terms of gathering social and environmental information, as an individual understands a situation without needing to go through it.

These networks of mirror neurons are also being discovered for the recognition and performance of emotions. Some areas of the brain, in particular the amygdala and the insula, seem to possess overlapping activation of neurons to the sight of emotional behaviours. Some experimental work has already been done, and chimpanzees appear to possess emotional awareness and display emotional reactions very similar than the ones observed in humans. Since humans and chimpanzees have approximately 97% DNA similarity and their lineages have diverged only 7-5 MA ago (e.g. Carrol, 2003) the evidence of chimpanzees being able to display neural activation and consequent empathy to the emotional behaviour of others can only be considered as very likely.

Unlike most reports of empathy, which are limited by their anecdotal nature, in this present study we tried to create a systematic method of data collection that allowed for the maximization of *trigger* collection, and investigated deeper into the phenomena by researching associated parameters that, in theory, will positively increment the empathic response.

Based on this project, we can discuss the possibility of the existence of empathy in chimpanzees, and corroborate the biological engraving of the empathic mechanism, as even chimpanzees with stories of isolation prior to the integration in the sanctuary displayed evidence of empathy. From the pool of available emotional responses, some relations between *trigger* and responses exhibited a strong association, and those shape the measures worth pursuing in future methodological studies of empathy.

In a future study, the biggest concern needs to be the collection of a larger set of data, which translates into a larger time window for observation and collection. The severe limitation of conducting behavioural work in semi-wild conditions is the inability to manipulate the behaviours to our advantage and therefore longer periods of time are needed in order to obtain the same amount of data if the observations were conducted in a laboratory. Although celerity is a concern, observations in semi-wild conditions do present the best results, as the environment resembles as much as possible the natural conditions of the wild, with hardly no human interference in the process of data collection. With a larger set of data, we can grasp interactions now invisible and obtain more reliable results.

The main difficulties found in the project were the limited observation of both groups (both enclosures where jointed by the night rooms which did not allow for a complete circling of the enclosures and the forest patch inside made it impossible to identify individuals) as well as the lack of interaction between individuals, especially in the adult group. Most individuals spent the majority of the time outside the night rooms engaging in solitary activities (Tables 13 and 14 referent to time usage by individuals are presented in the Annexes section).

The presented study contributes toward the understanding of empathy in non-human primates by presenting systematic data collection of relevant interactions and by sorting those emotional responses that are more likely to occur in empathic contexts from the pool of available responses.

In sum, this thesis aims to constitute a very important attempt to converge different fields of knowledge into promoting a clearer understanding of the empathic phenomena and, by studying empathy in a systematic fashion, rendering it the credibility that was lacking in the scientific community.

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Annexes

Annexes

Table 13. Proportions of emotional states in the juvenile group.

Individual	Relaxed	Excited	Playing	Other	Not Present	Agressive
Jao	0,59	0,02	0,07	0,17	0,15	0
Zac	0,44	0,04	0,04	0,16	0,32	0
Cozy	0,53	0,10	0,07	0,16	0,12	0,02
Thomas	0,34	0,03	0,34	0,15	0,13	0
Dinka	0,24	0,02	0,52	0,08	0,14	0
Charlie	0,24	0,02	0,50	0,09	0,16	0
Nina	0,35	0,02	0,34	0,10	0,20	0,01
Zeena	0,40	0,02	0,27	0,14	0,16	0,01
Sally	0,33	0,02	0,22	0,10	0,34	0
Zee	0,32	0,02	0,47	0,08	0,11	0

Table 14. Proportions of emotional states in the adult group.

Individual	Relaxed	Excited	Playing	Other	Not Present	Agressive
Abu	0,32	0,07	0	0,09	0,51	0
Amadeus	0,46	0,05	0	0,11	0,32	0
Nikki	0,39	0,06	0,01	0,11	0,37	0
Mimi	0,33	0,05	0	0,19	0,42	0
Guida	0,58	0,04	0,01	0,14	0,22	0
Jinga	0,51	0,05	0,02	0,23	0,20	0
Lika	0,30	0,02	0,02	0,08	0,57	0