An evolutionary and developmental approach to investigating empathy: Insights from physiology and behaviour in Pan and Homo

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An evolutionary and developmental approach to investigating empathy:

Insights from physiology and behaviour in *Pan* and *Homo*

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A Thesis Submitted for the Degree of

Doctor in Philosophy

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Declaration(s)

I confirm that no part of the material presented in this thesis has previously been submitted for a degree in this or any other institution. If material has been generated through joint work, this has been indicated where appropriate. All other sources have been referenced, and quotations suitably indicated.

Statement of copyright

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It is another Sunday night in lockdown #3 (March 2021), and while I keep staring at this thesis that looks like it will never end, I think about all the wonderful persons who are/were part of this journey with me. So, I decided to start writing this new part of what will hopefully one day become my completed thesis. Call it motivation or *procrastination*… but if you are reading this now, it means I did it!!!!

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Thesis abstract

Empathy, the sharing and understanding of others' emotional states, is a core feature of the human social experience. Research thus far has offered promising, yet contentious, evidence of its evolutionary and developmental origins, usually based on single isolated measurements. In this thesis, I address the evolutionary and developmental origins of empathy by using a mixed-methods approach that combines naturalistic observations, behavioural experiments, and non-invasive physiological approaches to investigate behavioural markers of empathy and its potential underlying mechanisms in young human children and our closest living relatives, the great apes. The **first goal** of this thesis was to investigate the ontogenetic development of empathic responding in sanctuary-living bonobos. Although my findings did not support the hypothesis that more complex forms of empathy develop in tandem with other skills and/or social experiences in apes, I did identify age-specific consolatory patterns. The **second goal** was to investigate the link between observable empathic behaviour in ecologically valid settings with corresponding inner arousal in chimpanzees. Results suggest that arousal – as measured with facial temperature change when chimpanzees experimentally witness the distress of a conspecific - might relate to their underlying motivation to comfort distressed others. However, it remains challenging to disentangle between an arousal response related to self-distress with one of empathy. The **third goal** was to experimentally investigate the underlying mechanisms of empathic responding in young human children. Results confirmed a physiological reaction of children when witnessing another's distress, which was predicted by the child's age and sex as well as – for some measures- model familiarity. Overall, the findings shed new light on the development of empathy in both humans and our closest relatives, as well as informing on the underlying mechanisms and their relationship to external behaviour. By doing so, this comparative study advances our comprehension of the evolutionary and developmental roots of empathy.

Keywords: Emotion; concern; prosocial behaviour; thermography; observations; apes; child development

Chapter 1 General introduction

In this chapter, I will introduce the theoretical concepts of empathy and the related concept of emotion regulation, focussing on their evolutionary and developmental foundations. First, I will describe the empirical approaches, evidence and challenges of studying empathy and emotion regulation in humans and other animals[1]. Then, I will introduce the importance of the developmental and evolutionary approaches, followed by considering our closest living relatives, the great apes, the study species of this thesis. Finally, I will outline the main aims and research studies described in this thesis.

1.1 A general introduction to empathy and emotion regulation

1.1.1 The theoretical concept(s) of empathy

Humans are a highly social species. We coordinate our activities and communicate information explicitly via language and other forms of communication, while social and emotional skills like empathy help us share and understand one another's underlying emotional states. Thanks to our capacity to "put ourselves in someone else's shoes", empathy enables us to resonate with another's positive (e.g., joy, amusement) and negative (e.g., sadness, grief, pain, suffering) emotions[2], thoughts and feelings. As such, empathy is central to the uniqueness of our human experience, from shaping our complex social and romantic lives to engaging with our wider political society and beyond. However, although empathy is known to be a crucial capacity for humans to effectively navigate their social environments (Hollan & Throop, 2011), many

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[1] Some parts of this chapter will be included in (Krupenye et al., In Prep.)

[2] There are vigorous debates about what the term "emotions" means for humans and other animals, particularly between the notion of *constructed emotions,* where emotions are social constructs emerging from an individual experience and consciousness, (Barrett, 2006, 2017a, 2017b) as opposed to emotions as biologically hardwired arousal related to the affective/emotional states. In the present thesis, I will not go into detail about these debates.

questions remain open. Indeed, we still know very little about the evolutionary history of empathy: particularly about the extent to which empathy is unique to our species, or whether components of this complex socio-emotional skill are shared with non-human animals (hereafter “animals”). Moreover, in line with Tinbergen’s four questions (i.e., causation, ontogeny, evolution and survival value; 1963), there is also a need to answer many fundamental questions about the roots of empathy, as well as its proximate mechanisms and ultimate functions (Preston & de Waal, 2002).

1.1.1.1 Empathy: a multi-dimensional construct

The current concept of *empathy* comes from the German word *Einfühlung,* or “feeling in(to)”, used in the late nineteenth century by the aesthetics’ theorist Theodor Lipps (1897). This introspectionist concept applies both to how we experience inert objects and how we understand the mental states of others. Lipp’s work inspired philosophers like Edmund Husserl, Wilhelm Dilthey, Max Weber and Edith Stein, but the rise of experimental psychology and behaviourism (Watson, 1913) in the early twentieth century upstaged Lipp’s empathy concept. In 1909, Titchener translated *Einfühlung* into the English word *empathy* (Titchener, 1909), drawing on the Greek “em” for “in” and “pathos” for “feeling”.

Nowadays, empathy is broadly described as the ability to share and understand the emotional states of others (Preston & de Waal, 2002). While there are many definitions of empathy in the literature (see Adriaense et al., 2020; Batson, 2009; Cuff et al., 2016), most contemporary definitions build upon Lipp’s original construction of the term, to refer to empathy as a multi-dimensional construct that includes affective and cognitive components (Blair, 2005; Davis, 1983; Decety & Jackson, 2004; Eisenberg, 2002; Preston & de Waal, 2002). *Affective* empathy broadly refers to the sharing of others’ emotional states towards a distressed other (Eisenberg & Fabes, 1990; Hoffman, 1984; Mehrabian & Epstein, 1972; Soto & Levenson, 2009), which might be observed when individuals orient themselves towards someone in need while showing facial expressions of concern (Davidov et al., 2020; Roth-Hanania et al., 2011). *Cognitive* empathy refers to the ability to understand others' emotional states and experiences (Hogan, 1969), which may be detectable when individuals *actively* enquire and explore another's distress with the goal of understanding the situation (hypothesis testing, Zahn-Waxler et al. 1992a). The behavioural expression of empathy is considered to be *prosocial responding to others' emotional states,* which implies the actions that help and benefit others without any direct benefit to the actor (Decety et al., 2016; Eisenberg & Spinrad, 2014). In an emotionally arousing situation, responding with self-distress instead of orienting towards another's distress results in personal distress (*over-arousal*, Eisenberg 2000) which is self-oriented in its nature as opposed to concern oriented towards the other. The emotion contagion PAM mechanism implies that some level of arousal is necessary to trigger empathic response. However, the term personal distress implies that this distress stops at *self*-oriented distress rather than *other*-oriented; consequently, the two are mutually exclusive, even if their origins are the same. In contrast, it is what the actor/subject perceives to be the source of the distress that is crucial distinction. Indeed, in personal distress, they themselves experience the distress as their own. It is worth noticing that not all prosocial behaviours are necessarily affectively based or empathic. For instance, often prosociality seems to be based on responding to requests in non-human primates (de Waal & Suchak, 2010; Tennie et al., 2016; Yamamoto & Takimoto, 2012).

Neurobiological and developmental studies support the distinction between affective and cognitive empathy (Decety, 2011; Jackson et al., 2006; Wicker et al., 2003; Zaki & Ochsner, 2012). Findings suggest that affective empathy is facilitated by bottom-up, evolutionarily-ancient neural processes, whereas cognitive empathy involves top-down neural processes (Decety, 2011; Singer, 2006; Stone, 2006) involved in cognitive perspective-taking and appraisal (Jankowiak-Siuda et al., 2011). In this respect, the affective and cognitive components of empathy are thought to involve interacting and particularly overlapping neural processes (Decety, 2011; Zaki & Ochsner, 2012). Nonetheless, the neural basis of empathy is still quite contentious and leaves space for discussion about the top-down vs bottom-up dynamic in place (Iacoboni, 2009; Shamay-Tsoory, 2011).

Relatedly, empathy relies on various other processes including self-other differentiation, self-reflection and integration of individual experiences to appropriately recognise and respond to emotional and mental states within a given social situation (Reniers et al., 2011). The process of self–other differentiation is crucial to avoid misperception and/or misattribution of emotional states that could be caused by one's self-distress and anxiety, itself caused by a lack of emotion regulation (Batson et al., 1997; Decety & Lamm, 2006). Therefore, emotional identification, processing and regulation, joint representations, self–other differentiation and integration of past experiences are crucial processes to the empathic experience (Reniers et al., 2014)

1.1.1.2 The roots of empathy

From an evolutionary perspective, precursors of empathy are thought to have evolved in the context of maternal/parental care which has expanded into an adaptation to social group living (MacLean, 1985; Preston, 2013). Indeed, offspring trigger an emotional response from their carers by displaying their affective states, with the distress of the offspring often leading to the distress of the parent/s (MacLean, 1985). The evolutionary origin of this emotional bond between caregiver and offspring is thought to explain the social familiarity effects found in empathy. Specifically, attention towards another's emotional expressions and corresponding empathic behaviours are often biased towards socially close individuals (see Preston and de Waal 2002 for a review). In particular, empathic responding in humans is known to be modulated by the affective bond between the persons (Singer et al., 2006), their similarity

(Krebs, 1975), and familiarity (Cialdini et al., 1997), while attention is oriented towards emotional expressions of familiar individuals (Berlo et al., 2020). Furthermore, social closeness has been shown to predict the likelihood of offering comfort to an individual in distress (i.e., consolation) in great apes (Romero et al., 2010; Clay & de Waal, 2013b; Palagi & Norscia, 2013) and some species of monkeys (Demaria & Thierry, 2001). These findings suggest deep evolutionary roots of affective processes supporting empathy in primates.

Proximately, processes such as associative learning might also explain this social familiarity effect. In particular, paying attention to socially relevant stimuli as a result of enhanced exposure does not require having the same functional explanation specific to caregiving and could be explained in more general ways. Furthermore, potential markers of empathy have been identified in fish (Silva et al., 2019; de Waal, 2019), leading researchers to rethink the evolutionary roots of empathy, and consider alternative explanations such as pair bonding, a strong and enduring bond and/or co-dependence on one another (but see Hooper et al., 2021).

1.1.2 Unpacking the concept of empathy

1.1.2.1 Empathy and Theory of Mind

By cognitively inferring the emotional experiences of another (Gallese, 2003), empathy shows some similarities with the concept of Theory of Mind (ToM) – the ability to attribute mental states such as intentions, desires and beliefs to others (Carlson et al., 2013; Frith, 1999; Premack & Woodruff, 1978). How closely the concepts of empathy and ToM are connected is debated (Schurz et al., 2021). For instance, Blair (2005) considers cognitive empathy and ToM as equivalent, as the representation of the internal mental state of another individual, while Reniers and colleagues (2011, 2014) consider that although cognitive empathy and ToM are likely to depend on similar underlying capabilities, cognitive empathy relates to the attribution of *emotional* states in contrast with *mental* states, resulting in the potential separation of the two concepts at neuro-anatomical and psychological levels. In line with this, studies demonstrate that empathy and ToM are supported by both shared and separate neuronal networks and underlying neurobiological mechanisms (Frith et al., 2003; Gallagher & Frith, 2003; Hynes et al., 2006; Saxe & Kanwisher, 2003; Saxe & Powell, 2006; Shamay-Tsoory et al., 2003, 2004; Shamay-Tsoory, 2011; Sommer et al., 2007; van der Meer et al., 2011; Völlm et al., 2006).

1.1.2.2 The Perception-Action Model (PAM) of empathy

One of the most popular models of empathy is the Perception-Action Model (PAM, Preston & de Waal, 2002). This model suggests that the perception of another's mental/emotional state and/or physical action elicits one's own representations of this state and/or action, which elicits spontaneous and physiological responses (see also de Waal & Preston, 2017). For instance, the PAM would explain the ability of young children to perceive and learn from their caregivers as a process of themselves generating states and actions in response to those of their caregivers. The synchronised actions and expressions implicit in the PAM are considered crucial for the development of emotion regulation (Field, 2008; Malatesta & Haviland, 1982), which is crucial for empathy (Ungerer et al., 1990). In addition to the developmental approach, this model can improve our evolutionary understanding of empathy by going beyond inclusive fitness and altruism (Preston & de Waal, 2002). For instance, the biases for similarity and familiarity, as well as previous experiences observed across species, can be explained by the shared emotional component of self and other representations described by the PAM. Mirror neurons are suggested to support the PAM at the neurological level (de Waal & Preston, 2017; Gallese et al., 1996; Rizzolatti et al., 1996; but see Rizzolatti & Caruana, 2017). However, the function of mirror neurons and their potential involvement in empathy is still under debate (Baird et al., 2011; Bekkali et al., 2019; Decety, 2010; Lamm & Majdandžić, 2015). Finally, although I will not provide many details about it here, proximate explanations like associative learning processes and attentional affordances should also be considered. I discuss related and alternative models to the PAM in the following sections.

1.1.2.3 The 'Russian doll' model of empathy

Empathy is often considered an umbrella term to include every mechanism resulting in feeling, sharing, and understanding the emotional states of another. de Waal (2003) first introduced the 'Russian doll' model of empathy based on the idea that "the old always remains present in the new" (de Waal, 2007), with the external layers always being connected to the core (see Figure 1.1).

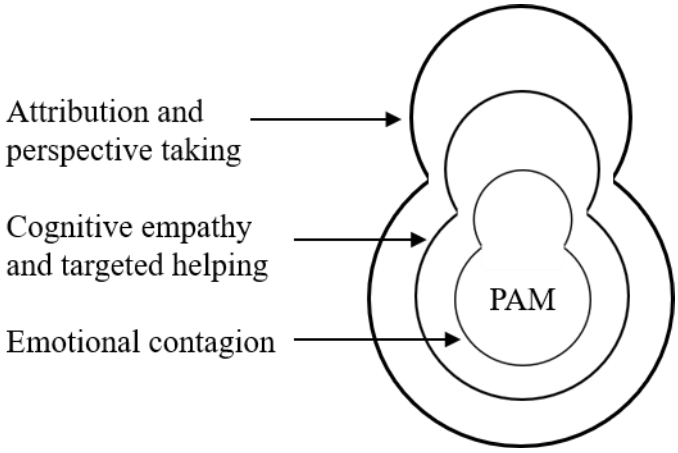

Figure 1.1 The Russian doll model of empathy (adapted from de Waal & Preston, 2017)

Accordingly, the PAM (described above, de Waal & Preston, 2017; Preston & de Waal, 2002) is at the core of the Russian doll, which generates the basic phenomenon of emotional contagion, upon which affective empathy relies. This simpler and automatic mechanism constitutes the socio-affective foundation for more complex processes to build upon, such as cognitive empathy and elements of ToM and perspective-taking, that allow for the understanding of another's state. At this stage, the individual does not only share the emotional state of the other or respond to a given signal but also looks for explanations. Such an ability is essential for a more complex behavioural response like targeted helping, where the needs of the other are identified and considered. However, the core emotional component of the model is essential to initiate the original emotion of the empathic response. Therefore, empathy is a complex phenomenon that embraces various levels of interconnected emotional and cognitive mechanisms. Understanding the emotional foundations and core of this phenomenon is crucial to access the additional cognitive and regulatory layers brought about during evolution. In the Russian Doll model, targeted helping requires perspective taking, therefore targeted helping and perspective taking are at the same level, while consolation is below. Consequently, perspective taking abilities are not necessarily required for consolation. Therefore, perspective-taking abilities are not necessarily required for consolation. Although the Russian doll model offers a valuable platform to explain the mechanisms of empathy, the linearity of the model's structure is debated and increasingly challenged (Adriaense et al., 2020). Indeed, the model infers that the inner components (i.e., emotional contagion) are essential for the development of the others (e.g., cognitive empathy, Hollis & Nowbahari, 2013; Yamamoto, 2017). However, this dependency is not confirmed by behavioural data (e.g., perspective-taking can occur without helping in chimpanzees, Yamamoto et al., 2009). Furthermore, the model infers that the inner components of the doll model are necessarily involved in the expression of the outer ones – with emotional contagion often considered as a preliminary building block of empathy (e.g., Palagi et al., 2015). Nevertheless, emotional contagion is frequently overlooked in the consolation or perspective-taking literature, and we have little data available to understand to what extent it is implicated in empathic responding (see Adriaense et al., 2020 for a review and discussion).

1.1.2.4 The ‘combination’ model of empathy

Another model for empathy is the ‘combination’ model of empathy proposed by Yamamoto (2017). This model is based on three components of empathy: 1/ matching with others (e.g., emotional contagion), 2/ understanding of others (e.g., perspective-taking), and 3/ prosociality (e.g., prosocial behaviours). These three components act independently but can interact with each other. For instance, while the combination of understanding others and prosociality might result in targeted helping, the combination of all three factors might result in sympathy or consolation (Yamamoto, 2017). In contrast with the Russian doll model (de Waal, 2003), this model is not linear and its different components are not dependent upon the inner ones. Therefore, such a framework offers a promising platform to investigate the different components of empathy independently and help untangle some of the current conceptual boundaries surrounding empathy and its mechanisms (Adriaense et al., 2020; Coplan, 2011).

1.1.3 Sex differences in emotion processing and empathy

In humans, research widely suggests that women show a higher ability to recognise emotional facial expressions than men (Campbell et al., 2002; Collignon et al., 2010; Hall, 1978; Hampson et al., 2006; Thayer & Johnsen, 2000), something that may consequently influence their empathic tendencies. This difference in identification of emotions seems to appear early in development, with 3.5-year-old American girls being as accurate as 5-year-old American boys (predominantly White and middle class) in selecting a picture that matches a given emotion (Boyatzis et al., 1993). The apparent superiority of expression processing skills of females compared to males also seems stable across development, with the more noticeable difference being observed in infancy and early childhood (McClure, 2000 for a review) and consistent in adulthood (Hall, 1990), but more research is needed to examine whether these differences emerge through socialisation, or are based on neurological differences between sexes. Nevertheless, there is a debate in the literature about the extent and specificity of this female advantage (Derntl et al., 2010; Grimshaw et al., 2004; McClure, 2000; Rahman et al., 2004). Particularly, some studies propose that these differences between females' and males' performances depend on the nature of the emotions displayed, with women/females being better at identifying facial displays related to sadness and fear (Mandal & Palchoudhury, 1985; Nowicki & Hartigan, 1988) and men/males being better at recognising emotions related to anger (Mandal & Palchoudhury, 1985; Rotter & Rotter, 1988; Wagner et al., 1986).

Despite the common stereotype, the literature suggests that the apparent and commonly accepted higher emotionality of women compared to men is based on the expression of emotions rather than how emotions are processed (Dimberg & Lundquist, 1990). When adult participants watched emotional video clips, women displayed more emotional expressions and a different pattern of skin conductance responses compared to men, while both sexes reported comparable levels of emotionality (or experienced emotion) (Kring & Gordon, 1998). Most of the sex differences in emotion expression also depend on the context/situation and the type of emotions based on cultural and social gender/sex-related display rules (Brody & Hall, 1993, 2008; Fischer, 1993; Fischer et al., 2004; Shields, 1987; Stoppard & Gunn Gruchy, 1993; Underwood et al., 1992), also described by Chaplin (2015) as the bio-psycho-social developmental model of gender and emotion expression.

From the perspective of social convention in Western, educated, industrialised, rich and democratic (WEIRD, Henrich et al., 2010) countries, expressions of anger and aggressive behaviours are more tolerated and/or appreciated in males as compared to females, with violent boys being judged more likeable and socially skilled than nonviolent ones (Hart et al., 1992; Serbin et al., 1993). By contrast, this is not observed for girls (Crick, 1997), who are in contrast expected to show more empathic behaviours than boys (Zahn-Waxler et al., 1991, 2001). These social pressures/rules may impact emotional development, with young girls consciously inhibiting expressions of anger from 4 years of age. From 7 years of age, boys start expressing more anger than girls, which is consistent with differences observed in adulthood (Potegal & Archer, 2004).

In conclusion, sex differences in emotion expression and processing is a complex phenomenon with various factors, including social pressures as mentioned above, but also genetic and hormonal (see Kret and De Gelder 2012 for a review). Particularly at the early stages of development, they are elicited by sex differences in gene expression (Cosgrove et al., 2007; Davies et al., 2006) and sex hormones in utero, causing brain and body differences between the sexes (Baron-Cohen, 2002; Zahn-Waxler et al., 2008).

1.1.4 Emotion regulation and empathy

To appropriately respond to someone else's emotional states, empathy also depends on emotion regulation, or the capacity to effectively manage one's own emotions (Bradley, 2000; Decety, 2011; Eisenberg & Eggum, 2009; Schipper & Petermann, 2013; van der Merwe & Dawes, 2000). Emotion regulation broadly refers to internal processes involved in managing one's behaviour, thoughts, and emotions within a given situation (Koole, 2009). Regulatory processes influence affective and behavioural responses (Decety, 2011; Gross, 1998); for instance, down-regulation of affect is essential for preventing "empathic over-arousal" (i.e., personal distress rather than orientation to the other's need (Eisenberg, 2000) to enable concern for others.

1.1.4.1 Expressive suppression and cognitive reappraisal strategies

The main emotion regulation strategies identified in the literature are *expressive suppression*, which occurs at the behavioural level, and *cognitive reappraisal*, which occurs at the cognitive level (Goldin et al., 2008). The strategy of expressive suppression is an inhibitory process that triggers a decrease in expressive emotional responses such as emotional facial and verbal expressions and gestures, without affecting the ongoing emotion experience (Gross, 2002). The strategy of reappraisal changes the sense of a situation to modify the course of emotional responses (neuro-anatomical studies: Beauregard et al., 2001; Lévesque et al., 2003; MacDonald et al., 2000; Ochsner et al., 2002, 2004; Phan et al., 2005; Schaefer et al., 2002; Urry et al., 2006), and by doing so, down-regulates emotional experiences and behaviours (Gross & John, 2003; Jackson et al., 2000; Ochsner & Gross, 2005). Emotion regulation and its strategies relate to other related Executive Function (EF) capacities. Indeed, studies in adults showed that difficulty in expressive suppression is linked to inferior cognitive abilities (Richards & Gross, 1999), while ability in cognitive-reappraisal is related to successful cognitive performance (Joormann & Gotlib, 2010; Raftery & Bizer, 2009; Wilkowski et al., 2010). Findings were similar in adolescents (Lantrip et al., 2016). The extent to which these strategies can be effectively measured or assessed in pre-verbal infants and animals is challenging to answer, as they require conscious (re-)evaluation by the subject that uses them (i.e., meta-awareness) hence making them difficult to study in non-linguistic individuals.

1.1.4.2 Neuro-anatomical bases of empathy and emotion regulation

Building on the idea that the same neural networks are involved in perception and action representation (Gallese et al., 1996a; Preston & de Waal, 2002; Rizzolatti et al., 1996), other theories emphasise that an understanding of the emotional and mental states of others is based on internal simulations of the state in oneself (Goldman & Sripada, 2005). Nonetheless, Decety and colleagues (Decety, 2011; Decety & Jackson, 2004) proposed that empathy stands on the interaction between neural processes underlying the affective and cognitive components of empathy, along with emotion regulation. In contrast, Schipper and Petermann (2013) argued that the affective and cognitive components of empathy develop earlier than emotion regulation processes, and that empathy deficits cause difficulties in emotion regulation. It appears sensible to suggest that the processes generating affective states are distinct from the processes that regulate them, but because both processes are involved in the behavioural expression, it is complicated to distinguish them by looking at behaviour only. As a result, it is important to try to look at both affective and cognitive components of empathy and emotion regulation in different settings using a multi-componential approach, i.e., one that looks at the different components of empathy both independently and together (Dadds et al., 2008; Jolliffe & Farrington, 2004; Lovett & Sheffield, 2007). Unfortunately, many different means to appraise empathy and other socio-emotional capacities are used in the literature, making it difficult to systematically compare and identify underlying components, particularly when it comes to developmental and comparative studies. Thus, it is crucial to develop standardized and reliable measures of empathy (Dadds et al., 2008; Piotrowska et al., 2015).

1.1.5 Investigating empathy in humans and animals

1.1.5.1 Pioneering experimental investigations of empathy with rodent models

Rodent studies from the last century formed the groundwork of early comparative research on empathy. In an original study conducted in 1959 (Church, 1959), rats were trained to press a lever that initially delivered a food reward and later delivered electric shocks to a conspecific in a neighbouring cage. Findings demonstrated that rats who had received electric shocks themselves were more likely to decrease the amount of time they would press the lever resulting in the delivery of shocks to a conspecific, than rats who had never received electric shocks. This work was the first to investigate the shared experience of pain in rodents and suggested that rats can recognise and relate to their own negative experience when observed in a conspecific going through the same situation. Furthermore, this behaviour also suggests that rats can discriminate their own affective state from those of their conspecifics, which is in line with some perspective-taking-like abilities (Sivaselvachandran et al., 2018). This study was followed by an investigation of ‘altruism’ and prosocial behaviours in rats (Rice & Gainer, 1962), which demonstrated that rats would help to improve the situation of a distressed conspecific suspended in the air by pressing the lever that would bring the conspecific back on the ground rather than pressing another lever (but see (Lavery & Foley, 1963 for alternative explanations). Following these pioneering works, rodent empathy research developed towards the use of two main routes and designs. The first assesses *emotional contagion* and involves experimental protocols that trigger negative emotional states like pain and fear in an individual to test how these negative states impact a conspecific observer (Jeon et al., 2010; Langford et al., 2006). The other investigates *prosocial behaviours* and is based on the induction of a distressed state in an individual to test a conspecific observer’s helping behaviours (Bartal et al., 2011; 2014).

1.1.5.2 Comparative behavioural approaches to empathy

There are several comparative behavioural approaches to investigate the evidence for empathy in animals (Clay et al. 2018). Based on the Russian doll model (de Waal, 2007, detailed in a section above), empathy can be investigated through its proposed different layers: from its core processes, with emotional contagion, to the most external ones involving more socio-cognitive mechanisms. The ethological approach explores behavioural markers of empathy.

Yawn contagion – i.e., the tendency to yawn when someone else is yawning – is considered to be an automatic and potential rudimentary form of state-matching that has been proposed by some to be related to empathy (Campbell & de Waal, 2011; Haker et al., 2013; Norscia & Palagi, 2011; Palagi et al., 2009; Platek et al., 2003; Romero et al., 2010). This is because both gender and social closeness (see *empathy gradient* in the above section) biases, characteristic of empathic abilities, are found in yawn contagion as well (e.g., Norscia et al., 2016; Norscia

& Palagi, 2011, but see Gallo et al., 2021). Furthermore, human studies demonstrated that children with autism – who are known to experience deficits in empathic abilities (Fletcher-Watson & Bird, 2020; Smith, 2009)- show less contagious yawning compared to typically developing (TD) children (Giganti & Esposito Ziello, 2009; Helt et al., 2010; Senju et al., 2007). These results support the opinion that yawn contagion is linked to empathy. Thus, although contagious yawning has been found in most hominoid species: i.e., chimpanzees (Campbell & Cox, 2019; Campbell & de Waal, 2011), bonobos (Demuru & Palagi, 2012; Palagi et al., 2014) and humans (Provine, 2005) as young as 2.5 years (Cordoni et al., 2021), this does not seem to be the case in gorillas (Palagi et al., 2019). This discontinuity implies that phylogenetic closeness does not automatically predict yawn contagion (Palagi et al., 2020). Moreover, although human foetuses show spontaneous yawning (Reissland et al., 2012), children do not show yawn contagion before the age of 4-5 years (Anderson & Meno, 2003; Helt et al., 2010; Millen & Anderson, 2011) which is later than empathy (Davidov et al., 2013, 2020; Roth-Hanania et al., 2011). The discussion about the proximate factors that support contagious yawning is still ongoing, and therefore, the link between yawn contagion and empathy remains controversial.

Another behavioural expression of the emotional mimicry mechanism considered to relate to empathic responding is *rapid facial mimicry* (RFM). RFM is an involuntary, *rapid*, and automatic response, in which individuals mimic others' *facial expression*s (Mancini et al., 2013). According to the Perception-Action model (described above, Preston & de Waal, 2002), the mirror neuron system generates shared representations during the perception of another's facial expression. As such, RFM is considered a pillar of synchronisation between individuals and constitutes a potential predictor of emotional and empathic contagion (Dimberg et al., 2000). Particularly, it has been observed in multiple non-human primate species (chimpanzees *Pan troglodytes* and gorillas *Gorilla gorilla*: Palagi et al., 2018; bonobos *Pan paniscus*: Palagi et al., 2020; orangutans *Pongo pygmaeus*: Davila-Ross et al., 2008; macaques *Macaca tonkeana* and *Macaca fuscata*: Scopa & Palagi, 2016; geladas *Theropithecus gelada*: Mancini et al., 2013), mainly in the context of play, but also recently during sexual contacts (Palagi et al., 2020).

Beyond state-matching and mimicry, comparative and developmental research in humans and other animals has shown that bystanders of social conflicts sometimes spontaneously approach victims in distress to offer them friendly contact or reassurance in order to alleviate their distress. This behaviour, known as *consolation*, is different from other forms of bystander-initiated affiliation in its assumed intrinsic motivation and prosocial function. Indeed, other consolatory-like behaviours – also called "third-party affiliation" (e.g., Call et al., 2002; Palagi & Cordoni, 2009) - might be driven by different proximate mechanisms serving selfish adaptive functions that are unrelated to empathy (e.g., Call et al., 2002; Schino & Marini, 2012). For instance, such affiliations can reduce self-distress as well as the risk of redirected aggressions, increase social reward and establish reciprocity for future events (Batson, 2011; Palagi et al., 2006; Watts, 2002). Consolation has first been described in chimpanzees (de Waal & van Roosmalen, 1979, followed by Fraser et al., 2008; Romero & de Waal, 2010), before being been reported in humans (Zahn-Waxler & Radke-Yarrow, 1990; Zahn-Waxler et al., 1985; Zahn-Waxler, Robinson, et al., 1992a; Eisenberg et al., 2006), bonobos (Clay & de Waal, 2013a, 2013b; Palagi & Norscia, 2013; Palagi et al., 2004), gorillas (Cordoni et al. 2006), and one species of monkeys – the Tonkean macaques (*Macaca tonkeana*: Palagi et al. 2014). Thus far, evidence from other studies on monkeys has remained inconclusive (de Waal & Aureli, 1996; Watts et al., 2000). Importantly, all these primate species demonstrating consolation are known for their high degree of social tolerance (Ciani et al., 2012; Matsumura, 1999). Consolation-like behaviours were also observed in non-primate species like dogs (*Canis lupus familiaris*, Quervel-Chaumette et al., 2016), rodents like prairie voles (*Microtus ochrogaster*, Burkett et al., 2016), and corvids like ravens (*Corvus corax*, Fraser & Bugnyar, 2010) – but the mechanisms of these behaviours are unclear, and more investigation is required to establish whether they are equivalent across species (Adriaense et al., 2020).

A hallmark feature of consolation is that this form of bystander-initiated affiliation is strongly predicted by social closeness, being strongest among kin, followed by socially close partners, and weakest among social-distant or unfamiliar individuals, i.e., “empathy gradient” (Fraser et al., 2008; Romero et al., 2010; Clay & de Waal, 2013a; Palagi & Norscia, 2013). Furthermore, more than a direct emotional response to the recipient’s distress, consolation is thought to reflect the bystander’s understanding of the victim’s state as well as an attempt to ameliorate their distress (de Waal & Preston, 2017). Indeed, consolation has been shown to function to reduce the distress of the recipient – based on rates of self-scratching behaviours- without immediate benefits to the actor (Clay & de Waal, 2013a; Fraser et al., 2008; Palagi & Norscia, 2013; Romero et al., 2010). Offering such comfort suggests that bystanders perceive the emotional state of another individual and thus provide the appropriate response to reduce their distress (Fraser et al., 2008; Palagi & Norscia, 2013; Romero et al., 2010). As a result, consolation is considered a marker of *sympathetic concern* (Fraser et al., 2008; de Waal, 2008; Romero et al., 2010; de Waal & Preston, 2017), which is defined as the “concern about another’s state and the attempts to ameliorate this state” (de Waal & Preston, 2017). Although the apparent involvement of perspective-taking suggests that consolation may reflect a cognitively advanced form of empathy, consolation nevertheless appears within the first years of human life (Roth-Hanania et al., 2011; Davidov et al., 2013) and has also been shown to be present in immature great apes (Clay & de Waal, 2013b, 2013c; Webb et al., 2017). This suggests that although the cognitive component of empathy develops over time, the initial building blocks of consolation, such as the ability to react to the emotions of others appear early in life, and the appreciation of others' emotional states does not necessarily require the most complex capacities, including attribution of mental states (i.e., perspective taking, de Waal 2008).

Finally, *targeted helping* – also known as 'instrumental helping' (Warneken, 2006; Warneken et al., 2007)- refers to the offer of targeted help that is based on the cognitive appreciation of the need of another in a given situation (de Waal, 1996; 2008). To provide such fine-tuned help, the actor must understand the situation of the other and provide a suitable solution. Empathy-related targeted helping, in contrast to other prosocial responses, is characterised by a fine-tuned response to an individual's specific situation or need (Pérez-Manrique & Gomila, 2018). In this case, targeted helping is considered to be connected to the cognitive component of empathy. This capacity seems to appear quite early in human development, with evidence that children as young as 18 months of age tend to help others to achieve their goals in various situations (Warneken, 2006). Several cases of targeted helping have been observed/suggested in nonhuman animals, such as some great apes (chimpanzees: de Waal, 2010; Melis et al., 2011; Yamamoto et al., 2012, although contested), cetaceans (Bearzi et al., 2017), and elephant species (Byrne et al., 2008; Douglas-Hamilton et al., 2006). However, detecting whether and to what extent an animal can understand another's goal and offer appropriate help is very challenging. This is because the same external behaviour can be triggered by different motivations and therefore different cognitive and physiological mechanisms. Consequently, despite the importance of the ethological approach for investigating behavioural markers of underlying processes, it is essential to also investigate the underlying processes themselves to explain the observed behaviours. This point is discussed in more depth in *Chapter 6*.

Thus far, most research investigating the evolution of empathy has depended on naturalistic observations with free-ranging animals or cognitive experiments with laboratory experiments. Conducting naturalistic observations gives a first-hand look at spontaneous behaviours expressed by the subjects in their natural environment, which provides important ecological validity to identify the evolutionary drivers shaping complex social phenomena like empathy. It is also often the only option to study behaviours expressed in situations that would be difficult and/or unethical to artificially set up, such as a distressing situation, in which empathic reactions arise (although previous work on rodents has included invasive and distressing protocols: see Meyza & Knapska, 2018 for a review). Naturalistic observations of consolation (e.g., Clay & de Waal, 2013a; de Waal & van Roosmalen, 1979) have provided valuable information on the function of this behaviour, how it develops in an individual by looking at different points in time (Webb et al., 2017), and also its phylogenetic history by investigating this behaviour in closely related species (e.g., Palagi et al., 2014). However, observing animals in natural settings precludes the capacity to control for external variables, which may influence behavioural outcomes, consequentially making it difficult to determine the cause of the observed behaviours. Therefore, experimental approaches in which researchers have a high level of control on environmental pressures and can control for confounding factors are essential to identify underlying mechanisms.

1.1.5.3 Investigating underlying mechanisms of empathy with a physiological approach

With the advance in novel technologies, the past few decades have seen the emergence of new tools to investigate the underlying mechanisms of emotion processing. These advances include the measurement of physiological mechanisms such as (cardio)vascular, and neuronal responses linked to changes in emotional states, including heart rate and heart rate variability analysed via electrocardiograms (ECG, Lischke et al., 2018), skin conductance / electrodermal activity (Hein et al., 2011), respiratory sinus arrhythmia (RAS, Liew et al., 2011a; MacGowan & Schmidt, 2020), and endocrinology (Zilioli et al., 2015). These measures provide quantifiable insights into the activity of the autonomic nervous system, which has been increasingly interpreted as relevant to empathy-related responding (Liew et al., 2003, 2011; Taylor et al., 2015; Zahn-Waxler et al., 1995). These kinds of psychophysiological measures are used to investigate emotional states in humans (Kreibig, 2010) and even some primates (Berntson et al., 1989; Berntson & Boysen, 1989; Parr, 2001). They have been validated by looking at the subject's physiological response to various relevant stimuli (e.g., distress-inducing) as well as their relation to the expression of prosocial behaviours. A recent study on 18-month to 5-year-old children highlighted that internal arousal (measured via pupil dilatation) predicted children's tendency to prosocially help: i.e., children who showed the greatest increases in internal arousal – as measured by pupil dilatation - when witnessing others in need, were more likely and faster to provide prosocial assistance (Hepach, Vaish, Müller, et al., 2017b). In line with previous research (Warneken & Tomasello, 2008; Hepach et al., 2012, 2016; Ulber et al., 2016), this suggests that children's prosociality might indeed be motivated by emotional processes, and therefore has an affective component.

Although techniques like pupillometry, ECG, skin conductance, RAS, and endocrinology open a relevant window on the physiological mechanisms underlying emotional responding, they present limitations and ethical issues, preventing their wide use with animals, including apes. Indeed, they are often quite restrictive in the way they limit the movement of subjects and are sometimes invasive. For instance, methods relying on direct contact with the subject (e.g., heart rate, electrodermal activity and electromyography, RAS) cannot be implemented on non-trained subjects and without physical restraint, which makes them difficult to use in ecologically valid conditions and/or with non-adult humans (e.g., young children, non-human animals). However, the advent of new technologies and methodologies such as Infra-Red Thermography (IRT) open new doors for the experimental study of physiological mechanisms, without restraining the subject/participant (Ioannou et al., 2014, more details below). As a non-invasive – defined as those that avoid "non-care-related insertions, injections or incisions"

(Ross & Leinwand, 2020)- and contact-free procedure, IRT enables wide use, beyond domesticated species or highly trained subjects.

In this regard, both natural observations and experiments show strengths and limitations for investigating the socio-emotional and cognitive mechanisms underlying empathy. No single measure can conclusively show or test for empathy nor emotions, which do not have a specific physiological signature, and both natural observations and experiments are required to detect different kinds of mechanisms. Indeed, natural observations can provide indicators of behaviour and offer insights into the selective pressures driving their evolution while experiments are needed to detect underlying mechanism. Consequently, given the multi-dimensional nature of empathy, it is crucial to combine across measures and approaches to estimate evidence of such a highly nuanced and complex multi-faceted capacity.

1.1.5.4 Infrared thermography: a technological advance in the field of affective science

A non-invasive, contact-free technology now emerging in the field of emotion research is infrared thermography (IRT, Ioannou et al., 2014), which measures the changes in body surface temperature resulting from changes in blood pressure activated by sympathetic nerves (Rubinstein & Sessler, 1990; Ioannou et al., 2014). This is because variation in emotional states is linked to modifications in the skin's blood flow via constriction and dilation of blood vessels, resulting in changes in blood volume and blood pulse amplitude, along with changes in surface skin temperature in specific areas of the face and body (Ioannou et al., 2014; Kreibig, 2010). This process is controlled by the Autonomic Nervous System (ANS, Kop et al., 2011; Levenson, 1992).

Empirical research in humans has demonstrated that emotion-based states induce distinctive changes in facial skin temperatures (Ioannou et al., 2014), and such changes have been recently reported following emotional stimulation in other animals as well, including great apes (Dezecache et al., 2017; Kano et al., 2016). For instance, a drop in skin temperature (caused by vasoconstriction) is associated with negative affect in humans (Ioannou et al., 2013; Ioannou et al., 2014; Nakanishi & Imai-Matsumura, 2008; Vinkers et al., 2013), non-human primates (Kano et al., 2016; Kuraoka & Nakamura, 2011; Nakayama et al., 2005), and other animals (e.g., pigs; Boileau et al., 2019), while an increase in nasal skin temperature is linked with positive affect in humans (Hahn et al., 2012; Ioannou et al., 2014). These last results on positive affect are less conclusive in non-human primates (see Chotard et al., 2018 for an overview). However, negative and positive emotional states seem to be linked to specific temperature variations for different facial areas (Chotard et al., 2018a). Affect has two dimensions: arousal and valence (see Adriaense et al., 2020 for a review). It seems that physiological mechanisms of affective states may be at least in part – arousal, but results are yet not clear for valence – measurable with infrared thermography in humans and other animals (e.g., rodents; Lecorps et al., 2016). Furthermore, protocols including more social contexts (e.g., response to the emotional state of another) are still needed to obtain a broader understanding of the underlying mechanisms of emotional responding. Although IRT represents a promising method in comparative affective science, it also presents some practical limitations that might be challenging to mitigate, including the importance of controlling external conditions (Kano et al., 2016) as well as physical activity (Nakanishi & Imai-Matsumura, 2008) on the variation in blood flow that can impact the measurement. I detail these limitations further in *Chapter 6*.

1.2 The value of the developmental and evolutionary approaches

1.2.1 Tinbergen’s four levels of explanation

In 1963, one of the founding fathers of ethology, Niko Tinbergen, suggested that behaviour can be explained from four levels: survival value (function), ontogeny (development), evolution (phylogeny), and causation (mechanisms). These four levels, categorised into ultimate and proximate causes (Laland et al., 2011; Mayr, 1961), offer mutually non-exclusive outlooks to understand and explain behaviour (Bolhuis & Verhulst, 2009). *Proximate* explanations look at *how* behaviour works and therefore investigates its mechanisms – including physiological, motivational or emotional- and developmental processes. On the other hand, the *ultimate* explanations look at *why* a behaviour is present or absent and hence investigates the adaptive value provided by a behaviour that has been selected by evolution, along with its phylogenetic history. This thesis aims at advancing our comprehension of these two levels of explanation, particularly the developmental and evolutionary roots of empathy and its underlying physiological mechanisms.

1.2.2 The contribution of the developmental approach

To identify the underlying processes of a phenomenon and how it interacts with other phenomena, it is crucial to understand its ontogeny as well as for understanding the causes of inter-individual and inter-group differences (De Haan & Gunnar, 2009). In particular, looking at the emergence and maturation of behaviours and/or abilities from its earlier developmental states informs on which of its components are essential to the development of others (i.e., precursors). This is particularly important for complex multi-componential phenomena like empathy, with its various components developing at different stages of life (Preston & de Waal, 2002).

Although the early emergence of a behaviour tends to suggest a heritable character, supporting a nativist view (Carey & Spelke, 1996; Spelke & Newport, 1998), a behaviour that emerges later might also be heritable if an individual is inherently equipped to develop this behaviour later in life, but requires the maturation of certain anatomical or neurological systems to appear and develop at a later stage (Karmiloff-Smith, 1994). Additional components may require explicit experiential inputs to grow, e.g., related to specific socio-cultural environments. In the case of empathy, the way individuals express their emotions and react to the emotion of others might also be culturally shaped (Butler et al., 2007; Fischer et al., 2004; Soto & Levenson, 2009). Therefore, combining different perspectives like cross-cultural and ontogenetic perspectives can mature our understanding of the roots of the behaviours (Liebal & Haun, 2012). Phylogenetic comparisons also allow for a valuable triangular method, which has the potential to inform on the presence of heritable traits in different species (Nielsen & Haun, 2016).

1.2.3 The contribution of the evolutionary approach

Evolutionary theory (Darwin, 1859) emphasises phylogenetic continuity between traits, whereby social, emotional and cognitive processes are biological adaptations anchored by shared evolutionary history. By identifying similarities and variations of different processes across related species, we can map their phylogenetic history (Haun, Jordan, et al., 2011). Over the past decades, comparative research has provided a valuable opportunity to investigate the evolutionary history of the social, emotional and cognitive skills that define our species and the conditions that might have promoted their evolution (Haun, Jordan, et al., 2011; Johnson-Pynn et al., 2003; Liebal & Haun, 2012; Tomasello & Call, 1997). Indeed, if a trait is found in every descendant of a common evolutionary ancestor, then this trait (i.e., homology) is considered to be inherited from that last common ancestor (LCA). On the contrary, if the trait is absent in some of the descendants but presents in one of them, it is likely to be a derived feature that has developed specifically in this species in response to various evolutionary pressures. Yet, not all evolved traits are adaptations that have undergone selection. Indeed, some traits arise as neutral by-products of selection on other traits (epi-phenomena, e.g., brain size; see Montgomery et al., 2016) or through other evolutionary mechanisms such as mutations and genetic drift (Foster, 2000; Hallatschek et al., 2007; Lynch et al., 2016) that yet do not exclude selection.

Comparisons among closely related species, such as humans and other great apes, allow us to identify shared, likely homologous traits, as well as derived traits that may be unique in one species as compared to another. Nevertheless, this approach does not necessarily inform about the drivers of those evolutionary patterns. In contrast, broader bottom-up comparisons across diverse species are needed to identify instances of convergent or analogous evolution and common selective pressures shaping trait variation (Losos, 2011). Intraspecific studies can shed light on a trait's apparent function (Bolnick et al., 2011; Richardson et al., 2014). Besides, experiential effects contribute to patterns of development and the extent to which adults of a particular population manifest a particular trait (i.e., variation is not explained only at the genetic level; Bonduriansky & Day, 2009). Finally, this approach would highly benefit from the broader inclusion of the extended diversity present in both intra- and inter-*Pan* species to provide a more accurate picture of the early hominid evolution (Boesch et al., 2002; de Waal & Lanting, 1997).

1.3 Our closest living relatives

In this section, I introduce the great apes and focus particularly on the study species of the thesis: bonobos, chimpanzees, and humans (*Homo sapiens*). I introduce their genetic relationships, territory and demographics, along with their similarities and differences in terms of social structure and cognitive and socio-emotional skills, and finally, neuro-anatomical evidence supporting their choice as study species to study the evolution of empathy.

1.3.1 The great apes

Human primates are part of the family of the *Hominidae* along with four other extant great ape genera: bonobos, chimpanzees (with 5 subspecies: *Pan troglodytes troglodytes, P. t. verus, P. t. ellioti, also known as P. t. vellerosus, P. t. schweinfurthii, and P. t. marungensis*), gorillas (with two species: *Gorilla gorilla and G. beringei*, with both species divided into two subspecies: *G. gorilla diehli, G. g. gorilla, G. beringei beringei, G. beringei graueri, respectively*), and orangutans (three species: *Pongo abelii; P. pygmaeus, P. tapanulii*). Chimpanzees and bonobos are the closest phylogenetic relatives of humans who split from the shared lineage with humans around five to seven million years ago (Prüfer et al., 2012), or even as early as eight million years ago (Langergraber et al., 2012 – see Figure 1.2). Therefore, given their evolutionary closeness to our own species, great apes – and particularly chimpanzees and bonobos- provide a unique window into our most recent evolutionary history.

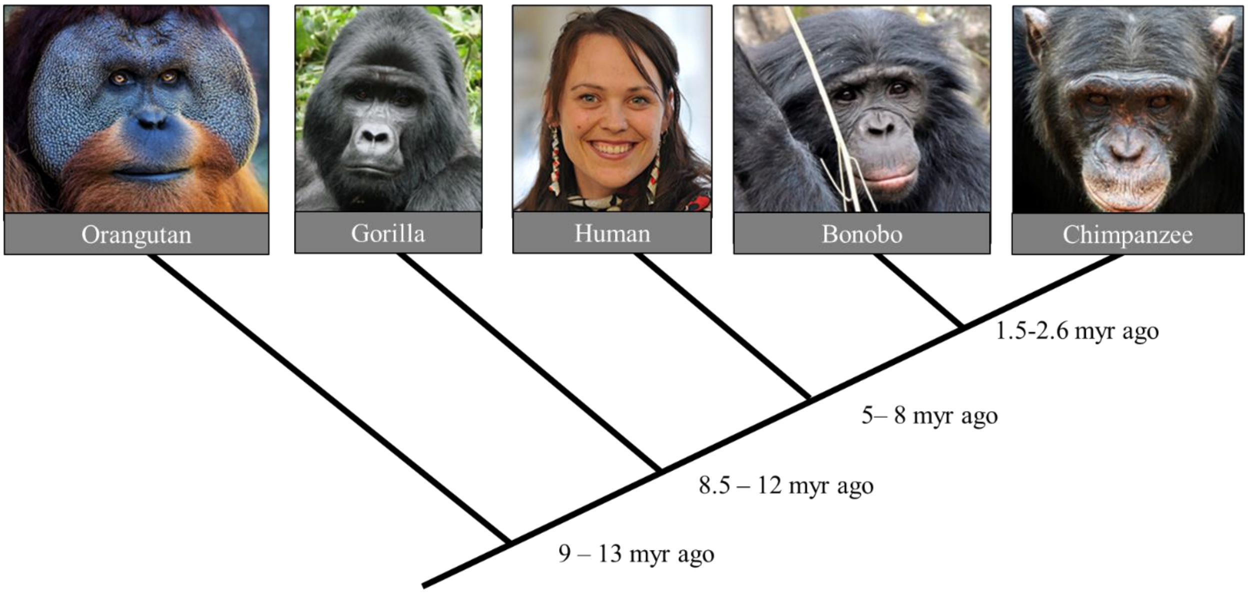

Figure 1.2 The evolutionary tree of great apes: *Pongo* and *gorilla* species, *Pan troglodytes,* and *Homo sapiens* (myr = million years) – with permission

1.3.2 Three study species: Bonobos, chimpanzees, and humans

1.3.2.1 Genetics and Hominin evolution

Bonobos and chimpanzees are closely related but genetically distinct African great ape species. The most recent data suggest that the two *Pan* species lineages diverged from each other between 1.5 to 2.6 million years ago (Langergraber et al., 2012). Both species are the closest living relatives of humans and share about 99% of their genetic material with us (Custance & Bard, 1994; Want & Harris, 2002; Tomonaga et al., 2004; Wildman et al., 2003), including even genetic similarities they do not share with each other (Prüfer et al., 2012). Therefore, the two *Pan* species embody key living models to rebuild our last common ancestor (LCA), and understand the social and ecological drivers that might have triggered the evolution of humanity.

1.3.2.2 Territory and demographics

Humans – the only extant members of the subtribe *Hominina*- have extensively colonised the Earth (and beyond) thanks to, but not limited to, human cognitive abilities, the expansion of cultural evolution, and the human body's adaptability to various environmental conditions. On the contrary, other great ape species are generally restricted to more limited geographic areas. The four subspecies of chimpanzees (Becquet et al., 2007) can currently be found in 21 African countries from Eastern to Western central Africa, while bonobos are endemic to the equatorial rainforests of the Democratic Republic of Congo. Both chimpanzees and bonobos are classified as *endangered* on the IUCN Red List. Great ape population estimates are made using a standard index of abundance that includes night nest count and distribution, often combined with predictive modelling. Although useful indicators, these estimates are uncertain due to the challenges coming with the field surveys, including political instability and limited access to remote areas. Sadly, chimpanzees are already extinct in four of their initial 25 range countries.

Last century, their wild population was estimated to be one million, compared to 172,000 - 300,000 today (Humle et al., 2016a). Regarding bonobos, the current estimates range from 10,000 to 20,000 individuals left in the wild (Fruth et al., 2016). Current trends predict that African ape populations will decline by eighty per cent in the next three to four decades. In contrast, the human population is in exponential expansion and constitutes the main threat to great apes' populations via the continuous destruction of their territory. This is a result of the transformation of wild areas into agricultural lands and human-wildlife competition for limited natural resources, along with the development of the illegal exotic pet trade and the commerce of bushmeat. Therefore, given their rapid decline, their status as a flagship species that help to protect ecosystems more generally, and their crucial relevance for understanding human evolution, it is vital to study these species and learn how to protect them.

1.3.2.3 Social structure

Bonobos, chimpanzees, and humans all live in highly complex societies. Human societies are structured in various social groups that range from family groups to communities, nations, and even beyond, thanks to the development of modern communicative technologies permitting global alliances. Along with their strong phenotypic resemblances, both chimpanzees and bonobos live in multi-male, multi-female fission-fusion societies counting on average 30-35 members in territories covering about 20-60 km^2 (Humle et al., 2016b; Mitani & Watts, 2005). However, groups might be much larger, with for instance the Ngogo chimpanzee community counting between 145 and 208 individuals since 1995 (Langergraber et al., 2013; Watts, 2018; Wood et al., 2017). In general, although some bonobo and chimpanzee females remain in their natal groups their whole life, others migrate when reaching sexual maturity, whereas males are philopatric and stay in their initial community (Goodall, 1986; Kanō, 1992). Both *Pan* offspring are dependent on maternal care for four to five years without the support of the father, resulting in long intervals between births of around five years (Goodall, 1986; Kano, 1992).

In chimpanzee communities, males are more closely related than the incoming females of the group (Hamilton, 1963). Male chimpanzees are highly cooperative (e.g., boundary patrols: Boesch, 2009; Nishida, 2011) and form strong alliances with other males in their communities (Duffy et al., 2007; Feldblum et al., 2021; Goodall, 1986; Mitani et al., 2000). They also dominate over all females (Boesch & Boesch-Achermann, 2000; Goodall, 1986) and generally show a clear linear hierarchal structure led by an alpha male (Boesch, 2009; Nishida, 2011). Nonetheless, they also maintain strong relationships with their mothers which is associated with social gain and reproductive success (Crockford et al., 2020). Similarly to chimpanzee communities, males bonobos are more closely related than the incoming females of the group (Ishizuka et al., 2020) and typically maintain a linear hierarchy among males, mediated through aggressive interactions (Surbeck et al., 2011, 2012). However, male bonobos do not form alliances with other males in agonistic contexts (Furuichi & Ihobe, 1994; Hohmann et al., 1999; Hohmann & Fruth, 2003), but instead, build strong bonds with the female of the group (Furuichi, 1997; Kanō, 1992; Surbeck et al., 2011; 2017). This starts with their mother from whom they gain most of their social status (Surbeck et al., 2011). A bonobo community is usually led by an alpha female and her mature male offspring (Furuichi, 1997; Surbeck et al., 2011).

In the wild, female chimpanzees do not usually form strong bonds or alliances with other females (Lehmann & Boesch, 2005), but do sometimes in captivity (Anestis, 2004). Although females are dominated by males in wild chimpanzee communities, this does vary between populations and females of the group also show an intrasexual hierarchy (Murray et al., 2007; Pusey & Schroepfer-Walker, 2013). Compared to female chimpanzees, female bonobos form strong alliances with other females (Moscovice et al., 2019; Tokuyama et al., 2019) as well as with males which strengthens female dominance (Hohmann et al., 1999; Hohmann & Fruth, 2003; Stevens et al., 2007; Vervaecke et al., 2000; White, 1988; White & Wood, 2007). Nonetheless, female dominance over males is not absolute, and although older females usually show high ranking positions (Vervaecke et al., 2000), dominance patterns are rather flexible and nonlinear (Vervaecke et al., 2000), where the system may be better described as co-dominant.

Chimpanzee societies show high rates of male aggression (Goodall, 1986), generally directed towards other males and sometimes towards females and juveniles – occasionally lethal (M. L. Wilson et al., 2014). In contrast, rates and severity of aggression are much lower in bonobo communities (Hohmann & Fruth, 2003). Furthermore, bonobos do not usually react overly aggressively towards neighbouring groups – some peaceful intergroup encounters have been reported (Furuichi, 2011; Hohmann, 2001; Sakamaki et al., 2018). For a complete review of the social structure of *Pan*, see Gruber & Clay (2016).

1.3.2.4 Cognitive and socio-emotional skills

Both *Pan* species can perceive conspecifics as intentional agents and attribute mental states to them (Krupenye et al., 2018; Lewis & Krupenye, 2021; Premack & Woodruff, 1978; Schleidgen et al., 2011). They are also sensitive to the emotions of others as they offer consolatory behaviours to distressed individuals following conflicts (Clay & de Waal, 2013a; de Waal & van Roosmalen, 1979). Experimental studies established that chimpanzees recognise the emotions of their conspecifics (Izumi & Kojima, 2004; Kano et al., 2008; Kret et al., 2014; Parr, 2003), that bonobos' attention is biased towards emotional signals of conspecifics (Kret et al., 2016b), and that both bonobos and chimpanzees are sensitive to human emotions (Buttelmann et al., 2009). Furthermore, bonobos are more tolerant than chimpanzees in co-feeding settings (Hare et al., 2007; but see Herrmann & Tomasello, 2006), and, with their greater levels of tolerance, even outperform chimpanzees when solving dyadic cooperative tasks (Hare et al., 2007). An eye-tracking experiment also showed that bonobos make more eye contact than chimpanzees (Kano et al., 2015), and they demonstrated more risk-aversion than chimpanzees in a risky decision task (Haun et al., 2011; Rosati & Hare, 2013). Taken together, these findings suggest that bonobos show higher levels of socio-emotional orientation than chimpanzees. Although bonobos outperform chimpanzees in social cognition tasks involving cooperation and tolerance, chimpanzees lead in physical cognition tasks (Herrmann et al., 2010) with their more developed tool-using abilities. Both chimpanzees and bonobos show highly developed cognitive and socio-emotional skills, yet to different degrees and in their own ways. Being human's closest living relatives, both species – studied together- can offer a rich and nuanced view of the cognition and socio-emotionality of *Pan* and our LCA.

1.3.2.5 Neuro-anatomical species differences in emotion processing

These species' differences in emotion processing have been supported by neuro-anatomical evidence. Firstly, bonobos have more grey matter in the dorsal amygdala compared to chimpanzees (Rilling et al., 2012). This area's activity is linked to the hypothalamic-pituitary-adrenal (HPA) axis and autonomic nervous system (ANS, Davis, 1997; LeDoux, 1998), and therefore constitutes a key aspect of a network that controls negative emotions like distress and anxiety, as well as sexual behaviours in non-human animals (Breedlove & Watson, 2013; Newman, 1999). This suggests that the bigger amygdala of bonobos could trigger distress, while also motivating sexual behaviour that helps alleviate tensions in bonobo communities (de Waal, 1987; Hare et al., 2007; Hohmann et al., 2009; Parish, 1996; Rilling et al., 2012). Bonobos also have a larger pathway linking the amygdala with the ventromedial prefrontal cortex than chimpanzees (Rilling et al., 2012). This pathway is implicated in emotion perception (Blair, 2008) and regulation (in humans: Davidson et al., 2000; Pezawas et al., 2005). Therefore, it might be implicated in the higher control of aggressive impulses in bonobos compared to chimpanzees (Davidson et al., 2000; Meyer-Lindenberg et al., 2006). Species' differences in pathway size may be amplified by higher testosterone levels in male chimpanzees that inhibit its functionality (Sannen et al., 2004; van Wingen et al., 2010; Wobber, Hare, et al., 2010). Finally, bonobos have more grey matter in the anterior insula than chimpanzees (Rilling et al., 2012). This region is linked to socio-emotional processing (Allman et al., 2010; Kurth et al., 2010), risk-taking (Bossaerts, 2010; Kuhnen & Knutson, 2005), and coactivates with the amygdala (Mutschler et al., 2009). This is consistent with bonobos being more risk-averse than chimpanzees (Heilbronner et al., 2008).

To conclude, studying both chimpanzees and bonobos, along with their intraspecies' variations (see Gruber & Clay, 2016 for a review), is central to deepen both our understanding of human evolutionary history – particularly in terms of empathy and emotional responding-, as well as our knowledge of these fascinating species and hopefully learn how to protect them.

1.4 Thesis aims

This review has revealed the complex nature of empathy and the even more complex issue of how to study it scientifically, particularly in animals. To this end, we still lack an understanding of its ultimate and proximate explanations (Tinbergen, 1963). This thesis aims at advancing our comprehension of the evolutionary and developmental roots of empathy. To do so, I investigate markers of empathy in our closest living relatives, the great apes, and in young human children using a mixed-method approach, that includes naturalistic observations as well as behavioural and physiological measurements in experimental settings.

Combining approaches and methodologies is a valuable way to deepen our understanding of this complex phenomenon (see *Chapter 2* for more details). Indeed, while naturalistic observations can help to identify empathy-driven behaviours and inform us on the adaptive function and phylogenetic history (*Chapter 3*), controlled experiments can help us comprehend the underlying physiological mechanism. Gathering insights from both our closest great ape relatives (*Chapter 4*) as well as from immature individuals in our own species (*Chapter 5*) can provide both evolutionary and developmental insights. Combining observations and physiological measurements is necessary to allow for an integrated interpretation of the output, thereby giving us access to a broader understanding of how these components relate to each other (*Chapter 4*).

The first study (*Chapter 3*) will focus on the ethological approach for studying the development of empathy in our great ape relatives, the bonobos, in naturalistic contexts: through giving consolation to bystanders following an instance of distress. I use systematic observations of post-conflict contexts to investigate how consolatory responses develop with age in sanctuary-living bonobos, considering the effectiveness and selectivity of the consolation response across age as well as the impact of rearing.

Following this ethological framework based on great apes, the second study (*Chapter 4*) combines for the first time – to my knowledge- naturalistic observations and physiological experiments using infrared thermography (IRT) to investigate the link between observable empathic behaviour and corresponding inner arousal in chimpanzees. This multi-methods approach, i.e, an empirical approach that combines both behavioural and physiological measurements, offers a way to shed new light on the underlying mechanisms of empathy in our closest living relatives in more ecologically valid settings.

Building on evolutionary insights, my third empirical study (*Chapter 5*) takes a comparative developmental approach to experimentally investigate the mechanisms of empathic responding in young human children. Using IRT, I measure the physiological and behavioural reactions of children when witnessing the distress of a familiar *vs.* unfamiliar individual. Combining both behavioural and physiological measures, I investigate how the nature of children's empathic responses varies across development as well as examine markers of cognitive empathy including exploratory communicative responding, information seeking, and emotion regulation.

Finally, in my thesis, I introduce the development of a new IRT protocol to track regions of interest and extract the physiological IRT values from the videos (*Chapter 2*). I will also report on a qualitative exploration of the facial thermal profile to better understand the scope of using this measure for future comparative and developmental studies on empathy.

Chapter 2 General methods

In this chapter, I start by presenting some challenges I met during my PhD, and explain how these shaped the resulting content of this thesis. Then, I introduce the different approaches and methods I used, starting with behavioural observations of naturally occurring behaviours, like consolation, and continuing with my experimental approach and use of thermography to investigate arousal. Finally, I will describe the main statistical protocols used, i.e., Generalised Linear Mixed Models (GLMMs).

2.1 Mitigating circumstances

2.1.1 Bonobo and chimpanzee data collection

In August 2018, I conducted a 6-week research trip to Lola ya Bonobo sanctuary (LYB), DR Congo with the intention of running experiments with thermal-imaging technology and complementary observations to examine the physiological processes that may drive empathy in bonobos. I received ethical approval from Durham University Animal Welfare and Ethics Review Board and the Scientific Coordinator and Scientific Committee of "Les Amis des Bonobos du Congo[3]". I obtained funding from the National Geographic Society to conduct this fieldwork. I was assisted by a local assistant (H. I.).

The fieldwork at LYB was a valuable and enriching opportunity that enabled me to pilot novel experimental methods for the project and led me to reshape and improve the research project. This field trip gave me the occasion to conduct initial experiments using infrared thermography technology and introduce the method to the staff, which provided me with valuable experience

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[3] www.friendsofbonobos.org

in how to implement this research with great apes. I was able to adapt the collection of emotional stimuli thanks to a collaboration with the local staff and community.

While this field trip was a valuable learning experience, I faced many challenges and ultimately had to rescope my project and swap field sites, as the data collection did not go as planned. The goals had been, 1/ to observe post-conflict interactions to assess consolation and to record distress vocalisations to use as playback stimuli in the experimental phase, and 2/ to conduct a playback experiment using IRT. Although I managed to conduct some behavioural observations, substantial changes in group composition (owing to the reintroduction into the wild of a significant number of individuals one month before my data collection) meant my data collection was disrupted. The bonobos spent little time in the visible areas of the enclosures and social conflicts were rare. As a result, I was not able to collect the planned data, including the audio stimuli required for the experimental phase.

Therefore, I tried to adapt my paradigm to examine the IRT and behavioural response of bonobos to the distress states of familiar caregivers and unfamiliar caregivers. As the bonobos have strong attachments to their caregivers, examining their empathic responses towards them in comparison to unfamiliar individuals seemed a promising direction. I asked Congolese caregivers at the sanctuary to express different emotions (distress, happiness), to investigate the arousal responses of bonobos when viewing these stimuli, whereby the subject facial temperature was measured in response to the emotion of a familiar and unfamiliar human using the infrared camera. Although this collaboration was promising, rising instabilities in the bonobo social groupings following the reintroduction meant a sharp increase in escapes and other behavioural management issues, which the local staff were required to attend to. Therefore, it was not possible to conduct the planned projects.

While this was disappointing and ultimately required me to rescope my project, the experience was valuable. I adapted my study to conduct it at a chimpanzee sanctuary the following year (*Chapter 4*). Furthermore, to mitigate the lack of observations that occurred due to these disruptions and the curtailment of my trip, I was provided with access to an archival data set, described below, of observational data of naturally occurring post-conflict and post-distress situations collected in 2012 and 2016 at LYB by my supervisor Z. C., her student S. K. and their research assistants respectively (*Chapter 3*).

2.1.2 Developmental data collection with children

2.1.2.1 Cross-cultural data collection

My original plan was to go back to LYB in early May 2019 to collect data on bonobos and conduct observational and experimental data on Congolese children for a cross-cultural study funded by the Lucie Burgers Foundation for Behavioural Research grant I obtained in 2019. However, due to ongoing behavioural management issues, I switched to collecting data on Zambian children living in the communities surrounding Chimfunshi Wildlife Orphanage (CWO) in Zambia, where I was due to conduct my primate research. However, although my application for chimpanzee data collection was approved, the human part of the project was rejected, due to an unexpected general decision to cease cross-cultural research at this site.

2.1.2.2 Data collection with British children

A significant part of my initial project relied on experimental and behavioural data collected in Durham nurseries with young children, including spontaneous responses to distress taking place among peers. However, despite the significant amount of time I spent in the Durham nurseries, it was very challenging to collect post-distress data because of the high rate of intervention by the adult caregivers whenever infant distress occurred. Although I intended to return to collect more PC data from the nurseries in 2020, I was not able to go back due to COVID-19. COVID-19 also meant that I could not increase the sample size for my experimental study with IRT (*Chapter 5*) within the time frame of this PhD. As a result, I re-defined the main scope of this chapter and worked with a small data set.

2.1.3 Access to technical consultation for IRT

For my PhD, I sought additional supervision from Prof Camila Caiado from the Department of Mathematical Sciences at Durham University, to assist with establishing an automated coding system of infrared thermographic data for my PhD (*Chapter 4, Chapter 5*). We were mid-way through finalising the coding scheme when the COVID-19 crisis began. Prof Caiado then redirected her attention to modelling for Durham Council and the NHS and other governance responsibilities, which meant she was no longer able to supervise this aspect. Due to the uncertainties of the pandemic, it was unclear if or when supervision of this component could recommence. Therefore, in the interim, I coded the data for *Chapter 4* and *Chapter 5* manually. An additional chapter aimed at introducing and validating the automated coding method was planned, but due to the technical specifications, it was not feasible for me to finalise this without the assistance of Prof Caiado or develop an alternative coding scheme (other than manual temperature extraction) to validate. While it would be fruitful to initiate this collaboration with another expert, unfortunately, the extensive delays already brought about during COVID-19 meant it was not feasible to do so within the time frame of this PhD. Instead, I present the preliminary work I conducted in *Chapters 2* and *6*.

2.2 Assessing consolation behaviour via naturalistic observations

Here, I present the protocols for naturalistic observations and recordings of consolation, and behavioural data coding used in *Chapter 3* and *Chapter 4* of this thesis.

2.2.1 Data collection: naturalistic observations and recordings

Pioneering work on consolation behaviour, conducted by de Waal & Yoshihara (1983), introduced a standardised method to detect consolation through studying post-conflict affiliations, i.e., the Post Conflict (PC)-Matched Control (MC) method. According to the PC_MC method, each PC is matched with a 5-minute Matched Control (MC) focal conducted on the same victim, the following day at the same or at the closest possible time. This aims at controlling for baseline The PC-MC method has been widely used to verify the presence of consolatory behaviours in animals (Cheney & Seyfarth, 1989; Clay & de Waal, 2013b).

To detect consolation, I used video recordings of naturally occurring post-conflict (PC) and post-distress (PD) situations of bonobos at LYB (*Chapter 3*) and chimpanzees at CWO (*Chapter 4*). As consolation has already been previously detected in this bonobo population with the PCMC method (Clay & de Waal, 2013b), and consolation has equally been widely identified as present in chimpanzee colonies (de Waal & van Roosmalen, 1979; Fraser et al., 2008; Romero et al., 2010), MCs were not collected. Therefore, I considered the post-conflict affiliations observed in these contexts to be consolations. Nonetheless, a potential impact of not having matched controls for the PC affiliation data used in this thesis might be that I am missing out on the potentiality that my subjects are displaying affiliative behaviours similar to consolation outside of the context of PC as well.

Zanna Clay (Z. C.) and Stephanie Kordon (S. K.) and their research assistants conducted video recordings of naturally occurring post-conflict and post-distress situations, respectively from May to August 2012 (used in Clay & de Waal, 2013b), and from June to August 2016 on bonobos at LYB. Jake Brooker (J. B.) and his assistant (Zoë Goldsborough, Z. G.) conducted similar video recordings from March to July 2019 on chimpanzees at CWO. An overview of the data collection is given in Table 2.1.

Table 2.1 Overview of the data collected by species and field site, year, duration of the data collection, and the main researcher collecting the data

Species	**Field site**	**Year**	**Duration** (months)	**Researcher**
Bonobo	Lola ya Bonobo	2012	4	Z. C.*
Bonobo	Lola ya Bonobo	2016	2.5	S. K.*
Chimpanzee	Chimfunshi Wildlife Orphanage	2019	4.5	J. B.*

*The main researcher was assisted by an assistant

The apes were recorded in the visible areas of the enclosures following the methodology used in previous studies conducted in the same settings (Clay & de Waal, 2013a, 2013b). Post-conflict situations (PC) were recorded for 5 minutes after the onset of a conflict between two opponents leading to a clear losing party of the conflict (i.e., victim). Post-distress situations (PD) were recorded for 5 minutes after the onset of a spontaneous outburst of distress (without a conflict). Comments in the recordings included the date, start time, identities of the aggressor and victim, type of aggression and proximities of the bystanders (within 1m, 5m, 10m or >10m visible to the observer).

I was provided with access to the raw data of the coding of the bonobo videos from 2012, coded by Z. C. for a previous project (Clay & de Waal, 2013a), as well as to some elements coded by S. K. for the videos from 2016. I completed the coding initiated by S. K. and added other elements into the 2016 videos with the help of two student assistants: R. Y. O. and F. J. Regarding the chimpanzee videos, I was provided access to the raw data compiled by J. B. and his assistants.

2.2.2 Behavioural data coding

2.2.2.1 PC/PD affiliations

From the recordings, all occurrences of PC/PD affiliations were coded using an annotation tool for audio and video recordings called ELAN software (Version 5.9 - Computer software, 2020 - Nijmegen: Max Planck Institute for Psycholinguistics, The Language Archive[4]), commonly used to code the behaviours (e.g., Lausberg and Sloetjes 2009). *Consolations* are defined as *unsolicited* affiliative interactions initiated by a third party to an individual in distress during a PC or PD, usually involving physical contact and being interpreted as other-oriented and empathy-driven, from the perspective of the third party (or bystander, Clay & de Waal, 2013a; de Waal & Yoshihara, 1983). In contrast, if the victim initiated the contact, it was labelled as a *solicited consolation*, a behaviour that is then not interpreted as empathy-driven from the bystander's perspective as not spontaneous (Verbeek & de Waal, 1997). As I relied on videos, I sometimes adopted the video narrator's expert opinion on this criterion when the video was unclear. The narrators were well trained and had a better visual appreciation of the situation than me. The duration taken for a bystander to offer consolatory behaviour to the victim was recorded. *Reconciliation*, defined as affiliative contact between former opponents that could be initiated by the aggressor or by the victim (Kempes et al., 2013), was also recorded but not included in this thesis as I was focusing on empathy-driven behaviours from the bystander. Therefore, I divided PCs into four categories: PCs with 1/ no affiliation, 2/ only consolation, 3/ only reconciliation, and 4/ both reconciliation and consolation. For both consolations and reconciliations, the start and end time, the initiator (i.e., approaching individual) and recipient of the contact, the type of contact (see Table 2.2), and the recipient's response (engage, passive, avoidance) were coded. For the bonobo data only, I classified the nature of the affiliative behaviours given by a bystander in two groups of patterns: sexual and non-sexual behaviours.

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[4] https://archive.mpi.nl/tla/elan

Table 2.2 Ethogram of affiliative bystander contacts for sanctuary-living bonobos (adapted from Clay and de Waal 2013b)

Behaviour	Description
Sexual behaviours	
Genito-genital contact	Individuals embrace ventro-ventrally and swing their hips laterally while keeping their vulvae in contact
Mount	The individual makes lateral contact of their genitals behind the recipient and thrusts their pelvis onto the recipient's behind/back area
Genital touch	Touching the genitals of the recipient using any body part other than genitals (i.e., using hand/foot to touch recipient's genitals)
Copulation(1)	Penile intromission and hip thrusting with a male or female partner
Non-sexual behaviours	
Embrace	Individual places one/both arms around the recipient's body while facing the partner or in lateral position (includes clinging to the back of another individual)
Touch(2)	Any instantaneous soft touch to the recipient's body, other than to their genitals, using any body part other than the actor's genitals
Groom(2)	Directed cleaning/touching/visual inspection of the recipient's hair/skin
Contact sitting(2)	Sit in physical contact with the recipient
Hold(2)	Grasp/hold onto the recipient's body with one or both hands. Generally, when the recipient is walking or standing
Pat(2)	Pronounced tapping/patting contact onto recipient body using a flat hand
Inspect(2)	Visual and contact inspection of the recipient's wound or injured body part, after a conflict
Play	Individuals wrestle/run/jump/chase/tickle in physical contact accompanied by play face and/or laughing

(1) In case of doubt of occurrence of copulation (i.e., unclear if intromission occurred), this behaviour was coded as 'mount' instead. (2) These behaviours were then classified as "directed contact and touch".

2.2.2.2 Victim recovery time

I measured the time taken to recover as the latency to cease expressing any unprovoked victim response behaviours throughout the 5 min recording, after the initial conflict or distress (Baker & Aureli, 1997; Castles et al., 1999; Kutsukake, 2003).

Furthermore, I looked at the victim's degree of emotional arousal as a victim in *Chapter 4* following the ethogram below (Table 2.3).

Table 2.3 Ethogram of the bonobo victim's emotional distress

Behaviour	Description
Self-directed behaviours	
Self-scratching	The individual scratches a part of their own body with one or several of their finger(s) with a "go and back" movement
Self-touching	The individual touches a part of their own body with no movement
Self-grooming	The individual inspects their own body with their fingers while looking at the body part
Others*	
Coprophagy	The individual eats their faeces
Head shake	The individual repeatedly moves their head up and down or side to side
Hair plucking	The individual plucks their own hair from a part of their own body with their fingers

* These other behaviours were not observed in the chimpanzees of this study

2.2.2.3 Aggressive interactions

Aggressive behaviours and conflict intensity. I also coded the types of aggressive behaviours and conflict intensity, ranging from *low/medium* to high. Low/medium included threat (handshake, bipedal swagger threat/whistle bark, lunge), chase without physical contact, low contact aggression (e.g., quick poke/shove or push). High included: single grab/hit/slap, severe/multiple grab/hit or biting (adapted from de Waal 1988). In the case of a PD, there was no aggression type.

Redirected aggression. I coded the time of occurrence, type of aggression, and the identity of the recipient of *redirected aggression,* defined as aggressive behaviour by the victim towards a bystander after the initial conflict or tantrum, within a PC or PD leading to victim response behaviour of the recipient.

Renewed aggression. I coded the time of occurrence, type of aggression, and latency from the initial conflict of renewed aggression, defined as additional aggression by the same aggressor towards the victim after the initial conflict within the same PC.

2.2.3 Age classes

Previous ape studies on post-conflict affiliations considered three age classes (i.e., infant, juvenile, and adult, Cordoni et al., 2006; Fraser et al., 2008; juvenile, adolescent, and adult, Clay & de Waal, 2013a, 2013b) and showed developmental differences in the age-groups below and above 8 years of age. To confirm and investigate these findings further, subjects of this thesis’ studies (*Chapters 3* and *4*) were divided into two age classes: below and above 8 years old.

2.3 Assessing arousal via physiological changes with InfraRed Thermography (IRT)

2.3.1 IRT equipment

In *Chapter 4* and *Chapter 5*, I[5] used an infrared thermal camera (T530, FLIR, Stockholm, Sweden; a temperature sensitivity <40 mK, an IR resolution of 320 x 240 pixels, Accuracy (drift): ±0.3°C) to record the face of the participants with a 29mm Lens Field of View (FOV, 14° x 10° - FLIR T199588 Tele 14° Lens). The IRT camera was on a tripod at about 1 to 1.3 metres from the subject and aimed at the subject's face. I adjusted the angle and position of the IRT camera in real-time according to the movement of the subject. A high-definition camcorder (Panasonic HC-V770) recorded the subject's behaviour during the trial. I displayed the video stimuli on a 13" screen from a Dell laptop (maximum brightness and volume 60) placed at about 1 to 1.3 metres of the subject at eye height.

I used 'FLIR tools' software[6] to process the thermal videos recorded and measure the temperature of the four regions of interest (i.e., ROI; peri-orbital PO, nose bridge NB, nose tip NT, upper lip UL – Figure 2.1). More information about the choice of ROIs is provided below.

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[5] In order to acquire the theoretical background necessary to conduct thermography studies, I attended a workshop on Infrared Thermography in Newcastle (January 2018). I also obtained the Certificate of Technical Achievement from Teletherm Infrared Systems and Research for successfully completing the Teletherm instructional program and examination on the science and application of infrared thermal imaging for use in Veterinary clinical practice (http://www.thermology.com/veterinary_infrared_training.html) in April 2019.

[6] https://www.flir.co.uk/products/flir-tools/

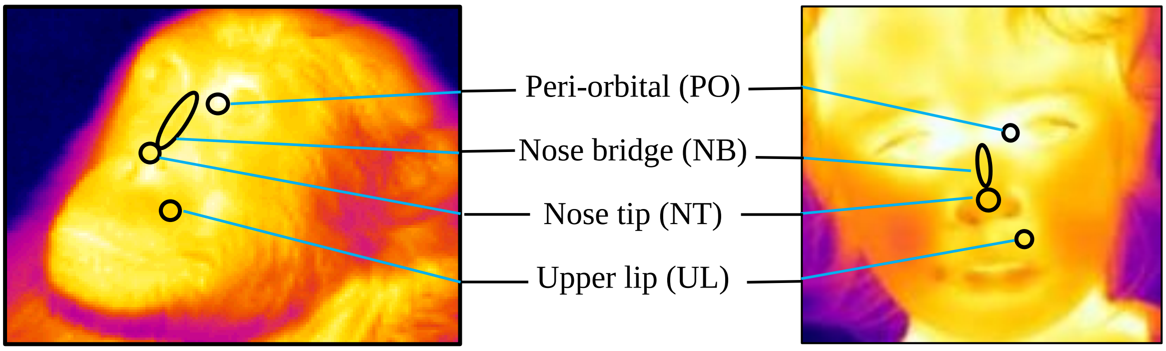

Figure 2.1 The four facial regions of interest I used in my infrared thermography experiments with the chimpanzees (*Chapter 4*) and with the children (*Chapter 5*) – with permission

I used an annotation tool for audio and video recordings called ELAN software[7] (Version 5.9 - Computer software, 2020 - Nijmegen: Max Planck Institute for Psycholinguistics, The Language Archive), to code the behavioural responses of children during the experiment (e.g., Lausberg and Sloetjes 2009).

As thermal responses can be sensitive to fluctuations in ambient temperature and humidity, the room/ambient temperature and relative humidity should be constant and, whenever possible, set at a value that allows thermoneutrality. To control for this, I monitored the temperature and humidity of the place/room at least every minute throughout the experiment, with an LCD digital psychrometer temperature and humidity meter with dew point and wet bulb temperature hygrometer (Preciva, Resolution 0.01%RH, 0.01 °C/0.01 °F – see *Appendix 2.1*) to control for variation, something which was entered into the analyses.

2.3.2 IRT: Technicalities, experimental settings and controls

As expanded upon in *Chapters 1*, *4* and *5*, IRT is a relevant emerging method to investigate how physiological processes modulate emotion. Moreover, due to its non-invasive nature, IRT

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[7] https://archive.mpi.nl/tla/elan

can be applied in more naturalistic contexts enabling comparative research. However, although there seems to be extensive potential in the use of infrared thermography, many questions remain as to what extent this technology can reliably address developmental and evolutionary questions about the origins of emotions. In this section, I detail the technicalities of the infrared thermography technology and present the settings and controls of IRT experiments, based on the work conducted for this thesis.

The IRT camera can detect and measure infrared radiation naturally emitted by an object, including a living subject. It then converts that infrared data into temperature values and an electronic image, i.e., a *thermogram*. Studies looking at skin temperature changes started developing protocols to obtain the representative temperature value of face and body regions of interest, (ROIs) from thermographic images individually captured or extracted from thermal videos and then processed with dedicated software (e.g., FLIR tools). Temperature measurements have mainly been conducted on the nasal area, the periorbital region, the upper lip, and the forehead (Chotard et al., 2018; Ioannou et al., 2014; Kano et al., 2016) where major vessels affect the subcutaneous temperature of the ROI, allowing the detection of subtle temperature change (Ioannou et al., 2014). The impact of anatomical factors, including various types of subcutaneous tissues (e.g., fat and muscular tissues) and irregularities on the surface of the skin (e.g., hair, scars, moles) of these facial ROIs is rather limited but can influence the thermal results (Merla et al., 2010).

The skin temperatures of different facial ROIs may vary in opposite directions following a given stimulus and within the same time window (Dezecache et al., 2017; Ioannou et al., 2016; Levine et al., 2001). This is because different regions of the facial skin show different blood vessel networks and consequently are exposed to unique physiological processes (Ioannou et al., 2014; Kreibig, 2010). Therefore, infrared thermography analyses based on the variation of facial skin temperature could benefit from the inclusion of several ROIs (Chotard et al., 2018).

Some studies have calculated the average temperature value of all the pixels included inside a selected ROI (Chotard et al., 2018), while others have identified and reported the temperature value of the warmest and/or coolest pixel (and neighbouring pixels) in the ROI (Kano et al., 2016). This latter protocol allows controlling for the uneven thermal distribution inside the ROI, resulting from the asymmetrical subcutaneous blood network and its inter-individual variability, as well as the methodological inconsistencies of potential manual fluctuations when selecting the optimal size and position of ROI in each frame (Kano et al., 2016). The influence of airflow patterns (for nasal skin temperature measurements) can be prevented/controlled by meticulous coding criteria (Kano et al., 2016).

During an IRT experiment, the infrared (IR) camera is placed between 0.5 and 3 metres from the subject to maximise the capture of ROI pixels. This distance depends on the sensitivity and resolution of the IR camera and lens. Contactless and wireless, the IR camera should not interfere with a subject's behaviour any more than a normal camera (Anbar, 2002; Head & Elliott, 2002; Kastberger & Stachl, 2003; Pavlidis et al., 2012; Vianna & Carrive, 2005). Ideally, the room temperature and relative humidity should be constant during the recording and, whenever possible, set at a value that allows thermoneutrality. The subject should be introduced to the testing space and allowed to acclimatise for at least 10 minutes before the commencement of recording (Kano et al., 2016).

Variation in blood flow linked to physical activity can impact the measurement (Nakanishi & Imai-Matsumura, 2008). Therefore, when working with un-constrained subjects, it is possible to minimise movement and attract them to the testing station by offering a limited amount of food rewards– however, this needs to be controlled for as food consumption can lower the nasal skin temperature (Chotard et al., 2018; Ioannou et al., 2015; Kano et al., 2016; van Baak, 2008). Working with wild animals in an ecologically valid environment calls for close monitoring of environmental and social conditions (e.g., Dezecache et al., 2017). Compared to other physiological measures, the facial temperature change is relatively slow, sometimes as long as 2 minutes following stimuli onset (Kano et al., 2016).

In conclusion, IRT is a valuable but still novel tool for psychophysiological monitoring. Coupled with other methods, IRT can provide valuable insights into the field of emotion and cognition research. It has also highly developed in the fields of animal welfare and veterinary research (Church et al., 2009), and shows promising applicability in the field of animal well-being (McManus et al., 2016).

2.3.3 Development of a new data extraction method for IRT data

In collaboration with Prof Camila Caiado from the Department of Mathematical Sciences at Durham University, we used R (version 3.6.3; R Core Team 2020) and Spyder[8] (version 3.3.6; The Scientific Python Development Environment) software to create a novel way to extract IRT data by continuously tracking a selected set of pixels for each ROI then extracting the temperature for every frame. The equipment used to collect the IRT data is provided in the section above.

In order to validate this method of thermal imaging analysis, I first identified the cleanest possible thermal footage from my dataset of a typically developing child recruited as part of my developmental study outlined in *Chapter 5* (17 girls; age range: 1.1 - 3.0 years old, mean = 2.0 years-old; SD = 0.5). As outlined in *Chapter 5*, data were collected from a day-care British nursery in the north-east of England during my experimental paradigm. I selected the trial with the least physical movements of the child and where the child was mostly facing the camera. The colour map in the FLIR software was manipulated to optimise the identification of the ROI

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[8] https://www.spyder-ide.org/

by the tracker. The nasal area was the only ROI that was reliably tracked by the tracker (Figure 2.2).

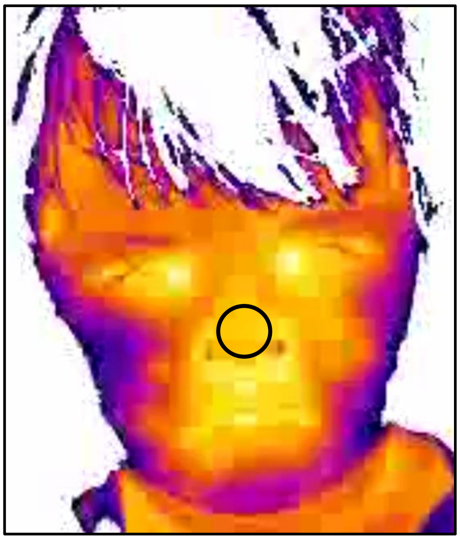
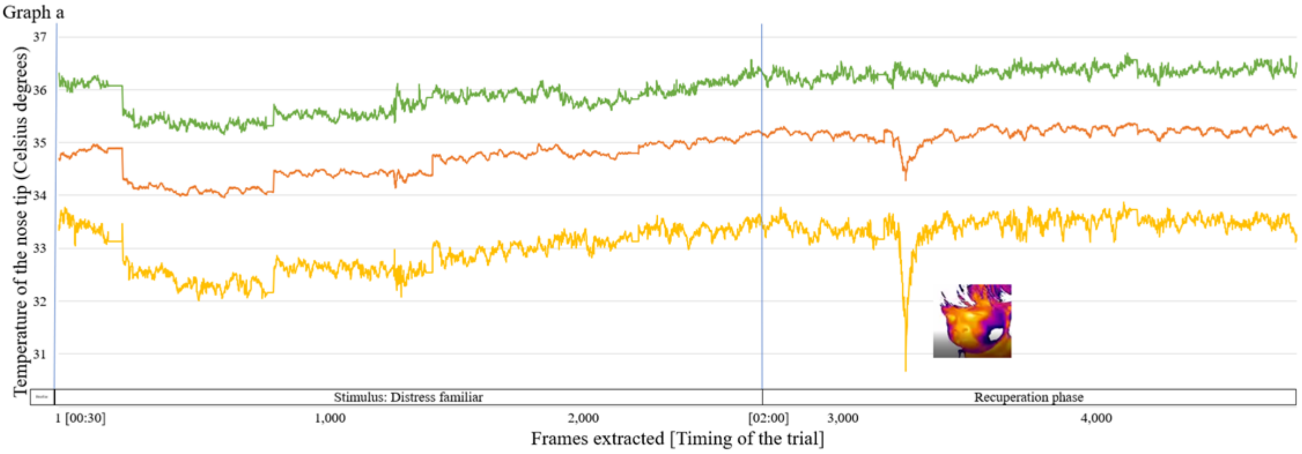


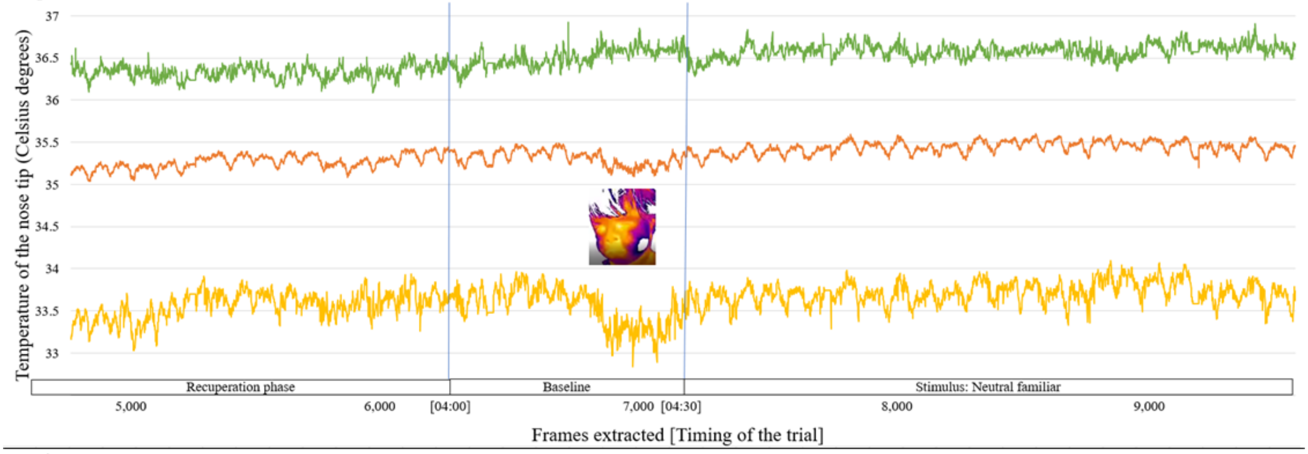
Figure 2.2 Screenshot of the IRT video used with the automated tracker (programmed in Python and R). The circle represents the ROI selected, i.e., the nasal area.

In order to examine the profile of the thermal response, data were extracted for the full duration of the trial. The only exclusion was the first 27 seconds of the video that were cropped because the child moved their head, leading to a loss of the tracker. The main programming functions/algorithms and a *step-by-step* methodology to extract the IRT data are provided in *Appendix 2.2*. A visual/qualitative representation of the data is provided in Figure 2.3. The pixels associated with a temperature below 30.0 Celsius degrees were excluded to prevent misreads.

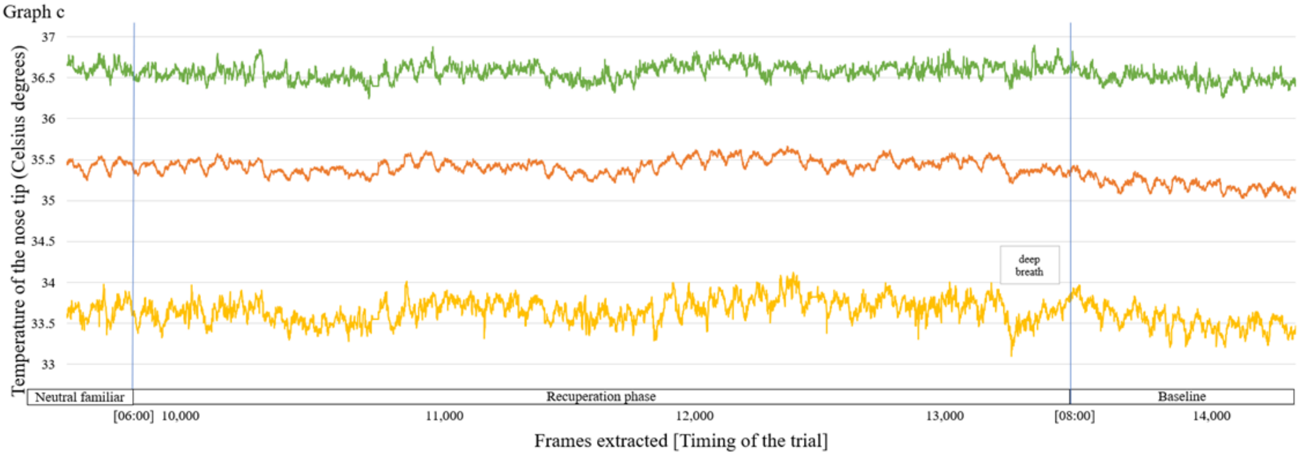
Graph a



Graph b



Graph c



Graph d

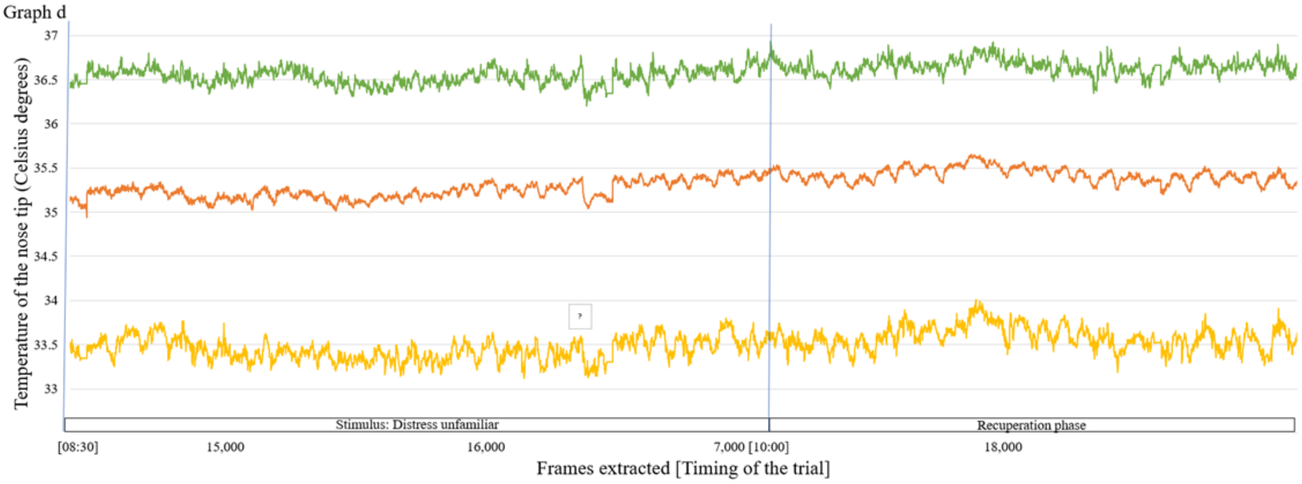


Figure 2.3 Graphic representations of the nasal skin temperature in Celsius degrees, as a function of the frames extracted during the trial and the timing of the trial (under brackets). The different phases of the trial are indicated in boxes. When a pattern stood out, I referred to the video to identify the cause of the temperature variation – usually due to a movement of the head. The colour code is as follow: Mean, Minimum, Maximum. Because of the huge amount of data included, a total of four graphs was required (graphs a, b, c, and d).

The qualitative representation of the *frame-by-frame* IRT data (Figure 2.2) shows that the thermal profiles obtained from this novel automatic temperature extraction method are rather noisy and difficult to interpret. Indeed, the temperature of the ROI varies following what seems to be a pattern that might be linked to the typical temperature variation of the facial skin of the ROI. I discuss this further in *Chapter 6*.

A recent study has based the thermal data extraction on a similar marking and tracking concept, for instance by using a MATLAB (R2018b) script (Brügger et al., 2021).

2.4 General protocols for statistical analyses: Generalised Linear Mixed Models (GLMMs)

I conducted all statistical analyses in R (version 3.6.3; R Core Team 2020). I employed Generalized Linear Mixed Models (GLMMs) for the main analyses of this thesis. To compute the GLMMs, I used the functions *lmer* and *glmer* (version 3.1-1) of the R package *lme4* (version 1.1-25; Bates et al., 2012, 2015), along with the optimizer “bobyqa” to improve model fit.

GLMMs are an extension of linear mixed models to allow for different types of response variable distribution, including Gaussian (e.g., relative temperature changes) and binomial (e.g., presence/absence of a given behaviour), that I use in this thesis. Furthermore, mixed-effects models account for both within-subject and across-subject variability and allow for dealing with data with several sources of random variability by including them into the models (i.e., random factors, Mundry, 2019; Sun et al., 2000). Therefore, GLMMs are an ideal tool to deal with the kind of data of this thesis that include repeated measurements per individual taken over different events occurring within a given time period (e.g., PC/PD and experimental trials, Mundry, 2019).

Model diagnostics. Before assessing model fit for any model, I first assessed model stability by using *glmm.model.stab* from *glmm_stability.r* (script by R. Mundry, with permission). This function derives estimates and standard deviations for data excluding levels of the random effects one at a time. The models assessed were defined as stable when no convergence issues were revealed (i.e., optimizer (bobyqa) convergence code: 0 (OK)).

Next, I visually checked the data distribution by plotting a histogram of the raw data. For all the models mentioned, I also visually inspected the distribution of residuals to confirm no severe violation in the assumption of normal distribution and homoscedastic residuals, by inspecting a histogram and a ggplot of residuals, as well as the residuals plotted against fitted values using the R function *diagnostics.plot* from *diagnostic_fcns.r*. Furthermore, I also checked the absence of collinearity among predictors (Queen et al., 2002), by inspecting Variance Inflation Factors (VIF, Field 2005) with the R function *vif* (version 1.0) in a package *car* (version 3.0-10; Fox et al. Package 'car', 2017) for the models excluding the random effects.

Full-null model comparison. As a test of a given model's overall predictive capacity, I compared each full model with a respective null model (Forstmeier & Schielzeth, 2011), which excluded all fixed effects and only kept the random factors and control variables (R function *anova* with argument test *Chisq*, Dobson and Barnett 2018). Only when the full model could explain the data significantly ($P < 0.05$) better than the null model, did I examine the contribution of fixed effects in the model (Forstmeier & Schielzeth, 2011; Mundry, 2014), using the R function *drop1* from the *lme4* package (Barr et al., 2013). The function *drop1* drops one factor at a time and compares the possible resulting model with the full model. When a full-null model comparison involving an interaction revealed non-significance, I ran the full-null model comparison again without the interaction. If this was not significant, only the values of the first comparison were reported. All p-values were two-tailed with alpha < 0.05.

Data interpretation. Throughout the thesis, I discuss the results of the models that were close to significance. That is because the data used in the thesis were sometimes noisy, particularly the physiological data, and the limit of $p < 0.05$ is still debated. Therefore, trends (e.g., $p < 0.09$) were highlighted and those that were particularly promising on a theoretical level were discussed, in particular when there were not many other significant results to discuss.

Chapter 3 Consolation across the age spectrum in sanctuary-living orphaned and mother-reared bonobos

3.1 Abstract

A core feature of empathy is sympathetic concern, which is concern about another's state and attempts to ameliorate this state. Consolation is considered a marker of sympathetic concern, whereby bystanders of social conflicts spontaneously approach distressed victims to offer friendly contact. Consolation has been demonstrated in human and non-human animals (henceforth animals), including great apes, suggestive of its deep evolutionary roots. Nevertheless, our understanding of the development of empathy in animals, particularly how consolation might change with age and social experience, is still extremely limited. For this study, I used archival recordings of post-conflict situations in order to investigate behavioural empathic responding across the age spectrum in bonobos (*Pan paniscus*), our closest living relatives. I systematically observed and analysed consolation and distress behaviours of N = 65 bonobos from across the age spectrum living at Lola ya Bonobo sanctuary (LYB) in DR Congo across two time periods (2012 and 2016), using a cross-sectional approach. I tested the main hypothesis that although immature and mature individuals may display comparable overall consolation patterns, their efficiency in alleviating their distress and their social awareness differ according to developmental constraints. Therefore, I predicted that, as compared to younger bonobos, older bonobos are more efficient in alleviating the distress of another (**effectiveness hypothesis**) and are more targeted in consoling socially-close individuals (**selectivity hypothesis**). I also predicted that younger bonobos, who may lack inhibition skills, are quicker to offer consolation, as compared to older bonobos (**latency hypothesis**). I also expected that the behavioural repertoire of consolation is broader in young bonobos who may offer non-sexual consolatory behaviours, including paedomorphic behaviours such as embrace, before becoming more specialised in older bonobos (**use and size of the consolation repertoire hypothesis**). Finally, I predicted that the more a mother consoles, the more her offspring consoles as well (**consolatory tendency hypothesis**). As LYB houses both orphan and mother-reared bonobos, I investigated the impact of rearing on the development of socio-emotional functioning. In contrast to my predictions, mature bonobos were not more efficient in alleviating the other's distress, nor were they more selective towards closely bonded partners as compared to immature bonobos. Results also indicated that mature bonobos tended to be faster than immature bonobos to console, and mother-reared bonobos tended to be faster than orphan bonobos to console. Then, there was developmental variability in the consolatory repertoire, with immature bonobos more likely to offer non-sexual consolatory behaviours versus adults, who were more likely to offer sexual ones. This was particularly true for the mother-reared individuals and directed towards kin (offspring and their mothers). I examined in particular the *embrace* behaviour, which was more characteristic of immature consoler than adults, supporting the notion that the *embrace* consolation gesture is likely an extension of the offspring's own early experience of being nurtured by its mother. Finally, there was no relationship between mother and offspring consolation tendencies. By directly investigating the effectiveness, selectivity, reaction time and rearing effect, as well as the nature and scope of consolation across age, this project sheds new light on the mechanisms of other-oriented behaviours as they develop in our closest living relatives, providing insights into the evolutionary and developmental origins of empathy.

Keywords: empathy; prosociality; kinship; trauma; development; Primates

3.2 Introduction

3.2.1 Consolation in primates and other animals

Empathy, the sharing and understanding of others' emotional states (de Waal & Preston, 2017), is a core feature of what it means to be human. One established form of empathy is **consolation**, defined as an unsolicited bystander affiliation to an individual in distress (Clay & de Waal, 2013b; de Waal & van Roosmalen, 1979). Offering consolation is thought to imply that bystanders perceives the emotional state of another individual and provides the appropriate response to reduce their distress (Fraser et al., 2008; Palagi & Norscia, 2013; Romero et al., 2010). Among primates, consolation has been reported in humans (Zahn-Waxler & Radke-Yarrow, 1990), bonobos (Clay & de Waal, 2013a, 2013b; Palagi & Norscia, 2013), chimpanzees (Fraser et al. 2008; Romero and de Waal 2010), and Tonkean macaques (*Macaca tonkeana*: Palagi et al. 2014), a species of monkeys known for their high degree of tolerance (Ciani et al., 2012; Matsumura, 1999), as well as captive barbary macaques *(Macaca sylvanus*: McFarland & Majolo, 2012). In contrast, consolation was reported as absent in other species of macaques (*Macaca mulatta*: Matheson, 1999; *Macaca fuscata*: Palagi et al., 2014), as well as in two species of lemurs (*Lemur catta* and *Eulemur fulvus rufus*: Kappeler, 1993). Therefore, consolation is not ubiquitous in the primate lineage, suggesting that its underlying cognitive and emotional capacities might vary between species. Consolation has also been reported in elephants (*Elephas maximus*: Plotnik, 2014), bottlenose dolphins (*Tursiops truncatus*: Yamamoto et al., 2015), corvids (*Corvus corax*: Fraser & Bugnyar, 2010), and rodents (prairie vole, *Microtus ochrogaster*: Burkett et al., 2016). More details about empathy and consolation are provided in *Chapter 1*.

To date, our understanding of the development of empathy in animals is still limited. Recent studies have demonstrated basic homologous patterns in the early emotion responses of children (Davidov et al., 2013), chimpanzees (Webb et al., 2017) and bonobos (Clay & de Waal, 2013a, 2013b), as well as later in life. However, in-depth insights remain outstanding, in particular, whether more complex forms of empathy develop in tandem with other skills and/or social experiences in apes, as they have been shown to in humans. Data on juveniles suggest that although the cognitive components of empathy develop over time, advanced cognition may not be essential for the expression of concern. Furthermore, although consolation is offered by both immature and mature great apes (Clay & de Waal, 2013a, 2013b; Webb et al., 2017), it remains unresolved whether they differ and the extent to which it is affected by early experiences.

3.2.2 Early deprivation: A barrier to empathy and emotion regulation development

Primates are characterised by a long period of maternal dependence. As a consequence, disturbances in early caregiving or maternal deprivation are expected to impact diverse aspects of development. In line with these assumptions, research has consistently highlighted the importance of early experience in the development of socio-emotional skills in humans (Moulson et al., 2009; Tottenham, 2014) and non-human primates (Parker & Maestripieri, 2011; Rosenblum et al., 1994; Suomi et al., 1975). Particularly, the species-typical adult patterns of behaviour are highly dependent on the early development of positive social and emotional relationships. Disruption in the formation and development of reliable social relationships can have negative effects on the development of social, emotional and cognitive functions in human (Moulson et al., 2009) and nonhuman primates (French & Carp, 2016).

Empirical primate research from the 1960s and 1970s highlighted that chronic disruption of the mother-infant bond and social deprivation disrupts development and triggers psychopathology (Harlow et al., 1965, 1971; Mason, 1960; Seay & Gottfried, 1975). Seminal studies by Harlow and colleagues (Harlow, 1965; Harlow et al., 1971) on rhesus macaques showed important long term behavioural alterations when infants are separated from their mothers and peers at birth and are reared in tactile isolation (but with auditory, visual and olfactory contact with peers) for a minimum of six to twelve months. These alterations include autistic-like behaviours, poor social abilities, increased aggressiveness, and inappropriate sexual behaviour (Harlow et al., 1965). The consequences are even more drastic under more severe social limitations. The first six months of life for a rhesus macaque are critical for the typical development of social, emotional and cognitive abilities. This period is also critical for neurobiological development (Kraemer, 1992). Similar patterns have been shown with great apes, notably chimpanzees (Bogart et al., 2014; Davenport et al., 1973; Morimura & Mori, 2010). In a comparison of age-matched mother-reared and orphaned juvenile bonobos, Clay and de Waal (2013b) showed that orphans scored higher on anxiety and lower on a metric of sympathetic concern than mother reared subjects, as indicated by lower rates of consolation.

Unlike in primates, where most of the evidence of the effects of early adversity is derived from experimental research, for humans, most of the empirical literature comes from nonexperimental data (Sánchez et al., 2001). Social deprivation studies have been based on poorly run orphanages where children suffered deprivations in social and emotional care at an early stage (Chisholm, 1998; Kaler & Freeman, 1994; Rosenberg, 1992). Children raised in such deprived settings develop atypical behaviours, as well as cognitive and emotional deficits comparable to those of nonhuman primates who grew up under comparable settings and conditions, e.g., low socio-emotional abilities, including sympathetic concern and emotion regulation (Hodges & Tizard, 1989; De Bellis, 2005; Beckett et al., 2006; Tottenham et al., 2010). Particularly, it has been reported that many of these children present deficits in attention, cognition, and language acquisition, with variations at a neural level (Bick & Nelson, 2016; McLaughlin et al., 2014; Pollak et al., 2010; Sheridan et al., 2012) leading to lasting socio-emotional disruption. Nonetheless, adapted care and attention at a later stage can alleviate these consequences (Hodges & Tizard, 1989).

Emotion regulation is also impacted by social deprivation. Indeed, a lack of coordinated activity (in relation to the PAM, de Waal & Preston 2017; Preston & de Waal 2002), early in life between an infant and its caregiver may lead to behavioural issues linked to an inability to evaluate and regulate emotions, leading to limited impulse control, emotional outbursts and risk-taking (Tronick, 1989). This has been termed under/over-regulation and mis/dys-regulation (Baumeister & Heatherton 1996). Failure to contain one’s emotions or exerting self-control in a counter-productive way can lead to difficulties with engaging in goal-directed behaviour, hence can be considered maladaptive (Aldao et al., 2010; Fischer & Munsch, 2012). For instance, it is linked to externalising behaviour problems in school-aged children (Eisenberg et al., 1996). Therefore, I also investigated the role of rearing experiences on the development and expression of empathy-related behaviours.

In this study, I used systematic observations of post-conflict and post-distress contexts to investigate how consolatory responses develop with age in sanctuary-living bonobos, considering the effectiveness, selectivity, and nature of the consolation response across the age spectrum, as well as the impact of rearing, along with the impact of mother’s empathic tendencies. In this way, the current study extends Clay and de Waal's work (2013b) which examined empathic responding in orphan and mother-reared bonobos.

I tested the main hypothesis that although immature and mature individuals may display comparable overall consolation patterns, their efficiency in alleviating their distress and their social awareness (i.e., of the victim’s social closeness) differ, as a function of developmental constraints in social and cognitive skills. Therefore, I expected age-related changes in the effectiveness, selectivity and speed of the consolation. I also expected differences in the use and size of the behavioural repertoire of consolation in the bonobos, reflecting evidence that consolation may change across the development. Below, I discuss my hypotheses and predictions further.

3.2.3 Effectiveness of consolation

Among humans, we see both effects of early developmental experiences and apparent gender differences in empathic responding. Children with troubled early experiences have difficulties with regulating their own distress (Pollak et al., 2005), which can impact their ability to offer comfort to others. Among adults, women usually outperform men in emotional tasks and underlying empathic abilities (Hall et al. 2000; McClure 2000; Schulte-Rüther et al. 2008; Christov-Moore et al. 2014 for reviews). Early experiments on monkeys highlighted that early adverse experiences impact the development of socio-emotional skills (Harlow, 1965), and in a naturalistic study, orphan bonobos scored higher on anxiety and lower on a metric of sympathetic concern than mother reared subjects (Clay & de Waal, 2013b). In adult apes, female chimpanzees (Romero et al., 2010) and gorillas (Cordoni et al., 2006) are more likely to offer consolation than males. Other factors may be critical when explaining a victim’s recovery after a distress. This is the case for the quality of the relationship between consolers and recipients, as well as the characteristics of the recipients themselves, for example, mother-reared juveniles recover sooner than orphan juveniles when victims themselves (Clay & de Waal, 2013a).

Therefore, I examined latency for victims to recover in order to test the prediction that consolations offered by older bonobos, with presumably more experience and technique in consolation, will correspond with quicker decreases of victim self-distress behaviours, as compared following consolations offered by younger bonobos. I also predicted that, as compared to mother-reared subjects, orphans will be less effective at consoling others, due to adverse consequences of their early life experiences on the development of their social and emotional skills (Clay & de Waal, 2013b; Harlow, 1965). Building on the literature, I investigated sex differences in the efficiency to alleviate others distress. I predicted that female bonobos will be more effective in providing an efficient consolatory contact, i.e., a contact that is more effective in alleviating another's distress, as compared to males. Finally, I investigated whether the nature of the contact impacts the recovery of the individual being consoled. I predicted that socio-sexual consolatory contacts – as compared to non-sexual contacts - will be more effective at consoling others due to their importance for group bonding in bonobos communities (Clay et al., In press). I controlled for the quality of the relationship between consolers and recipients, as well as the characteristics of the recipients themselves in the analyses.

3.2.4 Selectivity of the consolation

Considered as an extension of the mother-offspring bond shared across mammal species (MacLean, 1985), empathy is biased towards socially close or familiar individuals (Preston & de Waal, 2002). Consolation is correspondingly predicted by social closeness in primates, being strongest among kin, followed by socially close partners, and weakest among social-distant or unfamiliar individuals; this is known as the *empathy gradient* (Fraser et al., 2008a; Romero et al., 2010; Clay & de Waal, 2013b; Palagi & Norscia, 2013). This selectivity would be expected to increase with age along with social skills, including the ability to identify relevant social partners (in children: Hamlin et al., 2007; in bonobos: Krupenye & Hare, 2018). However, to what extent this selectivity towards socially close individuals increases with age is still to be explored. In a previous study conducted at LYB, juvenile bonobos who scored higher on measures of socio-emotional skills were more likely to offer consolation (Clay & de Waal, 2013a), suggesting that such skills are crucial to empathic responses. Social awareness and cognitive control over empathic-responding behaviours develop across age (Clay & de Waal, 2013a, 2013b; Cordoni et al., 2006; Webb et al., 2017). I expected that older subjects will respond more selectively to the distress behaviours of familiar individuals in comparison to less familiar individuals, with this difference being less strong in younger subjects who will respond more broadly.

3.2.5 Impact of mother's empathic tendencies

Bonobos, like all great ape species, have a prolonged immature period (Pereira & Fairbanks 2002). Thus, the infant has an extended and strong affiliation with their mother (Hoff et al., 1981; Plooij, 1984; Van Lawick-Goodall, 1967) who is their first and most influential bonding partner. Indeed, mothers support the development of the foraging abilities of their offspring in orangutans (Bard, 1992; Jaeggi et al., 2010; Van Schaik, 2004) and chimpanzees (Hirata & Celli, 2003; Lonsdorf, 2006). They are the most significant communication partner (Plooij, 1984; Schneider et al., 2012), and also play a crucial role in their offspring's socialisation process (King, 2004; Maestripieri & Call, 1996). Immature great apes learn both individually across development as well as through observing their mother (e.g., Hirata & Celli, 2003) and other members of the social groups (Cavalli-Sforza & Feldman, 1981). Given the importance of the mother-offspring bond, I was interested to examine the role this plays in her offspring's empathic development. Correspondingly, I expected a positive relationship between the empathic tendencies of a mother and her offspring(s). I expected both offspring of mothers with high empathic tendencies (in term of offering consolation) to show more empathic tendencies themselves, than those with mothers expressing lower empathic tendencies.

3.2.6 Latency and order of the consolation

The speed/delay of the consolatory behaviours is defined as the time between the onset of the distress/conflict and the offering of consolation by a bystander. If immature individuals learn socially from the behaviours of other group members, I expected that younger individuals might copy the consolations of others i.e., they would follow an initial consoler instead of being the first one to console. In this scenario, younger individuals are expected to be slower at reaching out to the distressed individual. However, if consolation is more of an "automatic" affective response, therefore less contingent on cognitive appraisal and self-regulation, I expected that younger individuals – who show poorer executive functioning skills, including inhibition-would be quicker at displaying consolatory behaviours than older individuals.

3.2.7 Development of a consolatory repertoire

In chimpanzees, the size of the gestural repertoire varies at different ages, with the greatest size found in the juvenile period and decreasing in adulthood (Hobaiter & Byrne, 2011). Yet, in that case, the gestural repertoire size was closely related to the number of gestures recorded per individuals. As bonobos grow older, I predicted that the nature or repertoire of the consolatory behaviour will change. The consolatory behaviours used by a bystander towards the victim of a conflict can be divided into two main categories: non-sexual and socio-sexual (Clay & de Waal, 2013b). Socio-sexual contacts appear early in the behavioural repertoire of immature bonobos, who use them predominantly during playful and other relaxed contexts (Hashimoto, 1997), but also start experiencing them in distressful situations, including following conflicts (de Waal 1987; Kano 1992; Furuichi and Ihobe 1994; Clay and de Waal 2013b; and Clay et al. in prep. for a review). Therefore, I expected younger individuals to use more non-sexual behaviours than socio-sexual ones when offering consolation to individuals in distress. This trend/distinction may not be salient anymore in bonobos reaching sexual maturity who developed their socio-sexual patterns of behaviours.

Furthermore, the “embrace” behaviour – described as when an individual puts one or both arms around the recipient’s body while facing the partner or in lateral position (as stated in *Chapter 2*)- is a behaviour commonly used by bonobos to console their peers (Clay & de Waal, 2013b). This behaviour is generally assumed to be a paedomorphic – or juvenile-like- behaviour, recalling the way infants and juveniles approach and get in contact with their mothers from birth, via clinging on to her fur (Anvari et al., 2014; Nakamichi & Yamada, 2009; Ross, 2001). In LYB, orphan juveniles also cling to surrogate human mothers at the sanctuary, a behaviour which may have thus been reinforced in this population. Such ventro-ventral embraces are also the step towards the first sexual experience young bonobos might encounter, as their mothers initiate genito-genital contacts in distressing situations such as following a conflict (Clay et al., In Press.; Hashimoto, 1997). Therefore, I expected consolatory embrace to be more common by younger individuals and mainly towards closely bonded partners. Finally, the nature of the consolatory behaviour offered by the consoler may depend on the age of the individual being consoled, with more paedomorphic behaviours offered to young individuals and more sexual behaviours offered to mature individuals by mature individuals – suggesting that the consoler is aware of the age of the individual in distress and therefore adapts their consolatory strategy.

I also predicted that younger individuals will show a broader consolatory repertoire overall than older individuals, these latest getting more “specialised” in the way they console, whilst the younger ones are still exploring how to console appropriately.

3.3 Methods

3.3.1 Ethical statement

The current study (and the pilot data collection conducted in 2018) was approved by the Psychology department and Ethics committee as well as the Animal Welfare Ethical Review Board (AWERB) at Durham University (UK). The data collections (2012 and 2016) were approved and carried out in strict accordance with the rules and requirements of the Scientific Coordinator and Scientific Committee of "Les Amis des Bonobos du Congo" (www.friendsofbonobos.org). The data collection from 2012 was financially supported by the Living Links Center of the Yerkes National Primate Research Center and Emory University's College of Arts and Sciences. The data collection from 2016 was financially supported by the John Templeton Foundation and approved by the ethics committee of the University of Utrecht, Netherlands.

3.3.2 Study site and subjects

This study was based upon an archival dataset amassed from observations that were conducted at Lola ya Bonobo sanctuary (LYB) in the Democratic Republic of the Congo during two time periods: May to August 2012 and June to August 2016. In 2012, observations were conducted by Z. C. and an assistant on 36 bonobos in two social groups (group 1, N=20; group 2, N=16). The bonobos were from all age (mean age: 11.1 ± 4.8-year-old, N = 103 subjects below 8-year-old and N = 23 subjects above 8-year-old) and sex-classes (17♀). In 2016, observations were conducted by S. K. and an assistant on 65 bonobos in three social groups (group 1, N=25; group 2, N = 22; group 3, N = 18). The bonobos were of all ages (mean age: 11.5 ± 6.3-year-old, N = 23 subjects below 8-year-old and N = 42 subjects above 8-year-old) and sex-classes (33♀). An overview of the individuals in the three groups is provided in Table 3.1.

Table 3.1 Overview of the individuals of the three groups who contributed to the 2012 and 2016 data sets (victims and/or bystanders)

	Group 1		**Group 2**		**Group 3**	
	Name	Year of birth	Name	Year of birth	Name	Year of birth
FEMALES	Kitoko*(Waka)	2016	Ndona*(Maya)	2016	Molendisi*(Kinshasa)	2015
	Liyaka*(Kisantu)	2010	Mvula*(Muanda)	2014	Elonga*(Likasi)	2012
	Kimya*(Salonga)	2009	Moseka*(Bandundu)	2012	Sanza*(Tshilomba)	2010
	Elikya*(Semendwa)	2005	Nyota*(Lisaka)	2011	Sandoa	2005
	Ndjili	2010	Malaïka*(Kalina)	2007	Kinshasa	2005
	Kinzia	2010	Mongata	2010	Likasi *[2016]*	2001
	Waka	2005	Minova	2009	Kalina	1998
	Katako	2004	Boma	2009	Isiro	1997
	Salonga	1997	Masisi	2005	Tshilomba	adult
	Semendwa(+Malaïka)	1996	Muanda	2003		
	Opala	1995	Lisala *[2016]*	2001		
	Bandundu	1997	Maya(+Mayele) *[2012]*	1993		
	Maya *[2016]*	1993	Kalina(+Bolingo)	1998		
	Lisala(+Nyota) *[2012]*	2001	Likasi(+Elonga) *[2012]*	2001		
			Sake	2005		
			Kisantu(+Liyaka)	1999		
MALES	Jukuu*(Elika)	2015	Mayele*(Maya)	2010	Minzoto*(Tshilomba)	2014
	Pole*(Opala)	2006	Bisengo*(Maya)	2005	Bolingo*(Kalina)	2011
	Wongolo*(Bandundu)	2008	Garamba	2009	Moyi*(Tshilomba)	2007
	Singi	2009	Bombo	2008	Lomako	2007
	Oshwe	2008	Kole	2006	Chibombo	2005
	Kodoro	2007	Eleke	2004	Maniema	2001
	Kasongo	2002	Yolo	2003	Fizi	2000
	Mambali	2002	Bili	2001	Boende	2000
	Dilolo	2001	Mbandaka	2001	Makali	1984
	Matadi	2001	Api *[2016]*	2000		
	Lomami	1999	Keza	adult		
	Kikwit	1998	Max	1986		
	Manono	1994	Ilebo	2002		
	Api *[2012]*	2000				
	Fizi	1999				

"*" indicate subjects born at the sanctuary (mother's name in brackets), as compared to orphans for who's year of birth might have been estimated by the vet team at their arrival at the sanctuary. Mothers carrying a dependent infant are indicated with: (+infant's name). Some individuals were transferred across groups between the two data collection periods, as indicated under brackets: [2012/2016].

In this study, bonobos were characterised as immature when below 8-year-old and mature when above 8-year-old (Table 3.2 for a summary).

Table 3.2 Summary of the group, sex and age class of the subjects (yo = years old)

		Group 1		**Group 2**		**Group 3**	
		Below/= 8yo	**above 8yo**	**Below/= 8yo**	**above 8yo**	**Below/= 8yo**	**above 8yo**
2012	Females	4	5	4	4		
	Males	2	9	3	5		
2016	Females	5	8	7	4	3	6
	Males	3	9	3	8	2	7

The age of the orphans was estimated upon arrival at the sanctuary by veterinarians using weight and dental data (Rosati & Hare, 2012; Wobber, Wrangham, et al., 2010). Orphans (N = 31 in 2012; N = 46 in 2016) were generally saved from the illicit bush-meat and pet trades as infants or juveniles. These individuals were integrated into a large mixed-age social group after a period of rehabilitation of several years in a nursery with a substitute human mother (see Figure 3.1). Some bonobos were born and reared by their mother at the Sanctuary (N = 6 offspring from N = 6 mothers in 2012; N = 19 offspring from N = 14 mothers in 2016), who also lived in the enclosures. Therefore, the three colonies were composed of a mixture of wild-born orphans and sanctuary-born bonobos.

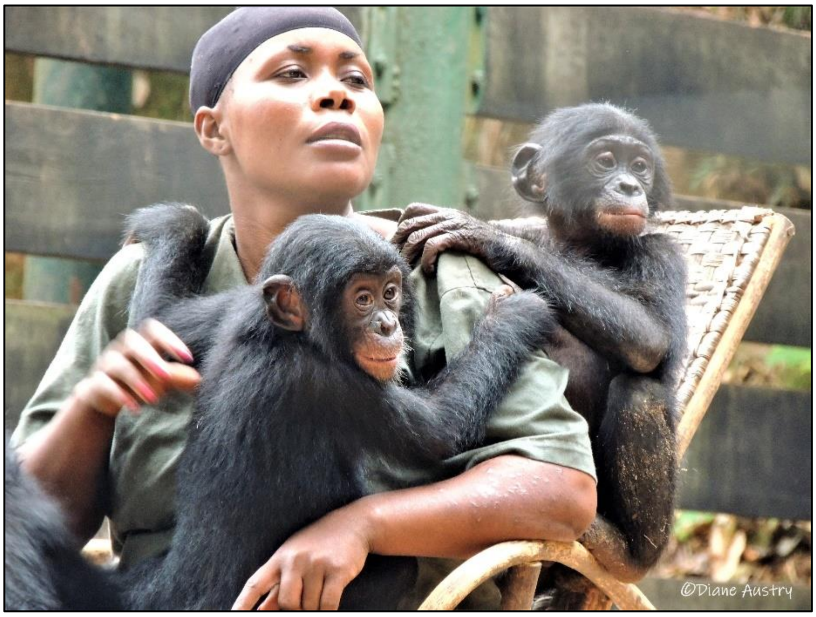


Figure 3.1 Maman S’arrive and two bonobo orphans at the nursery (August 2018)

LYB offers a valuable social and ecological environment that allows the bonobos to display the species’ natural behavioural pattern (André et al., 2008). During the day, bonobos were in semi-wild enclosure comprised of 8 to 20 ha comprised of grassy open areas, streams, swamplands, ponds, and primary rainforest (see Figure 3.2). Individuals spent the night together in dormitories of 75 m² divided into several separable rooms. Keepers distributed fruits and vegetables 3 or 4 times per day, and a mixture of soya milk around midday. Data were collected when bonobos were in visible areas of the enclosure.

Figure 3.2 Satellite view of the three enclosures housing group 1, 2 and 3, and the nursery, at LYB, Kinshasa, DR Congo (© Google Maps)

3.3.3 Materials

Social interactions from 2012 and 2016 were recorded with a high-definition Canon Vixia HF200 camcorder, and a high-definition Panasonic HC-V77 camcorder (20x Optical Zoom with 4-Drive Lens System), respectively. These were erected on tripods.

3.3.4 Procedure: Data collection and behavioural coding

Video recordings were made of spontaneous naturally-occurring post-conflict and post-distress situations following the methods described in *Chapter 2*. Consolation is characterised by being initiated by the bystander (de Waal & van Roosmalen, 1979) thus, only events in which the bystander initiated the recipient of the consolation, or when the contact was mutually initiated by the victim and a bystander (i.e., N = 213 in 2012, and N = 182 in 2016) were included. Therefore, N = 440 cases where victims initiated the contact (N = 407) or where it was unclear who was the initiator (N = 33) were excluded from the data set. As detailed in *Chapter 2*, the following data were coded: the occurrence and nature of a consolation, the nature of the aggressive behaviour (used to evaluate the intensity of the conflict), and the victim distress behaviour.

15-minute scan-sampling recordings were used to record the presence and proximities of group members during baseline periods. I used these scan samples to build affinity matrices on social affiliations. Close bonds per dyad were calculated with dyadic affiliation scores, i.e., numbers of scans in which a dyad interacted, divided by numbers of scans in which both individuals were present. Interactions included five behaviours (1-arm's reach, contact, grooming, sex, play) and were counted bidirectional. I calculated mean dyadic affiliation scores per individual. I identified close bonded partners relative to group levels by mean dyadic affiliation scores within the upper quartile of the group (Clay & de Waal, 2013a).

3.3.5 Data analysis

3.3.5.1 Inter-coder reliability testing

15% of the data set were coded by an independent coder. I used Cohen's kappa tests to test the coder agreement for identification of consolatory behaviours, nature of the aggression, and distress behaviours.

3.3.5.2 Statistical analyses: Generalised Linear Mixed Models (GLMMs)

I used generalised linear mixed models (GLMMs) to test the hypotheses about 1/ the effectiveness, 2/ selectivity, 3/ and the latency of the consolation, as well as 4/ the impact of mother's empathic tendencies on offspring consolation, and 5/ the development of a consolatory repertoire. I used the *lmer* function in *lme4* in R (Bates et al., 2012, 2015). I compared each full model with a respective null model (Forstmeier & Schielzeth, 2011), which excluded all predictors and only kept the random factors with likelihood ratio test (R function ‘anova’ with argument test “Chisq”, Dobson and Barnett 2018). Only when a full-null model comparison revealed significance ($P < 0.05$), did I discuss the results of the model for individual test predictors (Forstmeier & Schielzeth, 2011; Mundry, 2014). All p-values were two-tailed. I considered $P < 0.05$ as significant. More details are provided in *Chapter 2*.

In the models presented below, I included the control factors of severity of aggression in case of PCs, or its absence where PDs were taken (low/medium; high-intensity; spontaneous distress). Random intercepts were modelled to account for individual variation and repeated measures of the consoler (consoler ID), the victim being consoled (victim ID), as well as the PC or PD situation (PC/PD ID). Because the data were collected across two years (2012 and 2016), the ID of the consoler and victim were nested in the year of the data collection (random intercepts). The data analysed included the first consolation offered by a given bystander to the conspecific in distress within a given PD or PC. Several bystanders could provide a consolation within the same event, but if the same bystander provided more than one consolation, these were excluded from the data set. I assessed model stability and ran model diagnostics to ensure the number of variables included in the model was suitable for the sample size (see *Chapter 2*).

3.3.5.2.1 Effectiveness of the consolation

To analyse whether the age or sex of the consoler and/or the nature of the consolatory behaviour predict the effectiveness of the consolation, I fitted a GLMM for continuous data with a gaussian error distribution (identity link function) – the dependent variable being the duration of the distress expressed by the victim. The predictors in the model were the consoler’s age class (immature; mature), sex (male; female), and rearing status (mother reared; orphan), as well as the victim’s age class (immature; mature), and rearing status (mother-reared; orphan), along with the bond between the consoler and the victim (mother-offspring bond; closely bonded individuals; no closely bonded individuals – measured via scan sampling, relative to group levels by mean dyadic affiliation scores within the upper quartile of the group, as explained in section above), the nature of the consolatory behaviour offered (non-sexual; socio-sexual). I also included an interaction term between the consoler's age class and their rearing status. Control and random effects are stated above. Here, the data set included all occurrences of unsolicited consolation initiated by a bystander towards the victim (N = 206 PCs) or individual in distress (N = 189 PDs), with N = 35 consolers in 2012 (18♀ and 9 mother-reared individuals) and N = 48 consolers in 2016 (25♀ and 14 mother-reared individuals).

3.3.5.2.2 Selectivity of consolation

To analyse whether the affiliation/bond strength between the consoler and the distressed individual positively predicts the likelihood of the consolation and whether this selectivity increases with age, I fitted a GLMM for binomial data (binomial family) with a binomial error distribution (logit link function, McCullagh & Nelder, 1996). The dependent variable was the occurrence of consolation (i.e., for all bystanders who witnessed the conflict, whether the bystander – here, subject- offered at least one consolation to the victim or not). The predictors in the models were the affiliation between the consoler and the victim (categorical variable, mother-offspring bond and other closely bonded individuals; no closely bonded individuals), the consoler's age (immature; mature) and rearing status (mother reared; orphan). To test for the selectivity across age, I also included an interaction term between the consoler's age class and their affiliation with the victim. Control and random effects are stated above. The unit of analysis is the bystander. The dataset included all occurrences when a subject witnessed a distress/conflict as a bystander (N = 9,589), with N = 39 bystanders in 2012 (18♀ and 9 mother-reared individuals) and N = 61 bystanders in 2016 (30♀ and 15 mother-reared individuals).

3.3.5.2.3 Impact of mother's empathic tendencies

To analyse whether a mother's tendency to offer consolation predicts the offspring's tendency to offer consolation, I fitted a GLMM with a gaussian error distribution (identity link). The tendency to offer consolation was calculated as the number of consolations divided by the number of PCs or PDs the consoler had witnessed within the two observation periods. The dependent variable was the consolation tendency. The predictor was the bystander's mother's tendency to offer consolation transformed with the sqrt() function to fit a normal distribution. In addition to the control and random effects stated above, control factors included the affiliation between the consoler and the victim (mother-offspring bond and other closely bonded individuals; no closely bonded individuals) and the consoler's age (immature; mature) and sex (male; female). The data set included all occurrences when mother-reared subjects witnessed a distress and conflict as bystanders (N = 2,308), with N = 9 mother-reared individuals as bystanders in 2012 (4♀) and N = 14 mother-reared individuals as bystanders in 2016 (8♀; LY was excluded from this data set because her mother's – KS- consolatory tendencies were not available).

3.3.5.2.4 Latency and order of the consolation

To analyse whether the age of the consoler predicts the latency of the consolation, I fitted GLMMs for continuous data with a gaussian error distribution (identity link function). The dependent variable was the latency to offer a consolation (continuous; with all subject being within 1 to 5 metres from the victim at the start of the PC or PD). The predictors were the consoler's age (immature; mature), rearing status (mother reared; orphan), and sex (male; female). There was no interaction. Control and random effects are stated above.

To analyse whether the age of the consoler predicts who offers the first consolation, I fitted GLMMs with a binomial error distribution (logit link function). The dependent variable was whether the consolation was the first of the event or not (first; not first). First consolations that were also the only one of an event were also included as they attest to the motivation of the first consoler, independent as to whether someone will follow or not. The predictors in the models were the consoler's age (immature; mature), rearing status (mother reared; orphan), and sex (male; female). Control and random effects are stated above. No interaction was included.

To conduct these two sets of analyses, the dataset included all occurrences of consolation for N = 206 PCs and N = 189 PDs, with N = 35 consolers in 2012 (18♀ and 9 mother-reared individuals) and N = 48 consolers in 2016 (25♀ and 14 mother-reared individuals).

3.3.5.2.5 Development of a consolatory repertoire

To analyse whether the age of the consoler predicts the nature of the consolatory behaviour, I fitted GLMMs with a binomial error distribution (logit link function) to examine consolation events. The first model investigated whether the age of the consoler predicted the use of non-sexual as compared to socio-sexual behaviours (non-sexual; socio-sexual). The second model investigated whether the age of the consoler predicted the use of *embrac*e as compared to all other consolatory behaviours (embrace; others). The predictors were the consoler’s age (immature; mature), rearing status (mother reared; orphan), sex (male; female), victim age (immature; mature), and the affiliation between the consoler and the victim (mother-offspring bond; closely related; not closely related). Here, the dataset included all occurrences of consolation for N = 206 PCs and N = 189 PDs, with N = 35 consolers in 2012 (18♀ and 9 mother-reared individuals) and N = 48 consolers in 2016 (25♀ and 14 mother-reared individuals).

Finally, to analyse whether the age of the consoler predicts the individual’s size of consolatory repertoire, I ran a linear regression (anova) with the age of the consoler and the number of behavioural categories the subject has used at least once. Each individual only contributed one line of data to this analysis, avoiding pseudo replication. There are four categories of behaviours: socio-sexual contacts, play, embrace, and contact & touch.

3.4 Results

3.4.1 Inter-coder reliability testing

Inter-coder reliability was good to excellent for the identification of consolatory behaviours (k = 0.89), the nature of the aggression (k = 0.91, and the distress behaviours (k = 0.85).

3.4.2 Effectiveness of consolation

The full model did not explain the data significantly better than the null model – which only contained the intercept, control and random effect (henceforth referred to as the null model) ($\chi 2$ = 13.32, d.f. = 9, p = 0.149). Therefore, there were no reported effects of consolation effectiveness as a function of age or sex of the consoler and/or the nature of the consolatory behaviour.

3.4.3 Selectivity of the consolation

The full model explained the data significantly better than the null model ($\chi 2$ = 86.44, d.f. = 6, $p < 0.001$). The individual predictors are presented in Table 3.3.

The interaction between consoler age class and their affiliation with the victim did not show a significant effect on the likelihood to offer consolation (Table 3.3). However, when the model was re-tested without the interaction term, there was a significant effect of victim-consoler affiliation, with the bystander being more likely to console closely bonded conspecifics – including mother-offspring bond (Table 3.3; Figure 3.3.L). Mother-reared individuals were more likely to console than orphan individuals (Table 3.3; Figure 3.3.R), however, there was no effect of age class.

Table 3.3 Results of the full model testing the effect of console age, rearing, sex, and consoler-victim affiliation on the likelihood of offering a socio-sexual behaviour. S.E.: standard error; p: p-value.

Fixed effect	***Estimate***	***S.E.***	***z value***	***p***
(Intercept)	-2.166	0.231	-9.377	<0.001
Consoler age class * affiliation victim/consoler (mature*not closely bonded)	-0.336	0.249	-1.348	0.178
Consoler rearing (orphan)	-0.470	0.235	-1.999	**0.046**
Affiliation victim/consoler (not closely bonded)	-0.607	0.180	-3.371	**0.001**
Consoler age class (mature)	-0.336	0.249	-1.348	0.178

Significant values (P<0.05) are in **bold**

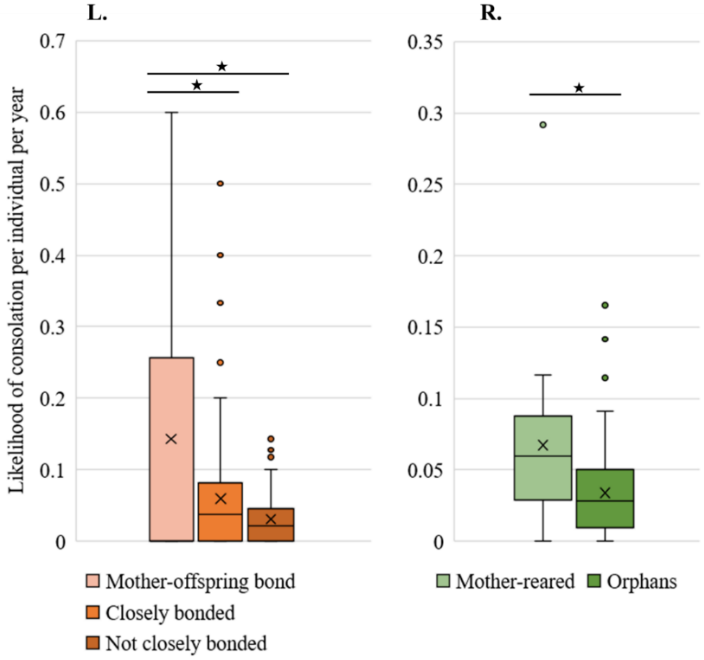


Figure 3.3 Effect of the social bond between the consoler and the victim (L), and effect of rearing (R) on the likelihood to offer consolation to the individual in distress (values per individual per year). Stars represent significant results. Crosses represent the means. Middle lines of the box represent the median number. Dots represent outlier data that are outside the 1.5 times the interquartile range (IQR), up and down.

3.4.4 Impact of mother's empathic tendencies

The full model did not explain the data significantly better than the null model ($\chi2 = 1.43$, d.f. = 1, p = 0.231). This indicates mother's tendency to offer consolation does not predict her offspring's tendency to offer consolation.

3.4.5 Latency and order of the consolation

The full model explained the data significantly better than the null model ($\chi2 = 18.33$, d.f. = 5, p = 0.003). The results are presented in Table 3.4.

Table 3.4 Results of the full model testing the effect of consoler age, rearing, sex, and consoler-victim affiliation on the latency of offering a consolation. S.E.: standard error; p: p-value.

Fixed effect	***Estimate***	***S.E.***	***t value***	***p***
(Intercept)	80.232	11.797	6.801	<0.001
<u>Consoler age class</u> (mature)	-24.039	12.630	-1.903	<u>0.061</u>
Consoler rearing (orphan)	36.742	12.864	2.856	**0.006**
Consoler sex (male)	-7.821	10.438	-0.749	0.456
Affiliation victim/consoler (mother-offspring bond)	-55.321	18.612	-2.972	**0.003**

Significant values (P<0.05) are in **bold;** almost significant values are <u>underlined</u> (P < 0.09)

Younger individuals tended to be slower at offering consolation than older individuals (estimate ± se = -24.04 ± 12.63, t = -1.90, p = 0.061 – Figure 3.4.A). Orphans were slower at offering consolation as compared to mother-reared individuals (estimate ± se = 36.74 ± 12.84, t = 2.86, p < 0.01 – Figure 3.4.B). Furthermore, subjects were quicker at offering consolation to their kin (mother/offspring), as compared to other closely bonded conspecifics or not closely bonded conspecifics (estimate ± se = -55.32 ± 18.61, t = -2.97, p < 0.005 – Figure 3.4.C). Subject sex did not affect the latency of consolation (estimate ± se = -7.82 ± 10.44, t = -0.75, p = 0.456).

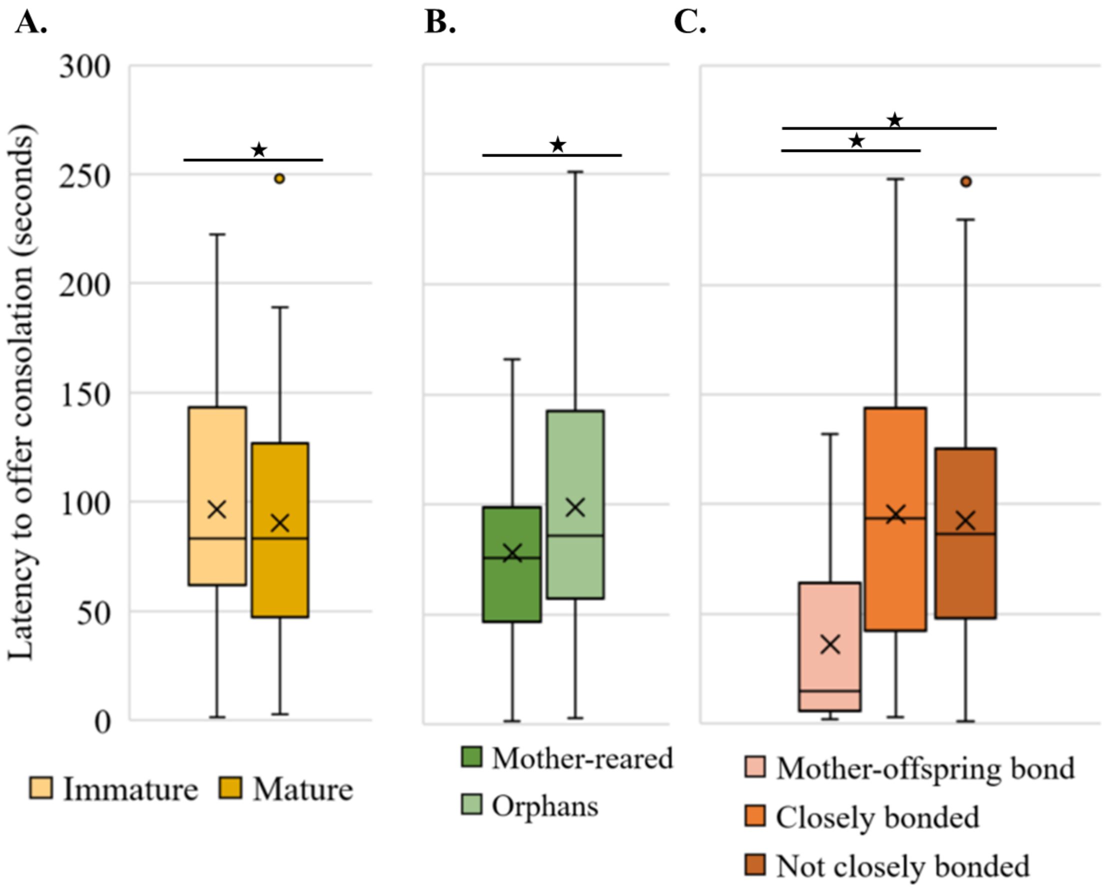


Figure 3.4 Latency to offer consolation as a function of the age class (mature; immature, A) and rearing status (mother-reared; orphan, B) of the consoler, and affiliation between the consoler and the victim (C). Stars represent significant results. Crosses represent the means. Middle lines of the box represent the median number. Dots represent outlier data that are outside the 1.5 times the interquartile range (IQR).

The full model examining the effect of age class on the likelihood to offer the first consolation did not explain the data significantly better than the null model – which only contained the intercept, control and random effect ($\chi2 = 1.04$, d.f. = 3, $p = 0.791$).

3.4.6 Development of the consolatory repertoire

3.4.6.1 Non-sexual vs sexual behaviours

The full model explained the data significantly better than the null model ($\chi2 = 32.25$, d.f. = 6, $p < 0.001$). The individual predictors are presented in Table 3.5.

Table 3.5 Results of the full model testing the effect of consoler age, rearing, sex, victim age, and consoler-victim affiliation on the likelihood of offering a non-sexual or socio-sexual consolatory behaviour. S.E.: standard error; p: p-value.

Fixed effect	***Estimate***	***S.E.***	***z value***	***p***
(Intercept)	-1.205	0.471	-2.556	0.011
Consoler age class (mature)	0.863	0.404	2.136	**0.033**
Victim age class (mature)	0.546	0.445	1.227	0.220
<u>Consoler rearing</u> (orphan)	0.769	0.440	1.749	<u>0.080</u>
Consoler sex (male)	-0.404	0.350	-1.154	0.249
Consoler/victim affiliation (mother-offspring bond)	-3.325	1.136	-2.926	**0.003**

Significant values (P<0.05) are in **bold;** almost significant values are <u>underlined</u> (P < 0.09)

Immature consolers were more likely to offer non-sexual consolatory behaviours than socio-sexual ones, while there is no such disparity in mature consolers (estimate ± se = 0.86 ± 0.40, z = 2.14, $p < 0.05$ – Figure 3.5.A). Mother-reared consolers tended to be more likely to offer non-sexual consolatory behaviours than socio-sexual ones (estimate ± se = 0.77 ± 0.44, z = 1.75, p = 0.080 – Figure 3.5.B), as compared to orphan individuals. Subjects were more likely to offer a non-sexual consolatory contact to kin (mother/offspring: estimate ± se = -3.33 ± 1.14, z = -2.93, $p < 0.005$ – Figure 3.5.C) as compared to socio-sexual behaviours. There was no effect of consoler sex (estimate ± se = -0.40 ± 0.35, z = -1.15, p = 0.249) or victim age class on the likelihood to offer non-sexual or socio-sexual consolatory behaviours.

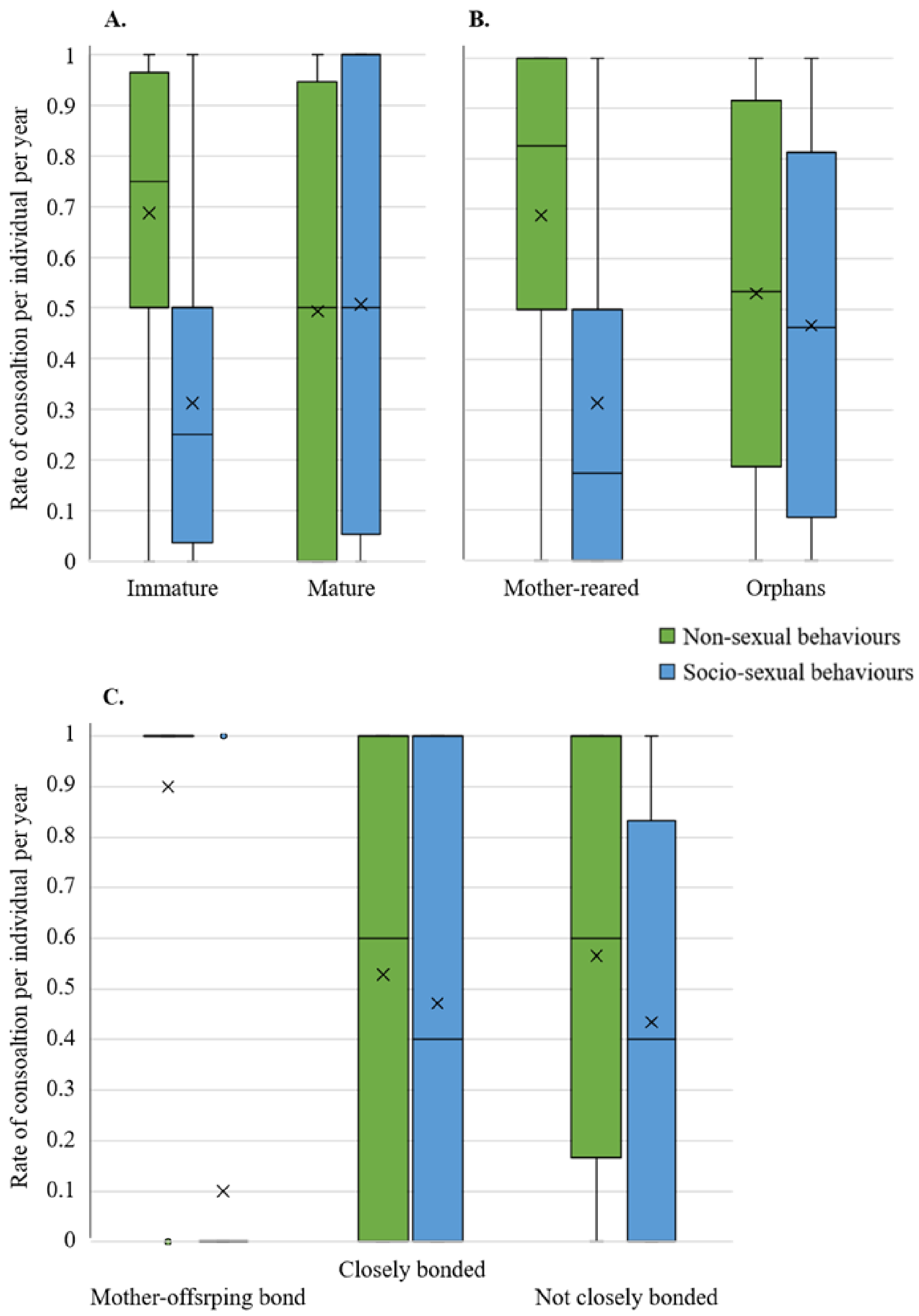


Figure 3.5 Effect of the age class (A) and rearing (B) of the consoler, and the bond between the consoler and the victim (C) on the rate of non-sexual and socio-sexual consolatory behaviour offered to the victim. The crosses represent the means. Middle lines of the box represent the median number. Dots represent outlier data that are outside the 1.5 times the interquartile range (IQR).

When examining the intricacies of the consolatory repertoire of immature and mature individuals, the average proportion of contact and touch behaviours by individual as similar (42 and 43%). However, mature individuals used socio-sexual behaviours more often than immature ones (42 vs 27%), who use embrace (18 vs 8%) and play (13 vs 7%) more often. Figure 3.6 represents the distribution of the proportion of the different consolatory behaviours offered by immature (Figure 3.6.a) and mature (Figure 3.6.b.) individuals.

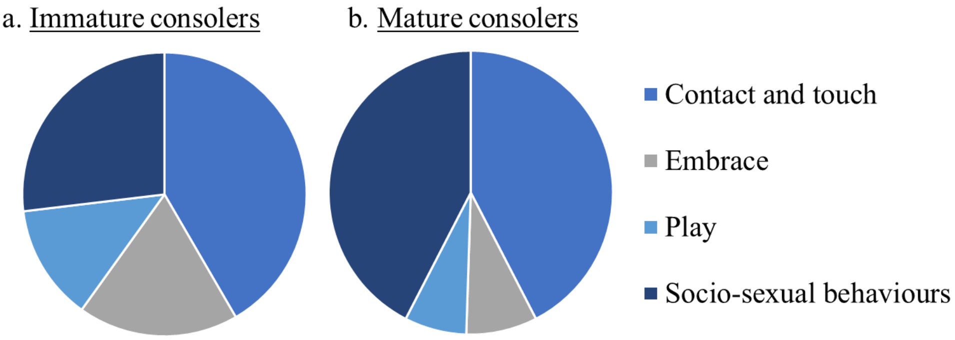


Figure 3.6 Graphical representation of the proportion of the different consolatory behaviours offered to a victim by immature (a) and mature (b) bystanders

3.4.6.2 Embrace behaviour

The full model explained the data significantly better than the null model ($\chi2 = 21.08$, d.f. = 6, $p < 0.002$). The individual predictors are presented in Table 3.6.

Table 3.6 Results of the full model testing the effect of consoler's age, rearing, sex, victim's age, and consoler-victim affiliation on the likelihood of offering a non-sexual or socio-sexual consolatory behaviour. S.E.: standard error; p: p-value.

Fixed effect	***Estimate***	***S.E.***	***z value***	***P***
(Intercept)	-1.409	0.556	-2.533	0.011
Consoler age class (mature)	-1.196	0.583	-2.051	**0.040**
Victim age class (mature)	-0.978	0.584	-1.673	0.094
Consoler rearing (orphan)	-0.810	0.526	-1.539	0.124
Consoler sex (male)	0.083	0.460	0.180	0.857
Consoler/victim affiliation (mother-offspring bond)	2.056	0.710	2.897	**0.004**

Significant values (P<0.05) are in **bold;** almost significant values are underlined (P < 0.09)

Immature consolers were more likely to use embrace to console peers than mature consolers (estimate ± se = -1.20 ± 0.58, z = 2-2.05, p < 0.05 – Figure 3.7.L). Subjects were more likely to offer an embrace consolation to kin (offspring/mothers; estimate ± se = 2.06 ± 0.71, z = 2.90, p < 0.005 – Figure 3.7.R) as compared to non-kin closely bonded or not closely bonded conspecifics. There was no effect of consoler sex (estimate ± se = 0.08 ± 0.46, z = 0.18, p = 0.857), rearing status (estimate ± se = -0.81 ± 0.53, z = -1.54, p = 0.124), or victim age class (estimate ± se = -0.98 ± 0.58, z = -1.67, p = 0.094) on the likelihood to offer embrace as compared to other consolatory behaviours.

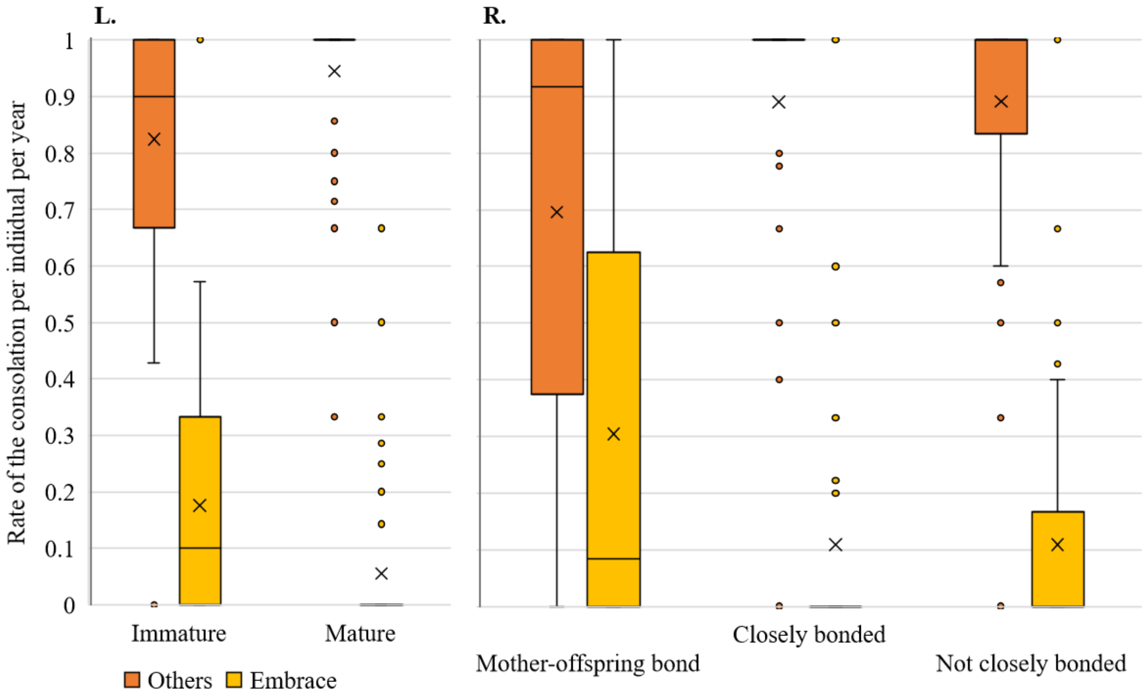


Figure 3.7 Effect of the age of the consoler (L) and bond between the consoler and the victim (R) on the rate of embrace and other consolatory behaviours offered to the victim. Crosses represent the means. Middle lines of the box represent the median number. Dots represent outlier data that are outside the 1.5 times the interquartile range (IQR).

Size of the consolatory repertoire

Results from a linear regression revealed that older subjects use less consolatory behavioural categories than younger ones ($R^2 = 0.20$, $p < 0.001$, $N = 83$).

3.5 Discussion

This study examined the development of empathy in bonobos in naturalistic contexts. The systematic observations of post-conflict and post-distress contexts revealed that mature bonobos were not more efficient in alleviating the other's distress, nor were they more selective towards consoling closely bonded partners as compared to immature bonobos. Results also indicated no relationship between mother and offspring consolation tendencies. However, mature bonobos tended to be faster than immature bonobos to console, and mother-reared bonobos tended to be faster than orphan bonobos to console. Finally, there was developmental variability in the consolatory repertoire. These results are discussed.

3.5.1 Effectiveness of consolation

Consolation functions to alleviate the distress level of the individual who is being consoled (Clay & de Waal, 2013b; Palagi & Norscia, 2013, 2013; Webb et al., 2017). Challenging my predictions, my findings did not reveal that the efficiency of consolation to decrease victim distress was predicted by the age, rearing status, or sex of the consoler, nor the nature of the consolatory behaviour offered. This suggests that such characteristics of the consolers may not be determinant in the assumed alleviation of victim distress. Instead, regardless of who the consoler is, receiving the physical contact itself might provide physical and emotional relief (comforting touch, Shamay-Tsoory & Eisenberger, 2021), particularly when it is offered spontaneously (as opposed to solicited: Palagi & Norscia, 2013). Such contact comes alongside the social support of a conspecific (Fraser et al., 2008b; Pallante et al., 2018) and might be enough for the victim to calm down. In that sense, the consolatory contact may be less cognitively complex in how it is processed than expected.

The present study used the duration of the behavioural distress as an indicator of the victim state. However, it is possible that other measures of anxiety or distress could have yielded other outcomes. Therefore, it is worth expanding our assessment of victim distress to other measurements to explore the effectiveness of the consolation. Combining behavioural metrics, like rate of self-scratching (Castles & Whiten, 1998; Clay & de Waal, 2013b, 2015; de Waal & Aureli, 1996; Koski et al., 2007; Palagi & Norscia, 2013) or scream duration (Castles & Whiten, 1998; Clay & de Waal, 2013b), with physiological measurements such as hormonal levels (e.g., Butovskaya et al., 2005; Hohmann et al., 2009) or infrared thermal imaging (Dezecache et al., 2017) measured before and after a given consolation-as indicators of anxiety, could provide crucial insights into the function of consolation and its underlying mechanisms.

3.5.2 Selectivity of offering consolation

In contrast to my prediction, I did not find that older consolers were more selective towards closely bonded partners than younger consolers. However, in line with Clay & de Waal (2013), I found an overall effect of consolation being directed towards socially close individuals. This might suggest that although the ability to identify relevant social partners (in children: Hamlin et al., 2007; in bonobos: Krupenye & Hare, 2018) and cognitive control may develop over time (Clay & de Waal, 2013a, 2013b; Cordoni et al., 2006; Webb et al., 2017), the maturation of these abilities is not crucial to the selectivity of empathic responding. However, it is also possible that these abilities develop and mature earlier than what the current sample can discriminate. Future work should focus on such capacities in younger individuals. The *empathy gradient* (i.e. the social bias of empathy*)* is thought to be an extension of the mother-offspring bond that connects socially relevant individuals (Preston & de Waal, 2002). The results of the current study might suggest that the social awareness underpinning this *empathy gradient* is already present in young individuals, who, although they console more than mature individuals (Clay & de Waal, 2013b), are more likely to console socially close individuals than more distant ones. When it comes to young bonobos, it is also conceivable that overall, they are more likely to interact with familiar individuals from a young age, particularly the friends and offspring of their mothers, and as a result, limit their social circle to those individuals. Therefore, any emotional response that could be triggered by the distress of an individual might also be mediated/regulated by how familiar this individual is – as it is the case for mature individuals. For immature individuals, different underlying mechanisms can be involved in this mediation; for instance, this selectivity might be motivated by a fear of the unfamiliar individuals, while advances in cognition might support higher emotion regulation skills and more filtered manifestation of empathy (e.g., in-group biases: Avenanti et al., 2010). Controlled experiments and physiological measurements are crucial to tease apart these hypotheses.

3.5.3 Impact of mother's empathic tendencies

Contrasting my initial hypotheses, I did not find a positive relation between the consolatory tendencies of a mother and her offspring(s), or an impact of age on this relation. This suggests that bonobos develop their empathic tendencies independently of those of their first direct social model, i.e., their mother, despite the mother being an apparently important social model in other aspects of her offspring's life (Jaeggi et al., 2010; Lonsdorf, 2006; Schneider et al., 2012). It is possible that rather than being learned, this tendency is biologically-inherited or shaped by factors such as rank or sex, as well as other social factors such as conspecific relationships (Perry, 2011; Rapaport & Brown, 2008; Suomi, 2005; Whiten & van de Waal, 2018). Internal mechanisms might also influence empathic tendencies. For instance, individual differences in empathic tendencies are stable through human (Eisenberg et al., 1999; Knafo et al., 2008; Zahn-Waxler, Radke-Yarrow, et al., 1992; Zahn-Waxler, Robinson, et al., 1992b) and non-human (Webb et al., 2017) primates lives suggesting that empathy might be included in a wider prosocial personality trait (Allemand et al., 2015).

3.5.4 Latency of the consolation

In line with my prediction, subjects were quicker to console kin (mother /offspring) as compared to other conspecifics, confirming the importance of social closeness (Preston & de Waal, 2002). I also expected younger individuals to be quicker at displaying consolatory behaviours than older individuals due to their presumed lack of impulse control. In contrast with my predictions, younger individuals tended to be slower at offering consolation than older individuals. Orphans were also slower at offering consolation to a conspecific in distress as compared to mother-reared individuals. These results were not explained by the alternative prediction that young individuals and orphans might wait for others to first approach the individual in distress before approaching themselves, as I did not find that immature individuals were more likely to wait to console after another consolation had already been offered. This prediction was based on the fact that the young may learn about some species-specific behaviours through observing their social environment (Cavalli-Sforza & Feldman, 1981; Hirata & Celli, 2003). This does not seem to apply to consolation behaviours, with the development of these behaviours potentially being less socially influenced. Furthermore, consolation might be triggered by different mechanisms in immature and mature bonobos, with – *potentially*- slower underlying processes leading to consolation in immature bonobos, in contrast to more efficient and swift processes in mature individuals. Then, immature individuals might share these processes with orphan individuals, whose cognitive and socio-emotional skills have been impaired by early trauma (humans: Beckett et al., 2006; bonobos: Clay & de Waal, 2013).

Another alternative is that it is riskier for individuals with less social capital or support to console, therefore they do it less (Clay & de Waal, 2013a). Indeed, while mature females have a strong social status in bonobo communities (Hohmann et al., 1999; Hohmann & Fruth, 2003; Stevens et al., 2007; Vervaecke et al., 2000; White, 1988; White & Wood, 2007), orphans have no mother to protect them (Surbeck et al., 2011). Furthermore, immature individuals with a less established social status may also be more vulnerable than older individuals in a conflict situation. Consequently, mature and mother reared individuals might feel more comfortable and can be bolder to get involved in risky situations. Future work should focus on the risks faced by different individuals in PC situation and how this influences their response.

3.5.5 Development of a consolatory repertoire

3.5.5.1 Non-sexual vs sexual behaviours

Immature consolers were more likely to offer non-sexual consolatory behaviours than socio-sexual ones, while there was no such disparity in mature consolers. This suggests that – although even infants as young as 1-year-old already were involved and performed sexual behaviours (Hashimoto, 1997)- the use of socio-sexual behaviours for consolation develops later in life. The use of socio-sexual behaviours for consolation might develop after the age of sexual maturity, when sexual behaviours acquire their reproductive function. Otherwise, subjects were more likely to offer a non-sexual consolatory contact to kin (offspring/mothers) as compared to socio-sexual behaviours, supporting the idea that young individuals learn and develop the use of socio-sexual behaviours with social partners other than their mother, and only a bit later in life (Hashimoto, 1997). Mother-reared consolers tended to be more likely to offer non-sexual consolatory behaviours than socio-sexual ones, as compared to orphans. This tendency might be explained by the fact that mother-reared consolers might also have been more likely to console their mothers with whom the exchange of socio-sexual contacts is limited (Hashimoto, 1997). Another possibility might be that it was more stressful for orphans to console, therefore they use socio-sexual contacts as a way for them to release stress. Future work combining behavioural and physiological measures should investigate whether the distress state of the consoling bystanders impact their consolatory strategies, in order to better understand the intrinsic motivations of consolation. There was no effect of consoler sex or victim age on the likelihood to offer non-sexual versus socio-sexual consolatory behaviours. This suggests that there are no sex-specific consolatory strategies. However, the sex of the victim rather than the sex of the consoler might influence the nature of the consolatory behaviour being offered. The human literature on consolatory strategies is limited, but expanding our knowledge of consolation to other ape species, including human, would deepen our understanding of the origins of potential sex-differences in humans, as a result of socialisation.

3.5.5.2 Embrace behaviour

When examining the intricacies of the consolatory repertoire, mature individuals used socio-sexual behaviours more often than immatures who use embrace and play more often. In most primate species, infants are born with grasping skills that permit them to cling safely to the mother's fur (Anvari et al., 2014; Kappeler, 1998; Nakamichi & Yamada, 2009). This is also in this *embracing* position that they access the breast to get the milk and regulate their body temperature for instance (Lubach et al., 1992). Therefore, infants experience this vital, close, physical contact with their mother (Ross, 2001). In human infants, embracing or hugging is considered to be a self-soothing behavioural strategy (Grolnick et al., 1996; Morales et al., 2005), and in adults, it is considered an affective touch interaction (Cohen et al., 2015). Such physical interaction has positive effects on both individuals involved, such as a decrease in heart rate (Grewen et al., 2003) and the risk of viral infection (Cohen et al., 2015), and even pain reduction (Goldstein et al., 2018). This explains the relevance of the embrace behaviour as a consolatory strategy in a high-intensity context. However, it remains unclear whether this behaviour is indeed other-oriented as assumed in a case of consolation, or instead reflects a self-soothing strategy from the consoler. Embrace consolations were mainly used by immature individuals of this study, supporting the potential self-soothing hypothesis, where younger individuals may need to regulate their own emotions following a high-intensity situation such as a post-conflict context and seek comfort. However, immature consolers were more likely to use embrace to "console" peers than mature consolers, which seem to contrast with the hypothesis that they would be seeking comfort via an embrace primarily from younger individuals rather than mature individuals. Yet, subjects regardless of age were more likely to offer an embrace consolatory contact to kin than other conspecifics, suggesting that this behaviour is somehow more intimate and targeted than others – in line with the maternal roots of this behaviour (Ross, 2001). A broader investigation of this behaviour across context, coupled with physiological measurements could help untangle the motivation and mechanisms underlying this behaviour.

There was no effect of the consoler’s sex or rearing status on the likelihood to offer embrace as compared to other consolatory behaviours. These results support the idea that the embrace behaviour finds its roots early in development without sexual specificity. There was no effect of the age of the victim either, suggesting that the consoler did not particularly adapt to this characteristic of the individual in distress. This result questions once again the other-oriented nature of the response: if a response is purely prosocial, we should expect this response to be recipient dependent more than consoler dependent.

Size of the consolatory repertoire

The finding that older subjects used fewer consolatory behavioural categories (i.e., socio-sexual contacts, play, embrace, contact & touch) than younger ones echoes results from the gesture literature, where the greatest gesture repertoire size is found in the juvenile period and decreases in adulthood (Hobaiter & Byrne, 2011).

3.5.6 Early deprivation: A barrier to empathy and emotion regulation development

Overall, although orphans consoled less than mother-reared, this study did not highlight other significant effects of rearing on the cognitive and socio-emotional skills of the bonobos. This suggests that adapted care and attention after an early trauma can alleviate its negative consequences on the development of the young individual (Hodges & Tizard, 1989).

3.5.7 Study limitations

While this study presents significant strengths, several limitations could have influenced the results and their generalisability, which are discussed below.

3.5.7.1 Age range

This study offers a new outlook on the development of consolation across the age spectrum in mother-reared and orphan bonobos. However, data on immature individuals mainly come from juveniles as opposed to infants. It is crucial to adapt our methods to take a closer look at the youngest age class to get in-depth insights on the evolutionary and developmental origins of empathy, either cross-sectionally or longitudinally.

3.5.7.2 Sample size

Furthermore, although the present study combines data of two time periods and therefore reaches a solid number of PC and PD events, the number of subjects included as victim and bystanders, as well as the amount of data per subject would benefit from a greater sample. In particular, the amount of mother reared individuals included in this study might have limited the power of the analysis on the impact of the mother's empathic tendencies. Therefore, future work, including a larger sample of mother-reared individuals might be able to characterise the variation in an individual's tendency to console with enough precision, to detect consistent relationships between the consolation behaviour of mothers and offspring.

3.5.7.3 Sanctuary settings and ecological validity

Finally, this study relies on the observation of bonobos housed in sanctuary settings. A large proportion of these apes were orphans saved from the illicit bush-meat and pet trades, while others were born at the sanctuaries. Therefore, although the study of this bonobo population living in a semi-wild environment might approach the behaviour of their wild conspecifics (André et al., 2008), we are restricted in our interpretation and generalisation of the outcomes of this study. Nonetheless, studying these populations offer the unique opportunity to investigate the effect of early deprivation on emotional and cognitive skills ethically, moving away from the early deprivation experiments conducted 50 years ago (Seay et al., 1962; Suomi et al., 1975, 1976). I discuss these points further in *Chapter 6*.

3.5.8 Conclusion

The present ethological study did not highlight significant developmental differences in bonobos efficiency to alleviate another's distress, how socially discriminant they are in selecting the target of the consolation and whether they tend to be first consoler or follower. This suggests that although the cognitive component of empathy develops over time, advanced cognition may not be essential for the expression of concern, or at least such skills might not be necessary for a consolatory contact to serve its consolatory role. Then, if cognitive abilities like perspective-taking are not required for consolation, what are the mechanisms underlying this empathic response? Are all unsolicited consolatory affiliations other-oriented, or what are the factors to identify to confirm the prosocial motivation of this response? To address this, it is crucial to conduct a broader investigation of consolation across age and context, coupled with experimental manipulations and physiological measurements in order to further untangle the motivation and mechanisms as they emerge in development.

Chapter 4 How do sanctuary-housed chimpanzees respond to others' emotions? A multi-componential approach

4.1 Abstract

Although empathy is important for effectively navigating the social environment, our understanding of its underlying mechanisms is still limited. Recent studies have demonstrated that children, chimpanzees, and bonobos show similar behavioural responses to the distress of others. However, detection of the underlying mechanisms is needed to confirm that the observed behaviour is empathy-based. Such an endeavour requires a multi-component approach in order to assess the complex basis of empathy-related reactions. Addressing this gap, this present study takes a multi-componential approach that combines naturalistic observations with non-invasive infrared thermography (IRT) experiments to investigate internal and external responses of sanctuary-housed chimpanzees toward the emotional states of others. For the IRT experiment, I showed short video clips of negative, positive, and neutral emotional social stimuli involving familiar and unfamiliar chimpanzees and humans to assess the thermal responses of N = 25 subjects at Chimfunshi Wildlife Orphanage (CWO). For the observational aspect, also conducted at CWO, I examined consolatory responses of these individuals as bystanders in response to naturally occurring post-conflict and post-distress reactions. This study is structured in two parts. **Part One** examines the link between observations taken during naturalistic contexts of bystander consolation and victim behavioural responses with the outcome of experiments measuring thermal responses of the same subjects while viewing a conspecific in distress. I hypothesised that inner arousal increases when chimpanzees witness the distress of a conspecific – and that this represents the underlying motivation to comfort a distressed individual (**hypothesis 1.1**). I also hypothesised that high and long-lasting levels of arousal at the physiological level indicate poor emotion regulation skills, thus translating into high levels of behavioural markers of anxiety, with emotion regulation increasing with age (**hypothesis 1.2**). In **Part Two**, I experimentally investigate the effect of stimulus valence and familiarity on facial thermal responses to human emotional stimuli. I hypothesised that external markers of the empathy bias (i.e., behavioural markers) are predicted by corresponding biases recorded at the physiological level (i.e., changes in the activity of the autonomous nervous system - **hypothesis 2.1**), and that IRT measurements would inform on both the *valence* and *arousal* dimensions (**hypothesis 2.2**). **Part One** shows that the temperature change in the periorbital region upon seeing a conspecific in distress in the experimental scenario predicts a subject's consolation rate in naturalistic settings, thus confirming **hypothesis 1.1**. Due to a limited sample size, I could not test whether thermal responses in the experiment predict victim anxiety behaviours in naturalistic settings (**hypothesis 1.2**). Results for **Part Two** show thermal variation in the nose tip region was predicted by human stimulus familiarity for positive emotion expressions – confirming **hypothesis 2.1**- as well as development stage – confirming **hypothesis 2.2**. As the use of IRT in comparative psychophysiological research is still in its infancy, this study also explores the temporal dynamics and physical pattern of the thermal response of chimpanzees to emotional stimuli, showing that the physiological response in anatomically close ROIs is similar. Overall, this project highlights the challenges and complexity of detecting the underlying mechanisms supporting empathy and provides new insights into the use of IRT as a method for studying emotional responding in chimpanzees.

Keywords: empathy; consolation; post-conflict affiliation; arousal; physiology; apes

4.2 Introduction

4.2.1 Multi-componential approaches to studying empathy and emotion contagion

Thus far, empathy research in animals has mainly relied on the observation of behaviours assumed to be linked to sympathetic concern, most notably consolation. However, identification of the underlying mechanisms shaping the observed behaviour is needed, as similar behaviours may be driven by different mechanisms. In order to understand the process of empathy, it is essential to implement a multi-component approach, as opposed to depending on observations, which can only ever measure the external dimension (see Adriaense et al. 2020 for a review, and *Chapter 2*).

Emotions are multi-componential (Anderson & Adolphs, 2014) with variation in behavioural, cognitive, and physiological components happening in a synchronised way (Mendl et al., 2010; Paul et al., 2005). The affective components are often divided along the dimensions of *arousal* (from lower to higher intensity) and *valence* (positive or negative; Russell 2003; Barrett et al. 2006). By conceptualising emotions in terms of universal core affective features, this *dimensional approach* can include the full scope of emotional states (see Mendl et al. 2010 for discussion).

Studies based on behavioural observations (e.g., Knapska et al. 2010; Reimert et al. 2017; Meyza & Knapska 2018) have provided important insights into the arousal dimension of an animal's emotional experience but have thus far yielded limited information on its valence (Briefer, 2018; Mendl et al., 2009; Paul et al., 2005). Arousal variation predicts changes in vigilance/attention, however, such variation does not automatically differentiate between positive or negative valence (Edgar & Nicol 2018). When evaluating the valence of an emotional response, researchers often rely on the context in which the behaviour is expressed (e.g., Church 1959) or behavioural indicators (e.g., Brosnan & de Waal 2003), therefore limiting the interpretation to detect its underlying basis (Huber et al., 2017; Mendl et al., 2009; Paul et al., 2005).

Similar methodological limitations also persist when it comes to investigating emotional contagion. Emotional contagion implies that the emotional state of the observer matches or is similar to that of the actor (Hatfield et al., 1994). Emotional contagion is considered an underlying mechanism for empathy as it involves the initiation of inner arousal in response to that of others (de Waal, 2008, 2011; de Waal & Preston, 2017a). However, detecting emotion contagion is theoretically difficult given that affective states do not always have clear behavioural or physiological signatures and the extent to which any subjective experience can be truly shared with others is difficult to assess. Nevertheless emotion contagion is often inferred from the presence of behavioural mimicry, yet individuals may present different behavioural responses while in potentially similar states, or present similar behavioural responses while in potentially different states (Isern-Mas & Gomila, 2019). The emotion contagion framework also tends to confuse variation in both arousal and valence, the latter being more challenging to assess (Mendl et al., 2009, 2010). Therefore, although emotional contagion is an important mechanism related to empathy, its presence and proposed link to empathy should be stated carefully (Huber et al., 2017).

4.2.2 The evolutionary roots of empathy: humans and great apes

Similar to human children (Zahn-Waxler et al., 1985; Zahn-Waxler, Robinson, et al., 1992a; Eisenberg et al., 2006), great apes (bonobos: Palagi et al., 2004; Clay and de Waal, 2013a, 2013b; chimpanzees: de Waal and van Roosmalen, 1979; Romero & de Waal, 2010; gorillas: Cordoni et al., 2006) sometimes spontaneously approach conspecifics in distress to offer them comfort. This behaviour – known as consolation- is considered as a marker of sympathetic concern (de Waal, 2008; de Waal & Preston, 2017; Fraser et al., 2008; Romero et al., 2010). I discuss this in *Chapter 1*.

In the human literature, there are robust empirical effects of similarity, familiarity, past experiences, explicit teaching, and salience for empathy (see Preston & de Waal 2002 for a review). In great apes, consolation is preferentially offered to socially close individuals (Romero et al., 2010; Clay & de Waal, 2013a; Palagi & Norscia, 2013). These findings suggest shared evolutionary roots among humans and great apes of the sensitivity to others' emotional expressions and its impact on empathy.

4.2.3 Investigating emotion contagion and empathy using infrared thermography

Comparative research addressing the mechanisms underlying empathy can benefit from non-invasive and contact-free technologies – particularly when combined with other approaches. Infrared thermography (IRT) is a promising non-invasive technology (Speakman & Ward, 1998) that can be used to assess underlying affective states in both humans (Ioannou, Gallese, et al., 2014) and animals (Chotard et al., 2018; Dezecache et al., 2017; Kano et al., 2016); something I present in *Chapter 2*. Importantly, IRT permits the measurement of the skin temperature in various experimental settings without restraining the subject (Ioannou et al., 2015), as well as in more naturalistic conditions. For example, an experimental study on captive chimpanzees reported a decrease in nasal skin temperature when hearing and watching fights of conspecifics (Kano et al., 2016), and a study conducted on wild chimpanzees showed a decrease in nasal skin temperature and an increase in ear temperature when hearing aversive calls of conspecifics (Dezecache et al., 2017).

Thus far, several studies demonstrate a link between negative emotional states and a decrease in nasal skin temperature (e.g. in humans, Ioannou et al. 2013; in monkeys, Nakayama et al. 2005; in pigs, Boileau et al. 2019). Studies investigating positive states and how they relate to the variation in facial skin temperature are more inconsistent (overview: Chotard et al. 2018). For non-human primates, divergences in IRT findings may be explained by the variation in the experimental stimuli but also variance in the regions of interest (ROIs) studied. Indeed, in one study of three monkey and two ape species, Chotard and colleagues (2018) found differences in temperature variations between positive and negative conditions, along with specific variations for different facial ROIs, explained due to their differences in blood supply. The induction of positive emotional states was linked to a decreased nose tip skin temperature and increased periorbital skin temperature, while the induction of negative ones was linked to increased upper lip skin temperature. Emotion research with IRT is still in its infancy, therefore we still need to understand better the potential variation between ROI and what implications that might have for findings.

Although IRT can thus be helpful to examine arousal changes, alone it may lack strong predictive power for detecting valence – just like the observation of the behaviour alone cannot properly inform on valence. Thus, it is crucial to combine multiple methods to understand the basis of an emotional response (Burkett et al., 2016; Oliveira et al., 2017). In a study on domestic chickens, Edgar et al. (2011) reported physiological (e.g., eye temperature, heart rate) and behavioural (preening, attention, vocalisations) reactions of hens witnessing the distress of their offspring. Because some of the changes were specifically reported in the distress intervention condition compared to the other conditions, it was possible to link the mother hens' responses to the condition of interest. Such combinations between physiological and behavioural measures are still lacking in the primate literature where a multi-componential approach is needed to validate and/or challenge assumptions made in the empathy literature. Addressing this issue, the present study combines observations and physiological measurements to investigate emotional contagion and its links to empathy in a great ape species.

This study is structured in two parts. **Part One** examines the link between consolation tendencies recorded in naturalistic settings and experimental data of a subject's thermal response to observing distress in conspecifics. In **Part Two**, I investigate the effect of stimulus valence and familiarity on chimpanzees' thermal response to human emotional stimuli in experimental settings. In *Appendix 4.1,* I explore the temporal dynamics and physical pattern of the thermal response of chimpanzees in order to examine how an emotional response translates into facial skin temperature changes.

4.2.4 Part One: How do chimpanzees respond to conspecifics' distress?

In **Part One**, I combined naturalistic observations with opportunistic behavioural experiments using infrared thermography (IRT) to investigate how chimpanzees experience affective states of conspecifics and whether this is predicted by their socio-affective behaviours in naturalistic situations. Importantly, chimpanzees show internal signs of arousal to emotional stimuli in the absence of a behavioural emotional response (Sato et al., 2019). Therefore, physiological measurements are crucial to identify the subject's arousal as observable measures alone are insufficient. Due to the methodological challenge of simultaneously measuring subjects' live physiological responses along with their prosocial behaviour, the connection between the two components can be investigated indirectly. This paradigm was used in previous empirical studies investigating physiological responses and their link with prosocial behaviours in children (Hastings et al., 2006). In the observational phase, I examined an individual's tendency to offer consolation to victims of naturally occurring social conflict (i.e., post-conflict situations). In the experimental phase, I assessed the thermal and behavioural responses of the same chimpanzees in response to video-based stimuli of familiar conspecifics in distress.

4.2.4.1 Hypothesis 1.1: Inner arousal predicts consolation tendency

In children, observing someone else in need of help appears to trigger internal changes in emotional arousal (Eisenberg et al., 1990; Hastings et al., 2006; Knafo et al., 2008) suggesting that children's prosociality (Posner et al., 2005) may be explained as an emotional response (Hepach, 2017; Hepach et al., 2013). This hypothesis was supported by studies using pupillometry that showed that children's affective arousal is strongest when observing others in need, where subsequent helping serves to reduce their arousal levels (Hepach, 2017; Hepach et al., 2017). In line with these findings, I hypothesised that the inner arousal will increase when chimpanzees witness the distress of a conspecific – and that this may represent the underlying motivation to comfort a distressed individual (**hypothesis 1.1**). Therefore, I tested the prediction that chimpanzees who show stronger changes in inner arousal (measured via IRT) in the experimental phase will demonstrate a higher tendency to offer consolation in naturalistic scenarios.

4.2.4.2 Hypothesis 1.2: Inner arousal predicts victim anxiety – investigating emotion regulation

If affective arousal serves as the motivation to help others, it is also crucial to investigate the mechanisms that regulate this arousal. Indeed, in order to effectively respond to someone else's states, empathy also depends on the ability to regulate one's own emotional responses to the situation (Bradley, 2000; Decety, 2011; Eisenberg & Eggum, 2009; Schipper & Petermann, 2013; van der Merwe & Dawes, 2000). Emotion regulation broadly refers to internal processes involved in managing one's behaviour, thoughts, and emotions, given a situation (Koole, 2009). More details about emotion regulation and links to empathy are provided in *Chapter 1*. IRT gives us access to the fluctuation of a subject's arousal, therefore allowing to investigate its potential regulation by looking at the strength of the arousal as well as its duration and latency to return to baseline (Moliné et al., 2017). However, it is relevant to note that while an increase in arousal might serve as the underlying motivation to help and comfort a distressed individual (Hypothesis 1.1 – see section above), it also might be a sign of personal distress (Parr, 2001; Sato et al., 2019).

Here, I was interested in whether an individual's apparent level of anxiety in naturalistic settings related to the strength of their emotional response as measured through the IRT experiment. To do so, I examined an individual's state of anxiety when they were a victim during post-conflict periods, using self-directed behaviour as a proxy for anxiety (Baker & Aureli, 1997; Castles et al., 1999; Kutsukake, 2003). Note that I assessed an individual's state of anxiety when they were a victim during post-conflicts periods rather than when in the role of bystander during post-conflicts periods. Although the latter might have been more suitable to assess the hypothesis of the effect of anxiety on consolation, practical limitations precluded me from attaining these data from the bystanders (i.e., the focal subject in these videos, collected for a previous project, was the victim rather than the bystander– see *Chapter 2*). I compared victim anxiety in naturalistic settings to the same individual's inner arousal (IRT) when witnessing a conspecific in distress in an experimental scenario. When viewing another's distress, regulatory processes influence affective and behavioural responses (Decety, 2011; Gross, 1998); for instance, down-regulation of affect is essential for preventing over-arousal (i.e., personal distress, Eisenberg, 2000) to enable concern for others (see *Chapter 1*). I hypothesised that high and long-lasting levels of arousal at the physiological level indicate poor emotion regulation skills, thus translating into high levels of behavioural markers of anxiety. In addition, I hypothesised that the processes regulating the strength of the arousal are not yet mature in younger individuals, but develop with age (Eisenberg & Fabes, 2006, **hypothesis 1.2**). Hence, I predicted that chimpanzees who demonstrate higher levels of anxiety in naturalistic settings would show stronger early and more prolonged arousal changes (measured via IRT) when watching a conspecific in distress in the experimental phase. Indeed, a fast and strong change would translate into over-arousal, while a slow return to baseline would translate into difficulty to regulate (Eisenberg & Fabes, 1992; Ungerer et al., 1990). I also predicted younger individuals would show stronger inner arousal in response to the affective stimuli and more difficulties to regulate their arousal (Eisenberg & Fabes, 2006).

In sum, according to my hypothesis, reduced emotion regulation skills will translate into a higher and longer arousal and thus greater anxiety in naturalistic conditions.

4.2.5 Part Two: How do chimpanzees respond to the positive and negative affective states of familiar and unfamiliar humans?

In **Part Two**, I examined whether changes in chimpanzee arousal (as measured via facial skin temperature) were predicted by the familiarity of human actors displaying positive and negative affective states.

4.2.5.1 Hypothesis 2.1: The social bias of empathy

Although the empathy bias towards familiar and socially close partners (Preston & de Waal, 2002, and see *Chapter 1*) has been widely demonstrated at a behavioural level (e.g., Clay and de Waal 2013b), the underlying mechanisms for these biases have not been investigated in great apes. I hypothesised that external markers of the empathy bias (i.e., behavioural markers) are predicted by corresponding biases recorded at the physiological level (i.e., changes in the activity of the autonomous nervous system) in regard to emotion responding (**hypothesis 2.1**). Furthermore, social awareness and cognitive control develop across age (Clay & de Waal, 2013a, 2013b; Cordoni et al., 2006; Webb et al., 2017). Therefore, I predicted that chimpanzees would show stronger inner arousal (measured via IRT) to the emotional states of familiar individuals (in this case their keepers) in comparison to strangers (in this case unfamiliar locals, Berlo et al., 2020; Kret et al., 2016), with this selectivity being stronger in older individuals due to developmental effects. Note that the familiar individuals used as stimuli here were not more familiar to older individuals than younger individuals as they arrived after the younger subjects were born.

4.2.5.2 Hypothesis 2.2: Stimulus valence predicts inner arousal

Emotional components are usually divided according to the dimensions of *arousal* and *valence* (Barrett et al., 2006; Mendl et al., 2010; Russell, 2003). While *valence* has been traditionally difficult to study, the investigation of thermal profiles might provide relevant information on both the *arousal* (i.e., the magnitude of the temperature change) and potentially the *valence* (i.e., the direction of the temperature change). Indeed, negative affect seems to trigger a drop in skin temperature (Kano et al., 2016) while positive affect seems to trigger a rise (Chotard et al., 2018). I therefore hypothesised that IRT measurements would inform on both the *valence* and *arousal* dimensions (**hypothesis 2.2**), with the direction and strength of the change in thermal response being predicted by stimulus valence. I predicted that the facial skin temperature will drop in the negative condition (Kano et al., 2016) and increase in the positive condition (Chotard et al., 2018). With changes in arousal preparing the individual for action, I also predicted that the change will be greater in the negative condition than in the positive condition that is not threatening and requires less of a quick behavioural response.

4.3 Methods

4.3.1 Ethical statement

This study was approved by and carried out in strict accordance with the rules and requirements of the Psychology department and Ethics committee as well as the Animal Welfare Ethical Review Board (AWERB) at Durham University (UK). It has also been accepted by the

Chimfunshi Research Advisory Board (CRAB). The field work was supported by the National Geographic Society and the Lucy Burgers for Comparative Research Foundation.

4.3.2 Study site and subjects

Subjects were 25 chimpanzees (*Pan troglodytes*) from all age (mean age: 22 ± 11-year-old, min = 2 and max = 42) and sex classes (16♀) from 5 different enclosures at Chimfunshi Wildlife Orphanage (CWO, Zambia – Figure 4.1), see *Chapter 2*.

Figure 4.1 Satellite view of the five enclosures housing groups 1, 2, 3, 4, and 5, i.e., the “escape artists”, at CWO, Zambia (© Google Maps)

Subjects of the present study were divided into two age classes: below and above 8 years old (see *Chapter 2*, Table 4.1).

Table 4.1 Sex, age class, and group of the subjects. Only Group 2 was observed in naturalistic conditions

	Females		**Males**	
	below 8yo	**above 8yo**	**below 8yo**	**above 8yo**
Group 1	3	9		2
Group 2	2	16	17	11
Group 3		8		
Group 4				10
Group 5		3		1

The chimpanzees lived in large outdoor enclosures ranging from 47 to 190 acres and containing grasslands and forests in the miombo woodland, a common habitat for wild chimpanzee populations. I studied four multimale-multifemale colonies with natural fission-fusion dynamics and one group composed of individuals who have been separated from the main groups because of repeated escapes. Each of the four main colonies was composed of a mixture of wild-born chimpanzees and chimpanzees born at CWO (see Davila-Ross et al. 2011). Wild-born chimpanzees come from various phylogenetic and geographical backgrounds, with a mixture of subspecies including *Pan troglodytes troglodytes* and *Pan troglodytes schweinfurthii*. The chimpanzees were fed up to three times a day. The main feeding took place around midday when most of the chimpanzees were brought into the indoor facilities for a couple of hours. They were provided with a variety of fruits and vegetables. During this time, the keepers and the vet had the opportunity to closely check on the chimpanzees, and provide medical attention and treatment (e.g., contraceptive pill) when necessary. Other smaller feeding consisted of throwing fruits, vegetables, or sometimes popcorn over the fence into the outdoor area to trigger foraging behaviours as enrichment. The time of these smaller feedings could vary depending on the presence of visitors but usually took place around 9 am and 4 pm. During these times, most chimpanzees were visible for observation. The chimpanzees could also forage on naturally fruiting trees present in the enclosures and hunt insects, amphibians, and small mammals occasionally, and during the night they slept in the outdoor area in nests they built. The indoor spaces of the four main colonies were made of several rooms separated by metallic bars to allow a separation of the chimpanzees by families in order to limit tensions during the feeding. Only the group of the “escape artists” lived in a small enclosure with no access to a large natural outdoor space (this changed in 2020: the four escape artists now have access to a large natural outdoor space!).

Chimpanzees from the five enclosures were potential subjects for the physiological experiment, while the naturalistic observations were conducted only in the enclosure containing the largest social group (i.e., 52 chimpanzees in enclosure 2 – recordings by J. B. and Z. G. – *Chapter 2*).

4.3.3 Behavioural observations

4.3.3.1 Spontaneous post-conflict and post-distress situations

Behavioural observations were conducted from March to July 2019 (*Chapter 2*) using two Panasonic HDC-HS100 camcorders, one with a Sennheiser MKE 400 shotgun microphone. Following a spontaneous distress (post-distress; PD) or a social conflict (post-conflict; PC), the observers followed the victim of aggression and recorded all occurrences of affiliative behaviours. To examine an individual’s degree of emotional arousal as a victim, I also examined measures of self-directed behaviours including self-scratching, self-touching, and self-grooming (see ethogram in *Chapter 2*, Table 2.3). The ethogram did include coprophagy, head shake, and hair plucking but these were never observed during the post-conflict periods. The procedures have been explained further in *Chapter 2*.

4.3.3.2 Inter-coder reliability testing

I computed Cohen's kappa tests on 20.5% of the data set (N = 33 PCs and PDs) to assess the absolute agreement between the main coder and two extra coders (coder A coded N = 19 events, and coder B coded N = 14 events) in coding i/ the occurrence of an interaction (based on the relative probability that one might randomly code an interaction), ii/ the identity of the interaction bystander (based on interactions that were agreed upon), iii/ the initiator of the first behaviour in an interaction (i.e., victim or bystander, based on interactions that were agreed upon), and iv/ the occurrence of a consolation (based on the relative probability that one might randomly code a consolation). The two inter-rater reliability coders were well trained in coding chimpanzee behaviours, and familiar with the main hypothesis of the study.

4.3.4 IRT experiments

4.3.4.1 Stimulus collection for Part One – Chimpanzees in distress

To create stimuli of conspecific emotional expressions, I extracted video clips from the post-conflict periods recorded for the observation data. I focused on scenes where an individual was in a distressed (*negative affect*). Distressed state refers to a post-conflict situation where the victim of the conflict vocalises and displays distress behaviours. The initial clips extracted ranged between 10 and 15 seconds and were looped to create a final stimulus of 90 seconds focusing on one individual. To control for sexual arousal, age/sex, and hierarchy effects, I included only non-swelling mature females as stimuli. Facial expressions were visible at various points, and only the individual of interest was visible and audible in the clip. The intensity of the different stimuli was rated by two independent coders to insure all the stimuli were of similar intensity (e.g., low, moderate, high intensity; moderate stimuli were selected).

4.3.4.2 Stimulus collection for Part Two – Familiar and unfamiliar humans enacting positive and negative affects

To examine the effects of social familiarity on emotion responses, I recruited 10 chimpanzee keepers and 10 villagers (unfamiliar to the chimpanzees) willing to enact positive affect (embodied with facial expressions, body movements, and mild volume vocalisations). All the keepers and villagers recruited were male from a broad age range (approximately 25 to 55 years old) and their clothes were similar with neutral-coloured T-shirts. This enabled comparability between the two conditions as only male caregivers were working with the chimpanzees during the data collection period.

To create the stimuli, I first showed the volunteers an example video and my local research assistant asked them to simulate the positive emotional response. I extensively trained the local research assistant and the emotional stimuli required for it. In the positive condition, the actor was asked to be happy (facial expressions of happiness with smiling and laughing – see Figure 4.2). I recorded several trials with each actor in order to select the best one. The realism (realistic, unrealistic) and intensity (low, moderate, high) of the clips were evaluated by myself and an independent coder, and those we judged as "unrealistic" (i.e., the person breaks character, e.g., laughing during the negative display, does not show the emotion required, e.g., neither in facial expression nor body language or vocalisation, exaggerates the emotion too much) and/or too intense (i.e., intense emotional expression with very loud vocalisations and intense facial expressions) or not intense enough (i.e., little to no emotion, no change in facial expression, in comparison to neutral, few vocalisations) were excluded.

Figure 4.2 Screenshot of a human positive facial expression used as stimuli in my experiment – with permission

To examine the effects of valence, I further asked the 10 keepers to enact sadness (facial expressions of sadness, hunched body movements, sobbing vocalisations – see Figure 4.3) for 80 seconds before visibly showing themselves to feel better for 10 sec; this final component ensured the vignette ended on a positive note.

Figure 4.3 Screenshot of a human negative facial expression used as stimuli in my experiment – with permission

4.3.4.3 Design and procedure

Data for the IRT experiment were collected within the same year but subsequent to the observational data collection, from July to September 2019. To collect the IRT data, I tested the chimpanzees in their indoor facilities after the midday feeding when they were resting and waiting to be released so as not to interfere with the feeding routine or the work of the keepers, see *Chapter 2*. This data collection took place from July to September 2019. I opportunistically presented the relevant video stimuli to an individual resting at the proximity of the feeding platform (ideally alone). The laptop, camcorder, and the thermal camera were placed on an apparatus out of reach from the chimpanzees (about 1.5 metres away – see Figure 4.4).

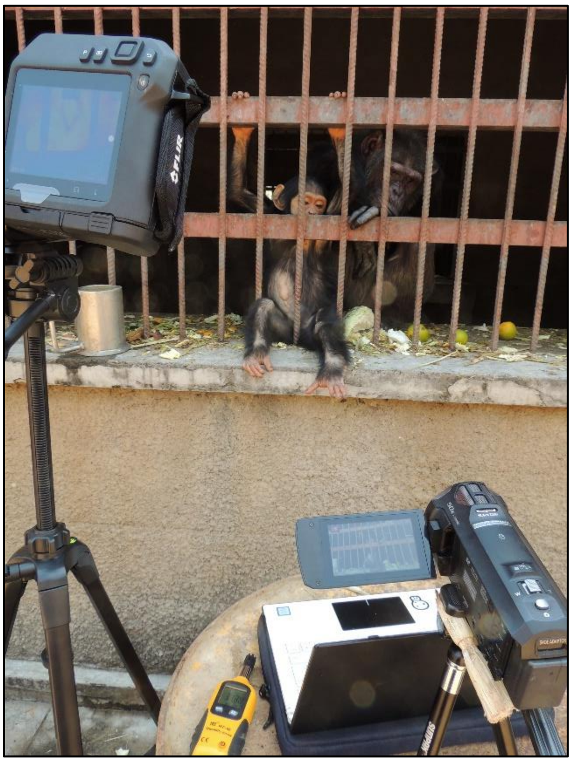


Figure 4.4 Experimental set-up, with the FLIR thermal camera, the camera recorder, the laptop, and the temperature and humidity data logger

I recorded the temperature and humidity at least once every minute and controlled for their potential variation within testing sessions in the analyses.

I played the video stimuli in a randomised order for 90 seconds (1.5 minutes), with a 30-sec baseline (moving car with white noise) and 2 min recuperation phase after each emotional condition. I used four human stimuli of each valence, and they were counterbalanced across subjects. Depending on the willingness and attention of the subject toward the stimuli, I played one or several stimuli over one testing episode or showed additional stimuli across several days. Details about the different phases of the stimulus are provided in *Chapter 2* (i.e., acclimatisation, baseline, testing, and recovery phases). When several individuals attended the stimulus at the same time, I focused the data collection on one single individual and noted the identity of the other chimpanzees in order to avoid testing them with the same stimulus later.

4.3.4.4 Data coding and processing

4.3.4.4.1 Naturalistic behavioural data

Data recorded during naturally occurring PCs and PDs are detailed in *Chapter 2*. This involves PC and PD affiliations, victim recovery time, victim distress and aggressive interactions.

4.3.4.4.2 Thermal data

4.3.4.4.3 Continuous measurements

With the help of two student research assistants, I extracted the temperature at four ROIs: the periorbital (PO), nose bridge (NB), nose tip (NT), and upper lip (UL) regions (see Figure 4.5).

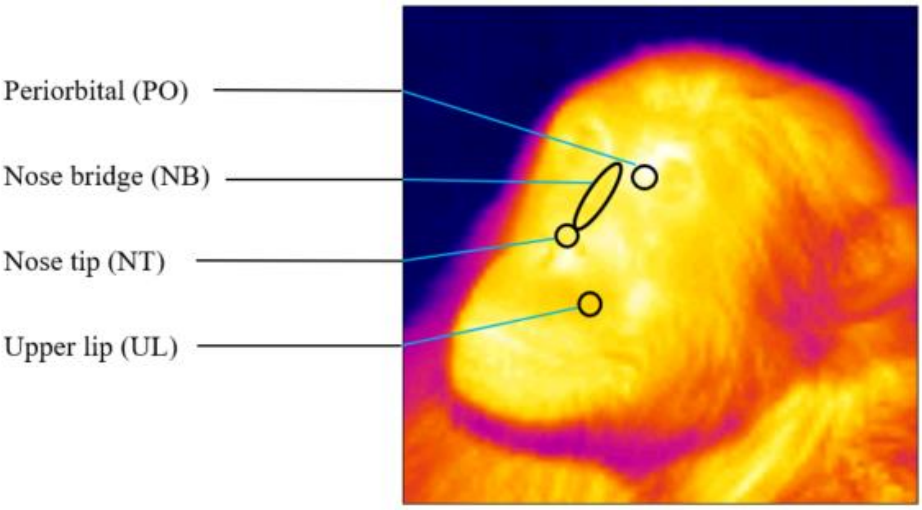


Figure 4.5 The four facial regions of interest I used in my IRT experiments

I recorded the minimum, maximum, and average temperatures every 10 seconds during baseline (i.e., 10-second intervals from −30 to 0 seconds relative to the stimulus onset), testing phase (i.e., from 10 to 110 seconds relative to the stimulus onset), and recuperation phase (i.e., from 10 to 120 seconds relative to the stimulus offset). I selected frames in which the face was in a similar angle, usually facing forward (Ioannou, Gallese, et al., 2014) and avoided the frames in which the facial image was blurred due to head motion (Kano et al., 2016). When I could not find the optimal frame (see criteria above) within ± 10 seconds, time points were excluded.

4.3.4.4.4 Time points

From the continuous measurements, I extracted four key measures after the stimulus onset and offset, i.e., i/ shortly after the stimulus onset (+20 sec), ii/ later after stimuli onset (+80 sec), iii/ shortly after the stimulus offset (+50 sec), and iv/ later after the stimulus offset (+110 sec) (see Figure 4.6). When a measure was not available but both the preceding and following measures were recorded (±10 seconds), I considered the average value of the two measures.

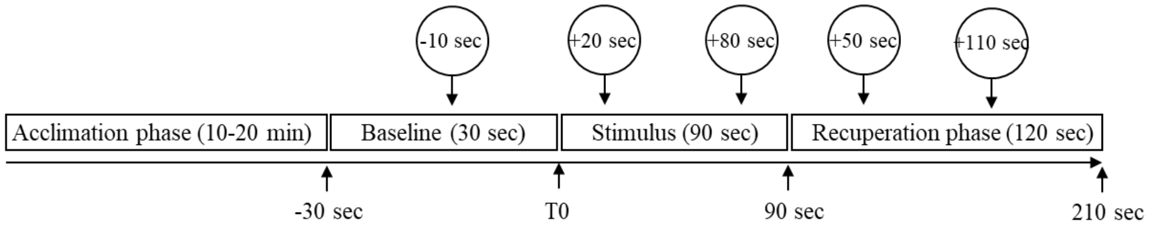


Figure 4.6 Key time points for thermal measurement extraction (in circles) during the three phases of the trial (i.e., baseline, stimulus presentation, and recuperation phase), and acclimation phase. The duration of each phase is indicated in brackets.

Raw thermal data (min, max, and average temperature extracted every 10 seconds) were visually inspected to check the overall time trend of the response. The measurement extracted during the baseline was subtracted from the data collected at 20 (i.e., early stimulus) and 80 (i.e., late stimulus) seconds after the onset of the stimulus, and 50 (i.e., early recuperation) and

110 (i.e., late recuperation) seconds after the offset of the stimulus. I inspected the distribution of the covariate and the distribution of the response. No data transformation on the temperature was conducted because they had a near normal distribution.

4.3.4.4.5 Experimental behavioural data

With the help of two research assistants, I coded behavioural variables during the trial in order to control for stimulus attention (i.e., looking at the screen), the production of facial expressions (presence/absence), the production of vocalisations (presence/absence), the production of self-directed behaviours (presence/absence), and subject movement (i.e., none, or up and moving). Behaviours within each category are mutually exclusive. The presence of other chimpanzees and their proximity to the subject were also recorded. The ethogram depicting the behavioural coding system is provided in *Appendix 4.2*. For a trial to be included in the data set, the subject had to look at the screen and record no major movement for a minimum of 75% of the trial.

4.3.4.5 Inter-coder reliability

4.3.4.5.1 For the IRT data

I computed intraclass correlations coefficients (ICC, Shrout and Fleiss 1979; Koo and Li 2016) on 15% of the data set. I used the function icc() from the irr package in R to assess the absolute agreement between three coders in extracting the facial temperature from the four regions of interest using the two-way random effect models and "single rater" unit.

4.3.4.5.2 For the experimental behavioural data

I computed Cohen’s kappa tests on 15% of the dataset to assess the absolute agreement between the main coder and another coder for duration and occurrences of the following: attention towards the display, presence of facial expressions, presence of vocalisations, presence of self-directed behaviours, movements, audience.

4.3.5 Statistical analyses

4.3.5.1 Generalised Linear Mixed Models (GLMMs)

I used generalised linear mixed models (GLMMs, Baayen et al. 2008) to test my hypotheses in Part Two regarding stimulus valence and familiarity. I detail how I use GLMMs in *Chapter 2*.

As temperature change data were close to a normal distribution, no transformation was required. I included subject ID as a random factor (nested with the familiarity and valence factors, which were added as random slopes). The response variables, fixed effects, and control variables are detailed for each model below.

4.3.5.2 Part One: How do chimpanzees respond to conspecifics' distress?

4.3.5.2.1 Testing for Hypothesis 1.1. Inner arousal predicts consolation tendency

To analyse whether the physiological response measured during the experimental manipulations predicted the tendency to express empathic behaviours in naturalistic settings, I ran four bivariate Pearson correlation tests. I examined whether 1/ the consolation rate per subject correlates with the change in facial skin temperature (in Celsius degrees, mean per subject) relative to baseline at +20 seconds and 80 seconds following the onset of the stimulus for the periorbital and the nose tip regions (see 4.4.2 for details). Consolation rate was measured as the number of unsolicited affiliative interactions initiated by the subject to a distressed victim *divided* by the total number of times that individual had been a bystander in post-conflict and post-distress periods then transformed to fit a normal distribution using a log function. This analysis was based on data from N = 13 individuals (9 ♀; mean age: 22 ± 13 years old) tested in the distressed conspecific condition. Each subject observed at least 30 PC and PD situations (min = 32; max = 149; average = 97). N = 6 initiated an affiliative interaction with a victim in distress during a post-conflict or post-distress period, while N = 7 never consoled. The human experimental condition was not included as it was deemed as having less ecological validity than responses to a conspecific.

4.3.5.2.2 Testing for Hypothesis 1.2. Inner arousal predicts victim anxiety behaviours – investigating emotion regulation and/or personal distress

I ran four bivariate Pearson correlation tests to test whether the physiological response measured during the experimental manipulation predicts the tendency to express anxiety behaviours in naturalistic settings, i.e., self-scratch rate during spontaneous post-distress and post-conflict interactions. The variables were the self-scratching rate transformed to fit a normal distribution using a log function, and the change in facial skin temperature (in Celsius, mean per subject) relative to baseline at +20 seconds and 80 seconds following the onset of the stimulus for the periorbital and the nose tip regions. This analysis was based on data from N = 13 individuals (9 ♀; mean age: 22 ± 13-year-old). I analysed data from the distressed-familiar-conspecific condition.

4.3.5.3 Part Two: How do chimpanzees respond to the affective states of familiar and unfamiliar humans?

4.3.5.3.1 Testing for Hypothesis 2.1. The social bias of empathy

To test whether stimulus familiarity predicts the physiological reaction of the subject, I fitted four general linear mixed models. The dependent variables were the change in facial skin temperature (in Celsius) relative to baseline at 20 and 80 seconds following the onset of the stimulus (familiar positive vs unfamiliar positive human) for the periorbital and the nose tip regions that fitted normal distribution. The predictors in the model were model familiarity (familiar vs unfamiliar), subject age (continuous; years), and sex (male, female), and the interaction between subject age and model familiarity. The control effect was the stimulus ID (i.e., videoed human’s ID, N = 4). Random intercepts were modelled to account for individual variation and repeated measures of the subject (subject ID). This analysis was based on data from N = 13 individuals (7♀, mean age: 21 ± 10 years old) tested in the familiar and unfamiliar human positive condition. I could not investigate the effect of familiarity for the negative condition because the quality of the video stimuli collected for the negative condition with unfamiliar individuals did not meet the quality required to be included.

4.3.5.3.2 Testing for Hypothesis 2.2. Stimulus valence predicts inner arousal

To analyse whether the stimulus valence for familiar human models predicted the physiological reaction of the subject, I fitted four general linear mixed models. The dependent variables were the subject's change in facial skin temperature (in Celsius) relative to baseline at 20 and 80 seconds following the onset of the stimulus for the periorbital and the nose tip regions that fitted normal distribution. The predictors in the model were stimulus valence (positive, negative) and subject age (continuous; years) and sex (male, female), and an interaction term between subject age and the valence of the stimulus. Although I also intended to include the control variable of audience (i.e., presence vs absence of conspecifics within arm's reach), I had to eventually exclude it from the model owing to convergence issues and model complexity. The control effect was stimulus model ID. Random intercepts of subject ID were modelled to account for individual variation and repeated measures. This analysis was based on data from N = 17 individuals (9♀, mean age: 21 ± 10 years old) who I was able to test across valence and familiarity conditions. I only used familiar human models to test stimulus valence because the quality of the video stimuli collected for the negative condition with unfamiliar individuals did not meet the quality required to be included.

4.4 Results

4.4.1 Inter-coder reliability

4.4.1.1 Naturalistic observations

There was an excellent (Koo and Li 2016) absolute agreement between the main coder and the two coders for i/ the occurrence of an interaction (based on the relative probability that one might randomly code an interaction, kappa = 0.91), ii/ the identity of the interaction bystander (based on interactions that were agreed upon, kappa = 0.95), iii/ the initiator of the first behaviour in an interaction (i.e., victim or bystander, based on interactions that were agreed upon, kappa = 0.97), iv/ the occurrence of a consolation (based on the relative probability that one might randomly code a consolation, kappa = 0.85), v/ the occurrence of self-directed behaviours (based on the relative probability that one might randomly code a consolation, kappa = 0.80). The absolute agreements are presented in *Appendix 4.3*.

4.4.1.2 IRT data

There was a **moderate** (Koo and Li 2016) absolute agreement between the three coders for the upper lip region (kappa = 0.727, p < 0.001), a good absolute agreement for the periorbital region (kappa = 0.878, p < 0.001), and excellent absolute agreement for the nose bridge (kappa = 0.982, p < 0.001) and the nose tip (kappa = 0.991, p < 0.001) regions. Results are provided in *Appendix 4.4*.

The variability of the measures can be explained by both the frame selection (20-second window) and the selection of the region of interest. Given the lower reliability of the coding of the upper lip, I excluded this region's data from the study.

4.4.1.3 Experimental behavioural data

The agreement between the two coders was good to excellent for the categories of behaviours when looking at duration and occurrences: attention towards the emotional display, kappa = 0.93; presence of facial expressions, kappa = 0.98; presence of vocalisations, kappa = 0.99; presence of self-directed behaviours, kappa = 0.81; movements, kappa = 0.98; and audience, kappa = 0.97.

4.4.2 Results for Part One: How do chimpanzees respond to conspecifics' distress?

Because most of the affective studies using thermography technology have looked at the nose tip region (Kano et al., 2016), I selected this ROI for the current study in order to facilitate results comparison. According to the temporal dynamics of the thermal response presented in *Appendix 4.1*, the temperature change recorded in the upper lip region does not correlate with the temperature change in the three other regions, so I included it independently in the analyses conducted below. Furthermore, for a given ROI, the temperature change recorded at the four experimental time points correlated. Therefore, I focus only on the earliest experimental time point, i.e., early stimulus, to test for the main hypotheses.

4.4.2.1 Results for Hypothesis 1.1. Inner arousal predicts consolation tendency

The consolation rate observed in naturalistic settings did not correlate with the change of temperature in the experiment in the periorbital region at +20 ($r = 0.402$, $p = 0.173$, $N = 13$) and +80 seconds ($r = 0.335$, $p = 0.263$, $N = 13$) after stimulus onset, nor with the change of temperature in the nose tip region at +20 ($r = -0.083$, $p = 0.809$, $N = 11$) and +80 seconds ($r = 0.033$, $p = 0.923$, $N = 11$) after stimulus onset.

When excluding the data for the $N = 7$ subjects who did not initiate any consolation, the consolation rate did positively correlate with increased temperature in the periorbital region at

+20s (r = 0.943, p = 0.005, N = 6). The average change was +0.2 Celsius degrees. This was not the case at +80s (r = 0.771, p = 0.072, N = 6) after stimulus onset. There was no significant effect on the change of temperature in the nose tip region at +20s (r = 0.100, p = 0.873, N = 5) and +80s (r = 0.486, p = 0.329, N = 6) after stimulus onset.

An overview of the consolation rates and change of facial skin temperature change per subject is provided in Table 4.2.

Table 4.2 Consolation rates and change of facial skin temperature means for the periorbital and nose tip regions at +20 and +80 seconds following the stimulus onset

		Regions of Interest			
		Periorbital		**Nose tip**	
ID code	**Consolation rate**	**+20 sec**	**+80 sec**	**+20 sec**	**+80 sec**
DA	0.111	0.6	0.85	0.2	-0.65
DV	0	0	1	-0.7	0
DI	0.027	0.4	1.4	-0.8	1.2
DR	0.010	-0.6	-1.45	*NA*	0
JA	0	-1	*NA*	0.1	*NA*
JO	0.061	2.7	-0.5	-0.9	-1.7
MG	0	2.5	*NA*	0.15	2
MS	0	-1.2	2.4	0.3	0.7
ME	0.010	-0.1	-0.1	0.1	0
MM	0	-0.2	0.55	0.3	0.55
NO	0	-0.6	*NA*	-0.7	*NA*
TR	0	0.2	*NA*	*NA*	*NA*
ZS	0.013	0.05	0.4	0.15	-0.1

4.4.2.2 Results for Hypothesis 1.2. Inner arousal predicts victim anxiety behaviours – investigating emotion regulation and/or personal distress

Out of the 16 individuals that I could include for this analysis, **N = 3** showed a minimum of 2 seconds of self-directed behaviour. Therefore, I could not run the analyses. The self-directed behaviour data is presented in *Appendix 4.5*.

4.4.3 Results for Part Two: How do chimpanzees respond to the affective states of familiar and unfamiliar humans?

4.4.3.1 Results for Hypothesis 2.1. The social bias of empathy

The full model for change in nose tip temperature explained the data significantly better than the null model, which contained only the intercept, control, and random effects- at +20 seconds (χ^2 = 17.27, d.f. = 3, $p < 0.001$; Table 4.3) and +80 seconds (χ^2 = 11.80, d.f. = 3, $p < 0.001$) after stimulus onset. This was not the case for the periorbital region (+20 seconds: χ^2 = 5.58, d.f. = 3, p = 0.134; +80 seconds: χ^2 = 2.96, d.f. = 3, p = 0.397).

Table 4.3 Results comparing full-null models with the change in skin temperature relative to baseline in the periorbital (PO) and nose tip (NT) regions at +20 and +80 seconds after stimulus onset

ROI	*Time point*	*χ2*	*d.f.*	*p*	*N obs*
PO	+20 sec	5.58 (1.62)	3 (2)	0.134 (0.445)	22
	+80 sec	2.96 (0.97)	3 (2)	0.397 (0.617)	22
NT	**+20 sec**	17.27	3	**<0.001**	25
	+80 sec	11.80	3	**<0.001**	22

Significant values (P<0.05) are in **bold;** in brackets are the result from full-null comparison without the interaction between familiarity and age

For the nose tip temperature, I then interpreted the model estimates. There was a significant interaction between subject age and stimulus familiarity on mean temperature change at 20s (estimate ± se = -0.08 ± 0.03, t = -2.93, p = 0.008; Table 4.4). When seeing an unfamiliar human displaying positive affect, nose tip temperature increased in younger subjects while it decreased in older ones. No effect of subject sex was detected for nose tip temperature change (estimate ± se = -0.19 ± 0.26, t = -0.72, p = 0.480).

Table 4.4 Results of the full model testing the effect of familiarity, age, and sex on temperature change in the nose tip region at +20 seconds

S.E.: standard error; P: p-value

Fixed effect	***Estimate***	***S.E.***	***t value***	***P***
(Intercept)	-0.211	0.619	-0.340	0.738
Familiarity (Unfamiliar) * Age	-0.077	0.026	-2.928	**0.008**
Sex (Male)	-0.190	0.263	-0.721	0.480

Significant values (P<0.05) are in **bold**

There was an interaction between subject age and stimulus familiarity on the mean temperature change of the nose tip at 80 seconds which approached significance (estimate ± se = 0.10 ± 0.05, t = -1.99, p = 0.065; Table 4.5). This developmental trend was not salient when the subject saw someone familiar, with the temperature decreasing similarly in young and older subjects. No effect of sex was detected (estimate ± se = -0.02 ± 0.50, t = -1.73, p = 0.105).

Table 4.5 Results of the full model testing the effect of familiarity, age, and sex on temperature change in the nose tip region at +80 seconds

S.E.: standard error; P: p-value

Fixed effect	*Estimate*	*S.E.*	*t value*	*P*
(Intercept)	0.258	1.128	0.229	0.822
Familiarity (Unfamiliar) * Age	-0.096	0.048	-1.991	0.065
Sex (Male)	-0.018	0.504	-1.725	0.105

Almost significant values are underlined (P < 0.09)

4.4.3.2 Results for Hypothesis 2.2. Stimulus valence predicts inner arousal

The full model for the change in the skin temperature of the periorbital region explained the data significantly better than the null model (which contained the intercept, control variables, and random effect) at +20 seconds after the stimulus onset ($\chi^2 = 24.71$, d.f. = 4, $p < 0.001$), but not at +80 seconds ($\chi^2 = 5.51$, d.f. = 4, $p = 0.239$). There were no significant effects for the change of the skin temperature of the nose tip at +20 ($\chi^2 = 1.58$, d.f. = 4, $p = 0.813$) and +80 seconds ($\chi^2 = 4.13$, d.f. = 4, $p = 0.389$ – Table 4.6).

Table 4.6 Results comparing full-null models with the change in skin temperature relative to baseline in the periorbital (PO) and nose tip (NT) regions at +20 sec after stimulus onset and +50 sec after stimulus offset as the response variable

ROI	*Time point*	*χ2*	*d.f.*	*p*	*N obs*
PO	**+20 sec**	24.713	4	**<0.001**	22
	+50 sec	5.511 (3.785)	4 (3)	0.239 (0.286)	21
NT	+20 sec	1.579 (0.592)	4 (3)	0.813 (0.898)	22
	+50 sec	4.130 (3.930)	4 (3)	0.389 (0.269)	23

Significant values (P<0.05) are in **bold;** in brackets are the result from full-null comparison without the interaction between familiarity and age

The temperature of the periorbital region at +20 seconds increased upon seeing the positive stimulus, and the temperature change was stronger in older individuals compared to younger ones (interaction valence * age: estimate ± se = 0.05 ± 0.01, t = 6.05, p = 0.007 – Figure 4.7). For the negative stimulus, the periorbital temperature increased similarly in young and older subjects. No effect of sex was detected (estimate ± se = -0.17 ± 0.40, t = -0.43, p = 0.677).

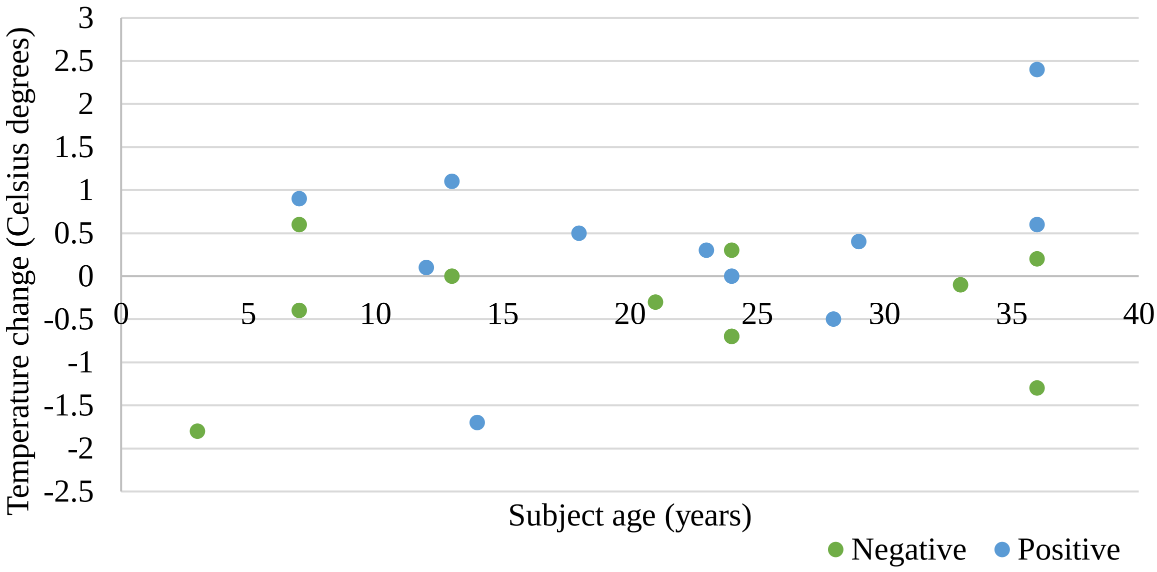


Figure 4.7 Change of temperature relative to baseline in the periorbital region at +20 seconds depending on the valence of the stimulus (human positive and negative stimuli) and the age of the subject (years)

Table 4.7 Results of the full model testing the effect of valence, age, and sex on temperature change in the periorbital region at +20 seconds

S.E.: standard error; P: p-value

Fixed effect	***Estimate***	***S.E.***	***t value***	***P***
(Intercept)	-2.211	0.768	-2.882	0.012
Stimulus valence (Positive) * Age	0.052	0.009	6.053	**0.007**
Sex (Male)	-0.172	0.404	-0.425	0.677

Significant values (P<0.05) are in **bold;** almost significant values are underlined (P < 0.09)

4.5 Discussion

The current study investigated the underlying physiological mechanisms of sanctuary-living chimpanzees and their relation to consolatory behaviours in observational settings. In line with an empathy-based argument I also examined whether the arousal responses of chimpanzees, as measured using IRT, were predicted by model familiarity and stimulus valence.

4.5.1 Part One: How do chimpanzees respond to conspecifics' distress? Multi-method approach

4.5.1.1 Hypothesis 1.1: Inner arousal predicts consolation tendency

When focusing on the data of subjects who initiated at least one affiliative interaction to a victim in distress (N = 6), the consolation rate positively correlated with increased temperature in the **periorbital** region at +20s when witnessing a conspecific in distress, with an average change of +0.2 Celsius degrees. In line with pupillometry studies examining prosociality in young children (Hepach, 2017; Hepach et al., 2017), this finding suggests that inner arousal – as measured with facial temperature change- might represent an underlying motivation to comfort a distressed individual. The results were not conclusive at 80 seconds after stimulus onset, suggesting that the thermal response appears within 20 seconds and disappears before 80 seconds. Although previous studies got convincing results focusing on the temperature change of the nose tip region in response to an audio stimulus of conspecifics fighting in chimpanzees (Kano et al., 2016), here, the results for the nose tip region were inconclusive. This contrast stresses the importance of investigating several ROIs (Chotard et al., 2018) to allow a mapping of the thermal response across the face and potentially account for individual differences, with the goal to increase the understanding of the thermal response within and across species.

Despite a rather limited sample size, this output encourages follow-up studies to pursue such investigation to disentangle the underlying motivation to help in chimpanzees. The multi-methods approach is very valuable, and the design of the current study allowed for conducting the experiment in sanctuary settings, making the research as ecologically valid as possible. However, other designs in more experimental settings could provide clearer results when it comes to the connection between inner arousal and behaviour, such as being able to record the inner arousal before a potential action.

4.5.1.2 Hypothesis 1.2: Inner arousal predicts anxiety behaviours

While IRT may be relevant for detecting empathic responding, it may otherwise be more indicative of personal distress. For instance, in the first infrared thermography study on primates, the nasal skin temperature of chimpanzees who witnessed another chimpanzee receiving an injection with a needle – or the needle alone- decreased (Parr, 2001). Rather than emotional contagion, this reaction suggests personal arousal in response to a familiar aversive situation as part of the individual's own experience (i.e., veterinary contacts). In a more recent study, chimpanzee nasal skin temperature decreased upon witnessing the realistic injury (with blood) of a human experimenter, but not when the experimenter pierced their (fake) thumb with a needle, here with no external cues of pain (no blood, Sato et al., 2019). This last situation might have been more difficult for the subjects to understand, suggesting that familiar signs of distress or pain are required to trigger the subject's physiological response. However, whether it relates to personal distress or empathy remains unclear. All in all, it is challenging to disentangle the thermal response of personal distress and the one of empathy. Yet, rather than being one or the other, future work should investigate the temporal physiological responses in order to identify a potential *arousal threshold* that would discriminate between the affective arousal as motivation to help and the over-arousal leading to self-distress. Unfortunately, due to very limited sample size, the analyses could not be completed to test this hypothesis.

4.5.2 Part Two: How do chimpanzees respond to the affective states of familiar and unfamiliar humans?

4.5.2.1 Hypothesis 2.1: Empathy gradient translates into inner arousal

While the nose tip temperature increased in younger subjects, in line with a previous study using positive stimuli (Chotard et al., 2018), it decreased in older ones which is usually expected in response to negative stimuli (e.g. humans, Ioannou et al. 2013; in apes, Chotard et al., 2018; Dezecache et al., 2017; Kano et al., 2016; monkeys, Nakayama et al. 2005). However, findings from studies investigating positive states and how they relate to the variation in facial skin temperature are inconsistent as compared to studies investigating negative states (overview: Chotard et al. 2018), probably due to variation in the experimental stimuli. For instance, Chotard and colleagues (2018) induced a positive emotional state in their subject using tickling and playing sessions and a negative emotional state using food-delay situations, while in other studies subjects witnessed an emotional situation (e.g., opportunistic naturalistic scenarios: Dezecache et al., 2017; experimental settings: Kano et al., 2016; Sato et al., 2019). In the current study, I investigated the physiological response of a subject in an empathy-triggering situation which may make the valence of the response difficult to assess.

The developmental contrast highlighted in this study might be explained by the familiarity of the model, with older individuals reacting more negatively to a stranger and to the novelty of such stimulus, while the younger ones were more responsive to the positive valence of the stimulus itself. Alternatively, this contrast might indicate that the mechanisms at the base of the physiological process mature/vary with age. Furthermore, this physiological reaction to a positive stimulus seems to be lasting (up to 80 seconds following stimulus onset). Future work should look at the dynamic of the response in order to investigate whether/how emotion regulation processes differ between positive and negative situations, with a potential stronger need to regulate arousal in a negative situation than in a positive one. Overall, these results support the hypothesis that the *empathy gradient* usually assessed via behavioural observations (e.g., Clay and de Waal 2013b) finds its roots at the physiological response to an emotional stimulus and develops with age, potentially alongside cognitive mechanisms.

4.5.2.2 Discussion of Hypothesis 2.2: Stimulus valence predicts inner arousal

The temperature of the **periorbital** region at +20 seconds increased upon seeing both the positive and negative stimuli, which contradicts the hypothesis that IRT measurements translate both the *valence* and *arousal* dimensions of the emotional experience. While the temperature of the nose tip is thought to decrease upon seeing negative stimuli (Kano et al., 2016), the result of the current study suggests a different trend for the temperature change in the periorbital region. This increase of the temperature following positive experiences is in line with previous studies, but such variation tends to be unclear (Chotard et al., 2018). Therefore, in contradiction with my hypothesis, the strength and direction of the change in inner arousal (measured via IRT) is not predicted by the valence of these stimuli. It is possible that the manner subjects process the emotional stimuli used in this experiment and their potential valence might not be as binary as assumed. Indeed, the thermal signature of empathy might itself translate to more complex temperature variations rather than the potential valence of a situation. Future work using different emotional stimuli to better define and understand the emotional thermal signature would help address this issue.

In contrast with a previous study (Kano et al., 2016), the results for the nose tip region were inconclusive. This suggests that the change of temperature in the nose tip region might not always reflect the change in inner arousal. Therefore, looking at different ROIs ensures we grasp the full pattern of the physiological response (Chotard et al., 2018). However, the variation in the experimental stimuli and settings across studies, as well as the limited sample size of this study, might explain the difference in results.

In addition, I found developmental effects, with the temperature change in the **periorbital** region being stronger in older individuals compared to younger ones when observing **positive** stimuli. For the **negative** stimuli, the **periorbital** temperature increased similarly in young and older subjects. Because we see a difference in the developmental trend only for the positive stimuli, this excludes the possibility of an anatomical difference between young and older individuals in the periorbital region that could have explained the results. Instead, this difference suggests that positive and negative events might be processed differently by young and older individuals, with younger individuals reacting more strongly than older ones to a positive stimulus.

4.5.3 Study considerations and limitations

In the current study, I tested a novel procedure using IRT in opportunistic – and relatively noisy- settings with semi-wild apes. While this study was pioneering in its mixed-methods approach, several limitations could have influenced the results and their generalisability. The use of thermography is still at its early stages in comparative affective science. Therefore, groundwork is required to understand the thermal measurements and how it informs on the physiological response of an individual. It was useful to test that such video stimuli with the camera set up can be played to chimpanzees in sanctuary settings. However, this also revealed many challenges and limitations of the design and validity of the measurements.

4.5.3.1 Experimental design: Indirect connection between the physiological and behavioural measurements (Part One)

The opportunity to concurrently measure the subject’s physiological response along with their behaviour is very limited. That is because most physiological measurements require that the subject is somehow restrained in their movements. However, new designs that allow for more connected measurements of the physiological and behavioural responses in children were developed using pupil dilation (Hepach et al., 2012; Hepach, Vaish, & Tomasello, 2017). Furthermore, heart rate modulation studies on geese used fully implanted transmitters allowing the recording of the heart rate in response to a live naturalistic social event (Wascher et al., 2008). The combination of several methods and technologies offers a valuable way to understand the link between physiological responses and prosocial behaviours.

4.5.3.2 Experimental stimuli

Previous studies conducted in laboratory settings have used visual contextual cues like conspecifics being injected with a needle (Parr, 2001), conspecifics with a face injury, a human experimenter with prosthetic wounds (Sato et al., 2019) to elicit emotional responses in apes. However, the outputs of these studies are somewhat disputed. For instance, the needle itself (Parr, 2001) has an aversive value, so it is unclear whether the response measured is to the conspecific in distress or the needle. Therefore, further work using various stimuli is needed.

In the present study, I used video clips of conspecifics in distress (Part One) and humans (Part Two) displaying negative and positive emotional states. Previous studies have presented subjects with real-life theatrical demonstrations (children: Gill & Calkins, 2003; Zahn-Waxler et al., 1992; apes: Sato et al., 2019), video (children: Eisenberg et al., 1990, 1996; Hepach et al., 2013), or audio stimuli (i.e., playback experiments, children: Gill & Calkins, 2003; Martin & Clark, 1982; non-human primates: Kano et al., 2016; Kuraoka & Nakamura, 2011) to elicit emotions in the subjects. Previous attempts to use still images or video footage failed at eliciting physiological reactions in chimpanzees (Sato et al., 2019). In the present study, the combination of visual and auditory stimuli successfully attracted the attention of the apes in a semi-wild context without manipulation or isolation. This opens the door to following studies with similar designs in sanctuary settings.

Finally, although it may be disputed that displaying human emotional expressions lacks ecological validity, the chimpanzees who took part in the study have an extensive experience interacting with humans from a young age. Therefore, I considered that humans can serve as relevant emotional stimuli, as has been demonstrated previously (Kano et al., 2016; Sato et al., 2019).

4.5.3.3 Experimental conditions

The mere presence of others influences the behavioural and emotional response of an individual, along with their arousal (i.e., *social facilitation*, Guerin & Innes, 2009; Mullen et al., 1997; Platania & Moran, 2001; Zajonc, 1965). In addition, the presence of other bodies that emit heat themselves can also influence the temperature of other bodies (Choi & Loftness, 2012; Ioannou, Gallese, et al., 2014). Therefore, the presence vs absence of conspecifics within arm's reach was initially included in the models. Unfortunately, I had to exclude this variable from the model due to overcomplexity. The discussion is expanded upon in *Chapter 6*.

In this testing environment, the environmental conditions were noisier than ideal when using IRT measurements (Ioannou, Gallese, et al., 2014; Kano et al., 2016). For instance, the open testing space allowed for the occasional wind, small changes of temperature and humidity (although no significant variation in temperature and humidity were detected), and variation in ambient lightning conditions, which may influenced the thermal response of the subject (Ioannou, Gallese, et al., 2014). Furthermore, because the testing occurred after the midday feeding, the digestive metabolism and/or occasional presence of food might have influenced the thermal response (Kano et al., 2016). Then, although trials when vocalisations occurred in the outdoor enclosure were excluded, some arousing auditory signals might have been missed by a human experimenter. Although these methodological challenges limit the interpretation of the findings, the sanctuary conditions still offer a valuable platform to study the behavioural aspect of the empathic behavioural-physiology connection that is otherwise impossible in other testing facilities with a limited number of individuals (Kano et al., 2016).

4.5.3.4 Sample size

Overall, due to the opportunistic data sampling, sample sizes were generally small (Kano et al., 2016; Sato et al., 2019). Larger sample sizes are ultimately needed to generalise the response patterns along with identifying individual differences.

4.5.3.5 Sanctuary settings

Finally, this study relies on the observation of chimpanzees housed in sanctuary settings. A large proportion of these apes were orphans saved from the illicit bush-meat and pet trades, while others were born at the sanctuaries. Therefore, although the study of this chimpanzee population living in a semi-wild environment might approach the behaviour of their wild conspecifics, we are restricted in our interpretation and generalisation of the outcomes of this study.

4.5.4 Conclusion

For the first time, this study combined observations and physiological measurements to allow for an integrated interpretation of the various measurements, including arousal and valence which are two crucial components of the emotional experience (Russell 2003; Barrett et al.

2006). The outputs of this study also highlight how complex measuring emotion is, and revealed/confirmed that IRT technology itself provides complex data that is challenging to interpret. Future work should combine IRT measures with other measures of physiological responses (e.g., heart rate or pupil dilation) as well as behavioural markers to mature our understanding of how the behavioural and physiological components of empathy relate to each other and disentangle the components of the emotional experience.

Chapter 5 How do young children respond to the distress of others? A behavioural and physiological investigation

5.1 Abstract

Empathy is a core feature of the human social experience; however, we know relatively little about how its affective and cognitive building blocks emerge in early life. In the present study, I used infrared thermography combined with behavioural observations to experimentally investigate how young British children (1-3 years of age) respond to others' distress. The three main goals were to investigate (**Aim 1**) the development of emotion contagion and empathy, (**Aim 2**) the development of exploratory communicative responding and information seeking, and, (**Aim 3**) the development of emotion regulation. In relation to **Aim 1**, I hypothesised that younger children, presumably lacking emotion regulation skills, would show a stronger physiological response than older children, and boys would react more strongly as compared to girls who seemingly show better emotion regulation skills. I also hypothesised that physiological and behavioural responses will be stronger when witnessing a familiar individual in distress as compared to an unfamiliar individual, and that children will produce context-appropriate facial expressions. Regarding **Aim 2**, I hypothesised that children will pay greater attention to another's distress than a neutral event, and that children will engage in more information-seeking in the distress condition, especially for familiar models. I also hypothesised that this behaviour will develop with age and be more salient in girls, who are more encouraged to express their emotions, than boys. Regarding **Aim 3**, I hypothesised that the development of emotion regulation in young children promotes sharing and understanding other's emotions, whereby children will use the (visual) support of their caregiver to regulate their arousal and seek reassurance via positive facial expressions. To do so, I measured the

emotional reactions – including behavioural responses and changes in facial skin temperature — of N = 30 typically developing young children (17 girls; age range: 1.1-3.0-years-old, mean=2.0-years-old; SD=0.5) from nurseries in the north-east of the UK by individually watching short video-vignettes of familiar and unfamiliar caregivers displaying emotional distress or neutral emotional expressions. Results from an analysis of changes to nasal temperature confirmed a physiological reaction of children when witnessing another's distress as compared to the control **(Aim 1**). Younger infants showed stronger thermal responses in response to distress stimuli compared to older children, and boys showed a stronger thermal response than girls; there was no interaction between these factors. Intriguingly, there were no sex or age differences in corresponding behavioural responses recorded during the experiment. Overall, children showed fewer indicators of positive emotions in response to negative stimuli than control stimuli. Regarding an empathy bias towards familiar others, there was no effect of model familiarity on children's behavioural responses, but some effect on their thermal response. When examining children's communicative responding and information seeking in response to observing someone in distress (**Aim 2**), children paid greater attention to distress than control stimuli. However, there was no effect of age, sex, model familiarity, or stimulus type on testing/enquiring behaviours such as social referencing and pointing. Regarding emotion regulation (**Aim 3**), the more children looked at the caregiver present in the room, the weaker their physiological response, suggesting that children used such social referencing to regulate their arousal. Furthermore, the more children looked at the caregiver present in the room, the more positive facial expressions they produced, indicative of the regulatory effect of the caregiver presence. There were no significant results on self-directed behaviours or stimulus avoidance. Overall, by combining physiological and behavioural measures, this study contributes to new theoretical and methodological advances into how internal affective

processes map onto external measures in early childhood, shedding new light on the development of empathy.

Keywords: empathy; emotion; concern for others; hypothesis testing; familiarity; thermography

5.2 Introduction

5.2.1 Empathic arousal and emotion contagion

As with other animals, humans experience *affective arousal* in response to observing others' affective states (Hastings et al., 2006; Knafo et al., 2008). Studies using pupillometry to examine the underlying mechanisms of prosociality in young children suggest that affective arousal acts as the intrinsic motivation to help others in need (Hepach, 2017; Hepach, Vaish, Müller, et al., 2017a). This response to others' states has been considered as a form of *emotion contagion*, which refers to emotional state matching between an observer and an actor (de Waal, 2008). As emotion contagion facilitates the experiencing of others' states (de Waal, 2008, 2011), it has been suggested by some to be a precursor for empathic responding (de Waal and Preston 2017, but see Nummenmaa et al. 2008). While emotional contagion is an important mechanism underpinning social interactions, it is difficult to empirically demonstrate, being often inferred or potentially confused with behavioural mimicry, despite the two being separable processes (Isern-Mas & Gomila, 2019). For instance, one can feel sad but not display the typical behavioural expression associated with sadness.

Studying physiological changes provides an opportunity to identify the occurrence of emotional contagion. In their thermographic study, Ebisch and colleagues (2012) found a congruency between the variation of maternal facial temperature changes- considered an indicator of the autonomic nervous system – while observing their children in a distressing situation and facial temperature variation occurring in their children. Thermal measures of the mother and child were recorded simultaneously supporting the supposition that empathy embodies a direct contagion of visceral-autonomic responses.

As emotion contagion can lead to personal distress, empathy requires regulation of one's own arousal in order to effectively suppress personal distress to appraise the situation and orient to the others' needs. As critical top-down mediators of affective states, regulatory processes influence affective and behavioural responses (Decety, 2011). Particularly, down-regulation of affect is essential for preventing *empathic over-arousal* (Eisenberg 2000) to enable other-oriented responses (see *Chapter 1*).

5.2.2 Typical development of empathy and emotion regulation

Theories of empathy development have long been dominated by the view that affective empathy appears first in development, with contagious crying considered as a marker of early emotional responding (Geangu et al., 2010; Hoffman, 2000; Simner, 1971). This is then followed by the onset of cognitive empathy in the second year of age; a trajectory that allows for an other-oriented response rather than self-distress (i.e., Hoffman's theory of empathy development, Hoffman 1975, 1984, 2000). Recent research however has challenged this 'stage' view by suggesting that infants can empathically respond to others' distress in the first year of life, with both affective and cognitive components of empathy in place to some degree (Davidov et al., 2013; Uzefovsky et al., 2020; Zahn-Waxler et al., 2018). A recent study by Davidov et al. (2020) found that infants as young as 3 months show concerned facial affect and exploration of the other's distress, which the authors took as evidence for empathic responding. Furthermore, these early expressions of empathy predicted prosocial comforting behaviours at 18-months. Following these findings, the author suggested that the capacity for concern and the underlying processes driving the motivation to help others are present very early on in human ontogeny. However, whether or not it is possible to detect and discriminate facial expressions of concern from other expressions, unrelated to empathy, at such a young age remains questionable.

To respond empathically, one needs to be sensitive to others' states and to perceive their emotional expressions. In an infant's first year of life, hearing the crying of another infant is likely to initiate contagious crying, a marker of personal distress (Dondi et al., 1999; Martin & Clark, 1982; Sagi & Hoffman, 1976). However, this distress response has been interpreted as evidence of *personal distress*, and found in newborns as well as infants of 1-, 3-, 6- and 9-months of age (Geangu et al., 2011). Upon hearing a crying peer, most 6-months old infants showed other-oriented responses as compared to self-focused reactions, which included looking toward the infant in distress, and some infants also gestured towards them or touched them, to communicate (Hay et al., 1981). Beyond the first year of life, many studies focusing on infants' and toddlers' responses to the distress of others investigated the affective, cognitive and behavioural components of the empathic response (e.g., Zahn-Waxler et al. 1992b, a; Demetriou and Hay 2004; Knafo et al. 2008). The *affective* component is reflected by facial expressions, vocalizations, and gestures. The *cognitive* component refers to the child's inquiry, or hypothesis testing behaviour.

During infancy and toddlerhood, the development of various neurophysiological and cognitive maturation processes enables children to better regulate their emotions and orient towards others (Cole et al., 2009), along with the development of new affective, cognitive and social skills (Carlson, 2005; Wellman et al., 2001). Regulation processes such as suppression and re-appraisal facilitate more tempered reactions to stressful situations (Stansbury & Gunnar, 1994), and increased control of arousal (Fox, 1994), which is necessary to stay focused on the others' distress and show concern. Emotion regulation is crucial for more cognitive forms of empathy, where personal distress is potentially re-appraised as other distress. More details about these regulatory strategies are provided in *Chapter 1*.

When the child fails to effectively regulate their own arousal to a distressing scenario, self-distress occurs (Abramson et al., 2019). The cognitive advances resulting from neural maturations during early childhood – which also include self-awareness and causal understanding – support developmental changes in the use of emotion regulatory strategies

(Kopp, 1989). Another important modification over childhood is the development of linguistic abilities, particularly during the second year (Ridgeway et al., 1985). Language allows the child to use language-based regulation strategies to promote more effective re-appraisal, i.e., by expressing themselves and enquiring directly about the situation. During toddlerhood, the development of motor abilities and increased flexibility in attention mechanisms (Gunnar et al., 1989) also promote emotion regulation abilities.

5.2.3 The underlying mechanisms of empathy

Compared to behavioural markers of empathy, along with their associated neurological mechanisms (Decety, 2015; Shamay-Tsoory, 2011, see *Chapter 1*), physiological markers of empathy remain less well understood. The autonomic nervous system (ANS) is considered a major component of emotional responding (Damasio, 1996, see *Chapter 1)*. Measures of ANS activity such as heart rate, respiratory sinus arrhythmia and skin conductance have been widely used to investigate emotional states in humans (Kreibig, 2010b) and may be relevant markers of empathy (Liew et al., 2003, 2011b; Taylor et al., 2015; Zahn-Waxler et al., 1995). This can be further validated by looking at the subject’s physiological response to various relevant stimuli (e.g., distress), as well as their relation to the expression of prosocial behaviours.

In children, physiological changes, as measured by heart rate variability, are linked to responses of the sympathetic nervous system to videos of others in distress (Eisenberg et al., 1988). Measures of ANS by measuring pupillary responses can also provide insights into underlying affective processes. Hepach and colleagues (2017a) showed that children’s tendency to help others is predicted by their pupil dilatation after observing others in need. In line with previous research (Warneken & Tomasello, 2008; Hepach et al., 2012, 2016; Ulber et al., 2016), this study suggests that children’s internal arousal shapes their intrinsic motivation to help others.

So far, most measures of ANS activity are either mostly restricted to artificial settings or require some degree of contact or invasiveness (Kreibig, 2010a). However, Infra-Red Thermography (IRT) represents a novel non-invasive, contact-free technology that has recently emerged in the field of emotion research. IRT records the thermal infrared signals emitted by the body and allows the measurement of the changes in skin temperature, which result from changes in blood pressure activated by sympathetic nerves (Rubinstein & Sessler, 1990). More information about IRT is provided in *Chapter 2*. Empirical research in humans has demonstrated that emotion-based states induce distinctive changes in the facial skin temperatures (Ioannou, Gallese, et al., 2014), and such changes have been recently reported in great apes too (Kano et al., 2016; Chotard et al., 2018; Dezecache et al., 2017). Although it has received minimal application as yet, IRT can be a valuable tool to use in developmental research with young children as it is contact-free, meaning children are not physically restrained and less biased by the presence of invasive equipment.

Different regions of the facial skin are irrigated differentially by blood vessel networks and are exposed to different physiological reactions (Ioannou, Gallese, et al., 2014; Kreibig, 2010b), leading to potential different temperature variations in different regions of the face at the same time (Dezecache et al., 2017; Ioannou et al., 2016; Levine et al., 2001). Hence it is important to look at several regions of the face when studying the variation of facial skin temperature. For the present study, I looked at four facial regions of interest (ROIs): the peri-orbital, the nose bridge, the nose tip, and the upper lip, following promising results in humans (Ebisch et al., 2012; Nakanishi & Imai-Matsumura, 2008) and non-human primates (Chotard et al., 2018; Ioannou et al., 2015). In particular, the nasal area, particularly the nose tip, has been identified as a reliable region of interest to detect physiological arousal in humans (Hahn et al., 2012; Kreibig, 2010b; Merla & Romani, 2007; Naemura et al., 1993) and non-human primates

(Kuraoka & Nakamura, 2011; Nakayama et al., 2005), due to its rich blood supply (Bergersen, 1993).

5.2.4 Aims

Given the limited information currently available regarding the underlying mechanisms shaping empathy development, the overall aim of the current study is to investigate the development of empathy using both physiological and behavioural measures. Simultaneously examining both inner arousal and external behavioural components allows for a more systematic investigation of the coordinated changes of the two measurable components of an emotional response. This is crucial to establish congruencies and validate assumptions about complex processes like empathy (see Adriaense et al. 2020 for a review). Furthermore, as behaviour or physiology may give differing insights, it is imperative to examine emotionality via a range of measures to understand the scope of its complexity.

To do so, I measured children's affective states in response to emotional stimuli using a combination of infrared thermal-imaging (IRT) and behavioural measures of their corresponding facial expressions and behaviours. I presented children with a series of empathy-eliciting video vignettes that showed familiar and unfamiliar women in distress, one being a familiar caregiver from their nursery while the other was a stranger. This study aimed to evaluate whether the nature and intensity of internal responses, as measured by IRT, mapped onto external behavioural measures i.e., facial and body expressions in response to others' distress. As this study included cross-sectional data from children aged 1 to 3 years old, I also looked at the developmental variation of the behavioural and physiological responses. Here, I investigated whether behavioural and physiological responses changed with age, and whether these responses become more targeted towards close social partners with age.

5.2.4.1 Development of emotion contagion (Aim 1)

The first aim was to examine the development of emotion contagion and empathy in young children. I tested the hypothesis that young children develop a system of emotion sharing that depends on the valence of others' emotions (in this case, negative and neutral – to add a novel angle to this thesis, as compared to the negative and positive valences investigated in *Chapter 4)* and the familiarity of the model, which can be detected by both physiological and behavioural markers. To investigate this, I measured children's physiological response (change in facial skin temperature) along with the production of negative (and positive) facial expressions, the production of self-directed behaviours, and the avoidance time of the stimulus (duration looking away from the screen), when witnessing the distress and neutral emotional expression of a familiar and unfamiliar caregiver. Participant age and gender were investigated.

5.2.4.1.1 Physiological response

Seeing others in need triggers internal physiological changes in children (Eisenberg et al., 1990; Hastings et al., 2006; Knafo et al., 2008), suggesting that prosociality (Posner et al., 2005) may be driven by children's emotional reaction towards someone else's emotional situation (Hepach, 2017; Hepach et al., 2013; 2017, see *Chapter 4*). Therefore, I predict that children's physiological response, as measured by IRT, will be stronger when responding to another's distress versus neutral expressions.

Furthermore, the *empathy gradient* predicts that empathy is strongest among kin, followed by socially close partners, and weakest among social-distant or unfamiliar individuals (Fraser et al., 2008a; Romero et al., 2010; Clay & de Waal, 2013b; Palagi & Norscia, 2013). Based on the hypothesis that the empathy gradient finds its roots at the physiological level, I predict that children's physiological response will be stronger when a familiar individual shows distress as compared to an unfamiliar individual (familiarity * valence interaction). In contrast, I do not predict such differences when the interaction is of neutral valence as it does not rely on the empathy gradient.

Neurological studies show an effect of gender, with greater neural reactivity to emotional stimuli in women compared to men, particularly for negative stimuli (Han et al., 2008; Williams et al., 2008). Women also display a different physiological response (i.e., the pattern of skin conductance) compared to men when watching emotional video clips (Kring & Gordon, 1998). Furthermore, during childhood, boys show lower inhibitory control than girls (Chaplin, 2015 for a review). I previously reviewed gender and/or sex differences and the development of emotional processing and expression in *Chapter 1*. Therefore, I predict sex differences in the physiological response of the children, with boys reacting more strongly to the distress situation as compared to girls. However, I do not predict such differences when the interaction is of neutral valence.

5.2.4.1.2 Behavioural response

Empathy is most commonly identified in responses to a negative emotional context (Abramson et al., 2019), with individuals who experience stronger negative emotions being more sensitive to those of other's (Edwards et al., 2015). For instance, negative affect predicts empathy in children (Edwards et al., 2015; Rothbart et al., 1994; Spinrad & Stifter, 2006) and adults (Andreychik & Migliaccio, 2015). Therefore, I predicted that children will produce more facial expressions typical of negative situations (such as concern, discomfort, distress, disgust, sadness, fear or anger), in the distress situation than in the neutral one. Nonetheless, although this predicted higher negative responsivity might translate into self-distress, I expected the development of emotion regulation skills to lessen the negative expression and allow for empathic responding in older children.

Throughout childhood, children learn how to process social and affective information, as well as how to react appropriately to diverse emotional situations (Eisenberg, 2002). In contrast with negative facial expressions, I predicted that children will produce fewer contextually inappropriate facial expressions, such as positive ones, in response to someone else's distress. However, younger children might produce them because of a lack of emotional experience, and older children might produce them as a way to get emotional support and/or as a coping mechanism (Fredrickson & Levenson, 1998; McEwen, 1993).

Self-directed behaviours are used as a measure of stress and arousal in the non-human primate literature (e.g., self-scratching, Castles et al., 1999; Castles & Whiten, 1998; Koski et al., 2007; Kutsukake, 2003; Palagi & Norscia, 2011), such as observing a conflict (e.g., Aureli, 1997). Indeed, in monkeys, self-directed behaviours such as self-scratching are linked to cortisol (Troisi, 2002), and are sensitive to anxiolytic and anxiogenic drugs (Schino et al., 1996). Therefore, I predict that children will show more self-directed behaviours when witnessing someone's distress as compared to the neutral condition. Furthermore, as empathic responding relies on orienting to the individual in distress, avoidance-based behaviours are more associated with self-distress than empathy (Liew et al., 2011a). Therefore, I predict that self-distress (as measured via self-directed behaviours) will result in greater avoidance behaviours during the distress stimuli more than the neutral ones, and that younger children will react with more self-distress and less empathy than the older ones, therefore showing less avoidance overall.

Selectivity towards familiar individuals is expected to increase with age with the maturation of cognitive skills that allow facial recognition and emotion regulation (Horning et al., 2012; this interaction has also been investigated in *Chapters 3* and *4*). Therefore, I predict that emotional facial expressions and self-directed behaviours will be stronger when the child witnesses the distress of a familiar individual.

Finally, if females are more responsive to other's emotions than males (Campbell et al., 2002; Collignon et al., 2010; Hall, 1978; Hampson et al., 2006; Kring & Gordon, 1998; Thayer & Johnsen, 2000) and more empathic (Zahn-Waxler et al., 1991, 2001), I predict that girls will be more behaviourally responsive than boys to the distress condition.

5.2.4.2 Development of exploratory communicative responding and information seeking (Aim 2)

The second aim was to examine to what extent behavioural markers of cognitive empathy – such as exploratory communicative responding and information seeking (hypothesis testing)- predicted physiological responding in young children. In particular, social referencing (Walle et al., 2017) happens when a child directs its attention to the non-verbal responses of a relevant social partner (i.e., the *referent*) towards a shared situation that may be confusing or arousing to them. By doing so, the child gathers information and improves their understanding of the situation (Klinnert et al., 1983), as well as regulates their emotional response in relation to the referent's reaction (Hornik & Gunnar, 1988; Parkinson & Simons, 2009). The ability to process and utilise the emotional communication of another is crucial for maturing an adaptive social functioning (Monlux et al., 2019; Walle et al., 2017). In the current study, we examined social referencing in the context of a child observing an emotional stimulus in the presence of their caregiver.

I hypothesised that child occurrence of cognitive empathy depends on the valence of other's emotions and their familiarity. I also expected that this selectivity to increase with age and be influenced by their sex. To test this hypothesis, I measured the duration looking toward the caregiver who remained in the room (i.e., social referencing), the occurrence of pointing behaviours towards the screen or the caregiver, as well as attention to the stimulus (duration looking at the screen). Inquiry behaviours, such as social referencing and information-seeking, suggest that the child attempts to understand the situation, as well as to share and/or seek information (i.e., hypothesis testing, Zahn-Waxler et al., 1992a, b). Based on the hypothesis that engaging in hypothesis testing is a sign of cognitive empathy (Zahn-Waxler, Radke-Yarrow, et al., 1992), I predict that children will engage in more information-seeking in the distress condition, especially for familiar models. The prediction is that infants will, i/ spend more time looking at their caregiver in the room, ii/ produce more pointing behaviours towards the screen, and iii/ focus longer on the stimulus (i.e., look at the screen). Furthermore, because girls score higher in seeking social support than boys**,** and boys score higher in avoidant coping (Eschenbeck et al., 2007), I predict sex differences in the communicative responding and information-seeking behaviours.

5.2.4.3 Development of emotion regulation and coping strategies (Aim 3)

The third aim was to examine the role of emotion regulation in empathic responding by linking the physiological and behavioural responses. I hypothesised that the development of emotion regulation in young children promotes sharing and understanding other’s emotions (see Southam-Gerow & Kendall, 2002 for a review). If emotion regulation abilities increase with time, including to deal with the distress of others (Eisenberg & Fabes, 1992), I predict that: i/ younger children will show a stronger physiological response compared to older children, ii/ children showing higher rates of self-directed behaviours will show stronger physiological response when witnessing the distress of another, iii/ children showing higher rates of social referencing will show a weaker change of temperature and less self-directed behaviours toward the emotion stimulus (distress) than children showing a low rate of social referencing behaviours, suggesting that they can better regulate their emotional responses, and v/ children showing higher rates of social referencing behaviours produce more positive facial expressions as a means to communicate with the caregivers and seek comfort (Hornik & Gunnar, 1988; Parkinson & Simons, 2009).

To test this hypothesis, I examined the relationship between changes in facial skin temperature with the production of self-directed behaviours, and the duration of social referencing to the caregiver in the room.

5.2.4.4 Examining the thermal profile (Aim 4)

See footnotes[9]

5.3 Methods

5.3.1 Ethics statement

This study was approved by the Psychology department Sub-Ethics committee at Durham University, UK, which includes full compliance to the General Data Protection Regulation Act (EU GDPR). I collaborated with the Nursery managers *(Appendix 5.1*) to contact and inform the parents and obtained their written informed consent to include their child to the study (*Appendices 5.2, 5.3, and 5.4*). Before conducting the experiment, I also obtained the child’s verbal assent and stopped a trial if the child requested (verbally or behaviourally). The caregivers who agreed to be recorded to create the emotional stimuli also provided informed consent (*Appendix 5.6*).

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[9] As well as the theoretical aims above, this study also aimed to validate the use of IRT for studying empathic responding in children. Thus, to do so, another goal was to conduct a qualitative visual exploration of the thermal profile (i.e., continuous physiological response across time) of children in relation to their behavioural response. However, unfortunately, the data were too noisy to be analysed, this goal could not be completed. I discuss this in the discussion of this chapter.

5.3.2 Participants

Typically-developing children were recruited from two day-care British nurseries in the north-east of the UK (Demographics of the sample: primarily white, Christian, with an average middle income (annual gross earning of £22,188 in 2020; the latest demographics data for Durham City are presented in *Appendix 5.7*, including ethnicity, religion, economy and employment data). I tested a total of N = 39 children of which N =30 were included in the analyses (17 girls; age range: 1.1-3.0-years-old, mean=2.0-years-old; SD=0.5 –Table 5.1). Of the excluded participants, three were excluded because of the low quality of the data collected (e.g., child movement and lack of attention towards the stimulus), one child fell asleep during the trial, and two requested to leave after showing lack of attention and boredom. Finally, three children were excluded because they were new at the Nursery and thus were evaluated to not have had time to develop a strong enough social relationship with their caregivers for this study (but who took part upon their request).

Table 5.1 Information about the children included in the IRT and behavioural data sets

	Girls		**Boys**	
	1 to 2-years-old	2 to 3-years-old	1 to 2-years-old	2 to 3-years-old
Nursery A	6	3	6	6
Nursery B	4	4	1	0
Total	**10**	**7**	**7**	**6**

In both day-care nurseries, the managers acted as gatekeepers by assisting in recruitment and facilitating access to their facility. In both nurseries, children progress through the different rooms depending upon their age and level of physical and emotional development, resulting in children of a similar age being gathered in the same area designed to meet their needs. As such, the youngest and less mobile babies are in Room A with about 1 to 5 babies in the room simultaneously (staff to child ratio: 1:3), before moving to Room B designed for more mobile babies and young children (about 3 to 10 children simultaneously, staff to child ratio: 1:3). Finally, Room C is adapted to young children who show more independence and mobility (about 10 to 20 children simultaneously, staff to child ratio: 1:4). The transition between rooms is gradual, with the child in transition spending more and more time in the next room allowing them to adapt to their new physical and social environment. Each child has a "key carer" with whom they develop a strong relationship. This key person spends more quality time with their *dedicated* children, including one-to-one interactions (e.g., play or reading sessions). Given the bond developed between a child and their key carer, I used this key person wherever possible as the familiar stimulus for our experiment (see below). To be included in the study, children must have joined the Nursery at least 8 weeks before participating, and must have attended the Nursery from three to five days a week over the course of these 8 weeks to ensure they had enough time to develop their familiarity with their new caregiver. All trials were conducted between 9-12 pm in April-June 2019.

5.3.3 Study design

Experiments were divided into four conditions (two test conditions of distress familiar/unfamiliar and two control conditions: neutral familiar/unfamiliar) in a within-subjects design. Prior to each condition, there was an acclimatisation phase of 5 mins for the participant to acclimatise to the ambient surroundings (see below). Each trial (corresponding to a condition) was composed of three phases: 30 seconds of baseline, followed by the experimental condition for 1.5 minutes and a recuperation phase of 2 minutes (Figure 5.1). This resulted in each trial lasting 4 minutes.

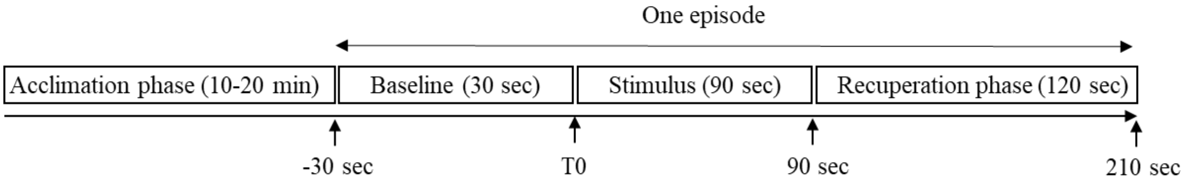

Figure 5.1 Illustration of the three phases of an episode of a trial (i.e., baseline, stimulus presentation, and recuperation phase), and acclimation phase. The duration of each phase is indicated under brackets.

There were four experimental conditions using a 2x2 design: familiar/unfamiliar in distress and familiar/unfamiliar neutral. The presentation of conditions by valence was of fixed order: distress-neutral-distress-neutral conditions in order to limit the emotional impact potentially triggered by two successive distressful conditions. As exposure to distress scenes can be over-arousing for the child, I also always ended with a neutral condition, as this was least arousing. If the first test condition was with a familiar caregiver, the second condition contained the corresponding control condition and the third and fourth episodes would contain conditions with the unfamiliar caregiver. From Nursery A, 66.7 per cent of the children (N = 14 out of 21) started the trial with the videos of their familiar caregivers, while this was the case for 55.6 per cent of the children from Nursery B (N = 5 out of 9, Table 5.2.). The slight unbalance for Nursery A is due to the exclusion at posteriori of some trials (see *Participants* section). The order of the stimuli and the identity of the caregivers acting in the videos were controlled for in the statistical analyses. A single trial was run once per child. However, if the trial was interrupted, this child was tested on a subsequent occasion for the missing conditions only.

Table 5.2 Representation of the children who started the trial by the familiar vs unfamiliar condition.

	Nursery A		**Nursery B**	
	>1 to 2-year-old	*>2 to 3-year-old*	*>1 to 2-year-old*	*>2 to 3-year-old*
Familiar	9	5	3	2
Unfamiliar	3	4	2	2

5.3.4 Experimental stimuli

I recruited Nursery caregivers, ideally "key carers" to create video stimuli. Only female caregivers were working at the Nurseries, therefore only females were used (ages approximately 25 to 55 years old). To create the stimuli, I asked caregivers to simulate an emotional response of either negative or neutral valence. In the *test condition* (empathy-eliciting video), the actor was provided with training and asked to pretend to be sad (facial expressions of sadness, hunched body movements, sobbing vocalisations) for 1:20 min before visibly showing themselves to feel better for 10 seconds by stopping any display of sadness and going back to neutrally reading a leaflet placed on their lap, concluding distress episode and mirroring the control condition; this final component was to ensure the vignette ended on a positive note for the child. See the video example here[10] and Figure 5.2.

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[10] https://www.dropbox.com/s/8xvcrqax7hmxhf0/Diane Austry PhDthesis_Chapter5_Distress stimulus_example.mp4?dl=0

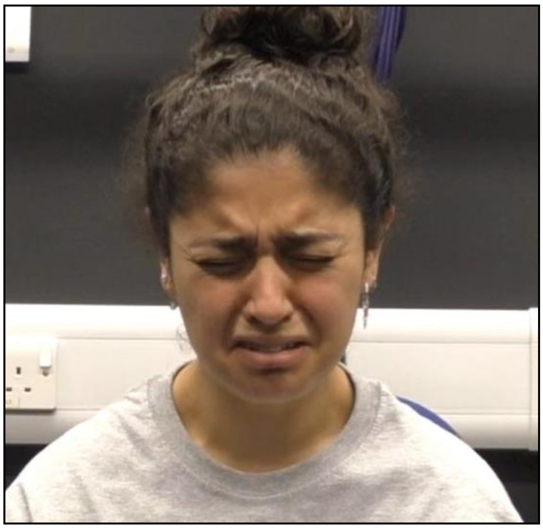

Figure 5.2 Screenshot exemplar of the negative valence stimuli I used in my experiment – with permission

In the *control condition* ("neutral"), the caregiver was asked to pretend to read a leaflet neutrally placed in their lap while emitting neutral vocalisations (such as 'hmmm') to match the presence of audio in the distress condition. Before recording, I showed each actor an exemplar video to model their performance. During the viewing of these videos, I pointed out the crucial criteria of the performance (e.g., movements, vocalisations) to ensure consistency. I recorded several trials with each volunteer caregiver. The realism and intensity of all of the video clips recorded was evaluated by myself and an independent coder, and the video clips that we judged as "unrealistic" were excluded i.e., the person breaks character, e.g., laughing during the negative display, does not show the emotion required, e.g., neither in facial expression nor body language or vocalisation, exaggerates the emotion too much) and/or too intense (i.e., intense emotional expression with very loud vocalisations and intense facial expressions) or not intense enough (i.e., little to no emotion, no change in facial expression, in comparison to neutral, few vocalisations) . There was perfect agreement between the coders as to this quality check. See the video example here[11] and Figure 5.3.

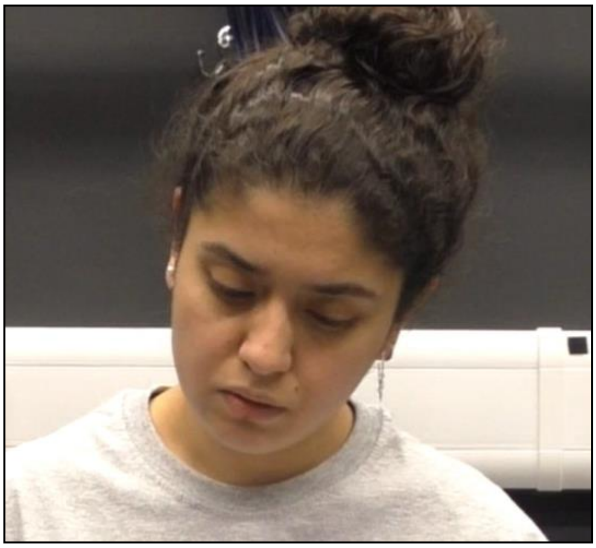

Figure 5.3 Screenshot of the neutral state I used in my experiment – with permission

To manipulate familiarity and control for various visual components, the caregivers from nursery A were used as the "familiar" individuals to the children in their nursery, whereas the same caregivers were used as the "unfamiliar" individuals to the children in nursery B, and vice versa.

5.3.5 Procedure

The experiment took place in a familiar and quiet room at the nursery. The IRT equipment is described in *Chapter 2*. These rooms were kept at a generally constant temperature and humidity throughout a whole session, with no direct sunlight or ventilation. Across testing sessions, the temperature and humidity varied only 0.13 Celsius degrees and 0.54% (SD values; with a minimum of 0.01 Celsius degrees and 0.14%; and a maximum of 0.28 Celsius degrees and 2.49%). Variation in temperature and humidity within each testing session has been

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[11] https://www.dropbox.com/s/fwf97gyh3fg99k9/Diane%20Austry%20PhDthesis_Chapter5_Neutral%20stimulus_example.mp4?dl=0

controlled for in the analyses. Before testing, the children were in another room of the nursery where the temperature and humidity were similar to the testing room. If the children were playing outdoors, I waited at least 15 minutes before starting the trial to allow for acclimatisation. All doors stayed closed during the experiment. No-one entered or left the room to prevent airflow that could disturb thermoneutrality, and thus maintain a stable and limited number of bodies that emit heat in the room during the experiment. A nursery caregiver was present during the experiment (see below), and was asked to limit their movements and avoid eye contact with the participant.

Because changing environment and being isolated can affect nasal temperature (Kano et al., 2016), I established a 5-minute *acclimatisation phase* with the child by playing quietly (colouring, looking at books, playing with cubes) until the child showed no behavioural sign of excitement or anxiety (for at least 5 min). This allowed the child to adapt to the temperature and humidity of the room, which is essential to obtain valid thermal measurements that are not biased by the environmental conditions (Ioannou, Gallese, et al., 2014; Kano et al., 2016). I was already familiar with the children as I had previously spent several weeks at the nursery.

The *baseline phase* was 30 seconds video of bubbles, aiming at measuring the basal/initial facial temperature of the child and behaviour before each of the experimental conditions (test and control conditions). I selected the bubbles from among other clips, as they successfully attracted the attention of the children while not being overly arousing.

Previous studies using IRT have used different lengths of stimuli and shown different delays to report facial temperature change (i.e., 10 seconds, Kuraoka & Nakamura, 2011; 2 min, Kano et al., 2016). In the current study, each experimental stimuli lasted 1:30 minutes, as I determined this duration as a threshold between the delay necessary for the emergence of a physiological reaction (i.e., possible change of facial skin temperature of the children), and the children’s attention span for this kind of task. Measurements were also extracted after the end of the stimulus display, during the “recuperation phase”.

To minimise movement during the trial, which can affect thermal-image quality, I secured young infants into a familiar infant chair whereas toddlers sat in a toddler-suited chair that they use daily at the nursery. The youngest children, who could not sit safely on their own (i.e., some of the infants aged below 1 year old), sat on their caregiver’s lap. The child faced a laptop screen positioned on a table 1 metre away at eye height. The experimenter then faced the child to operate/calibrate the infrared thermal imaging camera, placed on a tripod 1.2 metres away from the child at the child’s eye height. The child’s nursery caregiver sat on a chair 1 to 2 metres away from the child, but without any visual or physical contact unless necessary. A picture of the settings in the different nurseries is available (Figure 5.4). The child was free to seek contact with the experimenter or the caregiver who was present in the room (on the chair on the right side of the child –Figure 5.4), but the caregiver was instructed to not respond. If needed, I tried to attract the child’s attention toward the screen.

Figure 5.4 The experimental set-up, with the FLIR thermal camera, the camera recorder, the laptop, the temperature and humidity data logger, stop watch, and a chair for the caregiver in the room.

The *recuperation phase* followed immediately after the experimental or control condition (Merla & Romani, 2007). This phase was composed of 2 minutes of neutral silent clips displaying colourful moving shapes on the screen (Microsoft Windows© screensavers), which both attracted the child's attention to the screen, while remaining calm. Indeed, variation in blood flow linked to physical activity can impact the measurement (Nakanishi & Imai-Matsumura, 2008). Therefore when working with un-constrained subjects, it is important to minimise movement and enable a return to baseline (Ioannou et al., 2014). The duration of the recuperation phase (2 minutes) has been determined as a threshold between the delay necessary for the child to "physiologically recover" from the potentially distressing stimuli (i.e., back to the initial facial temperature), and the child's attention span for this kind of task (Ebisch et al. 2012; Ioannou et al. 2014 for a review).

During the trial, I closely monitored participant responses and ceased the experiment if any participant showed excessive distress. At the end of the test session, there was positive interaction at the end, when the child could pursue the picture drawing started at the beginning of the session, play a game or read a book with me to ensure the session ended on a rewarding note. Excessive distress during the experiment did not occur. Nonetheless, one child showed signs of discomfort (seemingly shy), even after spending a lot of time with me, so I did not go ahead with the experiment.

5.3.6 Coding

5.3.6.1 Coding of Infra-red thermal data

First, I looked at the thermal profiles for a subset of the data set (N = 15 children – see thermal video example here[12]) by extracting minimum temperatures every 10 seconds during baseline (i.e., 10-sec intervals from -30 to 0 sec relative to the stimulus onset), testing phases (i.e., from 10 to 110 sec relative to stimulus onset) and recuperation phases (i.e., from 10 to 120 sec relative to the stimulus offset) at the four regions of interest (ROI), i.e., periorbital (PO), nose bridge (NB), nose tip (NT), and upper lip (UL) regions (Figure 5.5). When I could not find the optimal frame (see criteria above) within ± 3 seconds, measurement time-points were coded as null values.

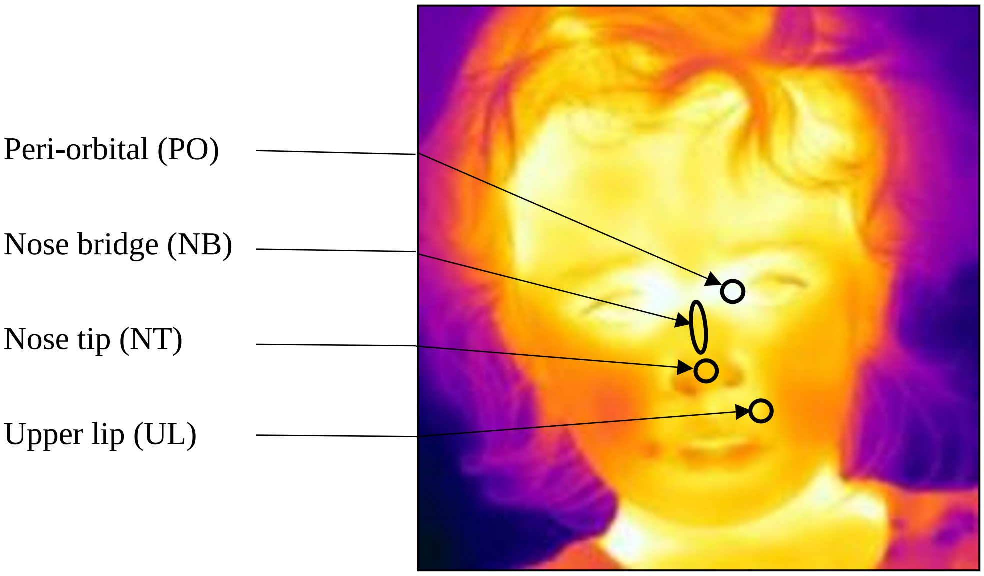

Figure 5.5 The four facial regions of interest – with permission

I extracted the temperature at three time points. The first was at the end of the stimulus display (+80 sec from stimulus onset). Compared to other responses of the autonomic nervous system,

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[12] https://www.dropbox.com/s/sf5e43027ydl93a/Diane%20Austry%20PhDthesis_Chapter5_Thermal%20video%20kid.mp4?dl=0

changes in facial skin temperatures are known to be relatively slow (Kano et al., 2016; Kuraoka & Nakamura, 2011). The second time point was at the end of the recuperation phase (+200 seconds from stimulus onset), aiming at recording a potential return to baseline (to test for emotion regulation) after the display of the stimulus. Finally, I also extracted the temperature during the baseline (-10 seconds relative to the stimulus onset) to compare the temperature extracted at the two time points to the baseline measurement to evaluate a *change* in facial skin temperature. Following Kano and colleagues (2016), I extracted the minimal temperature of an ROI to gain precision in finding when the optimal size and position of the ROI in each frame becomes challenging, particularly where the facial angle and position could vary. The optimal frames were selected within +/- 10 seconds for each of the four episodes that the children attended (Kano et al., 2016). This allowed for a higher quality of the frame extracted, as I could select those in which the face was in a constant angle (Ioannou et al., 2014) and avoid the frames in which the facial image was blurred due to the head motion (Kano et al., 2016).

I conducted an exploratory analyse with thermal profiles. Visual inspection of these profiles revealed considerable individual variation and noisy measurements within/between trials. Given the extensive variability, I, therefore, opted to select two time points to investigate for my analyses.

5.3.6.2 Coding of the behavioural data

Using a detailed ethogram, described below, I coded the following behavioural responses: 1/duration and occurrence of looking/attention towards four sources: the screen, the caregiver in the room, the experimenter, looking away from the screen or either adult), 2/ the duration and occurrence of facial expressions (i.e., concern and discomfort, along with other negative facial expressions, including distress; positive facial expressions; neutral facial expressions; others, see ethogram), 3/ the duration and occurrence of self-directed behaviours (e.g., self-scratching, see ethogram), and 4/ the duration and occurrences of pointing behaviours towards the screen. Behaviours within each category are mutually exclusive. Photographic illustrations are provided below.

5.3.6.2.1 Duration and occurrences of looking/attention

Participant attention towards the stimulus was recorded when their face was facing the screen with an angle of ±20 degrees for at least one second. The coding also involved eye gaze when possible. The participant was coded as looking away from the emotional stimulus when their face was outside of the 20-degree angle relative to the screen, and/or the participant’s gaze indicated that the child was not looking at the screen for at least 1 second. Note that durations when the participant looked at the caregiver in the room or the experimenter in the room were excluded (see ethogram below).

5.3.6.2.2 Coding of facial expressions

My coding system was inspired by the Maximally Discriminative Facial Movement coding system (MAX, Izard 1979) and some physical criteria identified and described in the empathy coding scheme from the MacArthur Longitudinal Twin Study developed by Zahn-Waxler and Robinson and their colleagues (Zahn-Waxler et al., 1992; Zahn-Waxler & Robinson, 1995), and used extensively in prior research (e.g., Knafo et al. 2008; Davidov et al. 2020).

For the coding of the facial expressions of concern, discomfort, and distress, I conducted the coding in two phases. I first coded all *negative facial expressions*, which included any signs of concern, discomfort, and distress (disgust, sadness, fear or anger were not observed). Then, from these negative expressions, I identified facial expressions of concern, distress or discomfort (all mutually exclusive). The ethogram is described in detail in *Appendix 5.8* and some illustrative figures are provided below (Figures 5.6-11).

Figure 5.6 Facial expression of concern from a 1.5-year-old girl in the unfamiliar distress condition (e.g., brow furrowed, open mouth) – with permission

Figure 5.7 Expression of discomfort from a 2.9-year-old boy in the familiar distress condition (e.g., avoiding look, hand in mouth) – with permission

Figure 5.8 Facial expressions of amusement and happiness (i.e., mouth smiling and cheeks raised) from a 1.5-year-old girl in the familiar distress condition – with permission

5.3.6.2.3 Duration and occurrences of self-directed behaviours

Figure 5.9 Self-directed behaviours from a 2.9-year-old boy in the familiar distress condition – with permission

5.3.6.2.4 Coding for social referencing and information seeking/sharing

Figure 5.10 Looks at the caregiver from a 2.9-year-old boy in the familiar distress condition. In this picture, I also recorded a facial expression of concern (not mutually exclusive with the looking behaviour) – with permission

Figure 5.11 Pointing behaviour from a 1.5-year-old girl in the familiar distress condition – with permission

While some studies of empathy aim to score the overall strength of the emotional response (Davidov et al., 2020; Zahn-Waxler, Radke-Yarrow, et al., 1992), I used the duration and the number of occurrences of a given behaviour that a child expresses as metrics for the analyses. I looked at each behaviour individually and controlled for the general expressivity of the child by comparing all measures recorded after the onset of the stimulus with the measurements recorded during baseline. This prevented us from overestimating the reaction of a child to the stimulus when this child was also very expressive during the baseline.

5.3.7 Data analysis

5.3.7.1 Inter-coder reliability: IRT data

15% of the total data was blind coded by two research assistants, which were then compared using intraclass correlations coefficients (ICC, Shrout and Fleiss 1979; Koo and Li 2016). I used the function icc() from the irr package in R to assess the absolute agreement between the main coder and two sub-coders in extracting the facial temperature from the four regions of interest. Using the two-way random effect models and "single rater" unit.

5.3.7.2 Inter-coder reliability: Behavioural data

Inter-coder reliability of each behaviour in each of the three categories (i.e., looking/attention, facial expressions and self-directed behaviours, social referencing behaviours) was calculated between two coders using Cohen’s kappa on a minimum of 15% of the data set (i.e., 5 children). The coders were not blind to the aim of the project; but coded the videos without knowing the episode (i.e., distress or neutral, familiar or unfamiliar). To limit inferences between categories, each category was coded separately.

5.3.7.3 Analyses: Behavioural data

All behavioural data collected during the test phases and coded with ELAN were coupled to a baseline period. Within the 30 seconds following stimulus onset, I extracted the duration of each facial expression and behaviour recorded and subtracted the duration recorded during the 30-seconds baseline. Therefore, data were close to the normal distribution, centred around zero.

5.3.7.4 Analyses: Thermal data

Raw thermal data (min, max, and average temperature extracted every 10 seconds) were visually inspected to check the overall trial period for 15 children (out of 30). The measurement extracted during the baseline was subtracted from the data collected at 80 and 200 seconds after the stimulus onset. I inspected the distribution of the covariate and the distribution of the response. No data transformation on the temperature was conducted because they were near normal distribution.

5.3.7.5 Statistical analyses

I used generalised linear mixed models (GLMMs, Baayen et al. 2008) to test my hypotheses, see *Chapter 2*. I included participant ID as a random factor in the models (nested with the familiarity and valence factors, which were added as a random slope). The response variables, fixed effects, and control variables are detailed for each model below.

5.3.7.5.1 Testing the development of emotion sharing (Aim 1)

I examined whether changes in the following physiological and behavioural measures were predicted by stimulus valence (i.e., distress vs neutral) and model familiarity (familiar vs unfamiliar): i)/ Change in facial skin temperature relative to baseline (Response Variable, RV – relative change at 80 and 200 seconds following the onset of the stimulus – for each relevant region of interest - continuous), ii/ duration of concern facial expressions (RV – continuous) and presence/absence of concern facial expression (RV - binomial), iii/ duration of other negative facial expressions (RV – continuous), iv/ duration of positive facial expressions (RV – continuous), v/ occurrence of self-directed behaviours (RV – continuous), and vi/ duration of avoidance behaviours (RV – i.e., the child looks away from the screen - continuous).

To detect developmental and sex-based differences, age in months and participant sex were also included as variables in the models.

Trial order (1 to 4), stimulus ID (i.e., caregiver identity), and nursery (A/B) were included as control variables in each model. To control for the potential interaction between random and fixed effects, Participant ID nested with stimulus familiarity and valence was included as a random slope (*Model 1*, Table 5.3.). Overall, I ran 11 full GLMM models (“lmer” function for Gaussian data).

Table 5.3 Variables entered into the model comparison to test the development of emotion sharing (*Model 1*)

Variable	**Level**
Fixed effects	
Stimulus Familiarity	Familiar; Unfamiliar
Stimulus Valence	Distress; Neutral
Participant Sex	Male; Female
Participant Age	Continuous (in months)
Control variables	
Trial order	1; 2; 3; 4
Stimulus ID	3 combinations of 2 familiar/unfamiliar caregivers
Nursery	Nursery A; Nursery B
Random slope	
Familiarity + Valence | ID	
Random Effect	
Participant ID	
Interaction	
Familiarity * Valence	

For models with thermal measures as response variables, I ran separate models with the temperature (Celsius) and humidity (percentage) variation within a testing session (standard deviation values) entered as a sole fixed effect to test for their potential effect.

5.3.7.5.2 Testing the development of exploratory communicative responding and information seeking (Aim 2)

I constructed three models to examine whether i/ social referencing (RV - total duration looking at the caregiver), ii/ pointing behaviours (RV - occurrence of pointing towards the stimulus), and iii/ attention towards the screen (RV - total duration of time looking at the screen) were predicted by stimulus valence and familiarity along with participant age and sex. I again controlled for trial order (1 to 4), stimulus ID and nursery by adding them as control variables, with the random effect of participant ID nested with the familiarity and valence as a random slope (*Model 1*, Table 5.3).

5.3.7.5.3 Testing the development of emotion regulation and coping strategies (Aim 3)

I examined whether the physiological response (i.e., change in facial skin temperature relative to baseline, at 80- and 200-seconds following stimulus onset– for each of the three regions of interest) predicted behavioural responses related to emotion regulation- this included i/ the duration of self-directed behaviours, ii/ duration of social referencing, and iii/ avoidance behaviours (time looking away from the screen). I included familiarity, valence, age and sex as fixed effects; trial order, stimulus ID, and the nursery as control variables; participant ID as a random effect and participant ID nested with stimulus familiarity and valence was included as random slope (*Model 2*, Table 5.4). For this analysis, I used data for the distress trials and excluded data for the neutral trials.

Table 5.4 Variables entered into the model comparison to test the development of emotion regulation and coping strategies; Response variables: self-directed behaviours, social referencing behaviours, and avoidance behaviours *(Model 2*)

Variable	Level
Fixed effects	
Physiological response	Temperature difference of the ROI
Participant Sex	Male; Female
Participant Age	Continuous (in months)
Control variables	
Stimulus Familiarity	Familiar; Unfamiliar
Trial order	1; 3
Stimulus ID	3 combinations of two familiar/unfamiliar caregivers
Nursery	Nursery A; Nursery B
Random slope	
Familiarity + Valence | ID	
Random Effect	
Participant ID	
Interaction	
Familiarity * Valence	

I also ran bivariate Pearson correlations to investigate the relationship between the physiological and behavioural responses. To do so, I used the average of the data in both the familiar and unfamiliar in distress situations for each child to examine whether the physiological response (response variables: change in facial skin temperature, the average of the values for the familiar and unfamiliar in distress for each of the three regions of interest – neutral situation excluded) correlates with the i/ participant age, ii/ the production of self-directed behaviours (duration of self-directed behaviours), and iii/ the time avoiding the stimulus. I also examined whether rates of social referencing correlate with i/ the physiological response, ii/ the production of positive facial expressions, iii/ the production of self-directed behaviours (duration of self-directed behaviours), iv/ the time avoiding the stimulus (time looking away from the screen), and v/ the age of the children. Then, I ran partial bivariate Pearson correlations[13] to investigate the effect of familiarity on the above correlations that revealed significance.

5.4 Results

The results are based on a sample of N= 30 children. Each child completed 4 trials (familiarity and valence combination), resulting in a total of 120 trials. The description of the IRT data is provided in *Appendix 5.9*.

5.4.1 Inter coder reliability: IRT data

There was a moderate (Koo and Li 2016) absolute agreement between the three coders for the peri-orbital (kappa = 0.677, $p < 0.001$) and the upper lip (kappa = 0.643, $p < 0.001$) regions,

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[13] I used Bivariate Pearson correlation rather than regression because I did not have predictions as to the directionality of which variable (physiology/behaviour) affected the other.

and an excellent absolute agreement for the nose bridge (kappa = 0.994, p < 0.01) and the nose tip (kappa = 0.998, p < 0.001) regions (Table 5.5).

The variability of the measures can be explained by both the frame selection (20 seconds window) and the selection of the region of interest. Given the lower reliability of the coding of the upper lip, I excluded this region data from the study. Yet, I cautiously included the peri-orbital area to expand our understanding of this ROI.

Table 5.5 Intraclass correlations coefficients (ICC) for absolute agreement of three codes using the two-way random effect models

Average measures for the regions of interest	**Intraclass Correlation**	**95% Confidence Interval**		**F Test with True Value**			
		Lower Bound	*Upper Bound*	*Value*	*df1*	*df2*	*Sig*
Peri orbital	0.677	0.442	0.811	3.91	59	118	<0.001
Nose bridge	0.994	0.990	0.996	163.34	59	118	<0.001
Nose tip	0.998	0.996	0.999	653.21	59	118	<0.001
Upper lip	0.643	0.342	0.800	3.84	59	118	<0.001

5.4.2 Inter coder reliability: behavioural data

The Cohen's kappa was good to excellent for the three categories of behaviours when looking at duration and occurrences: attention towards the emotional display, kappa = 0.91; facial expressions, kappa = 0.85; social referencing and information seeking/sharing, kappa = 0.83. The facial expression of concern was coded as a subset of the negative facial expressions.

5.4.3 Results for the development of emotion contagion (Aim 1)

For the nose-bridge area: χ^2=12.59, d.f. = 5, *p* = 0.027 and nose tip area, both at 200 seconds: χ^2=10.04, d.f. = 4, *p* = 0.040), the full models explained the data significantly better than the null models (which only contained the intercept, control variables, random effect and random slopes). The full model also tends to explain the data significantly better than the null model for the nose bridge area at 80 seconds: χ^2=9.73, d.f. = 5, *p* = 0.083, as well as for the production of positive facial expressions: χ^2=8.33, d.f. = 4, *p* = 0.080 (interaction between familiarity and valence dropped).

Full-null model comparisons were not significant for the other models (Table 5.6). Over-dispersion was no issue in any model, and no considerable collinearity was detected following inspection of VIF.

Table 5.6 Results comparing full -null models

Response variables: change in skin temperature relative to baseline, from stimulus onset	***χ2***	***d.f.***	***p***
peri orbital region 80 sec	1.976 (1.964)	5 (4)	0.852 (0.742)
peri orbital region 200 sec	4.697 (2.439)	5 (4)	0.454 (0.656)
nose bridge region 80 sec	9.727 (1.639)	5 (4)	0.083 (0.802)
nose bridge region 200 sec	12.591 (11.579)	5 (4)	**0.027 (0.021)**
nose tip region 80 sec	8.055 (2.135)	5 (4)	0.153 (0.711)
nose tip region 200 sec	11.067 (10.043)	5 (4)	0.050 **(0.040)**
Response variables: behavioural expressions	***χ2***	***d.f.***	***p***
Concern facial expressions (duration)	7.739 (3.878)	5 (4)	0.171 (0.422)
Concern facial expressions (binomial)	2.496 (3.013)	5 (4)	0.777 (0.556)
Other negative facial expressions (duration)	6.095 (0.674)	5 (4)	0.297 (0.674)
Positive facial expressions (duration)	8.672 (8.326)	5 (4)	0.122 (0.080)
Self-directed behaviours (occurrences)	4.158 (4.153)	5 (4)	0.527 (0.386)
Stimulus avoidance (duration)	3.746 (2.948)	5 (4)	0.587 (0.567)

Significant values (P<0.05) are in **bold;** almost significant values are underlined (P < 0.9); in brackets are the result from full-null comparison without the interaction between familiarity and valence

At 80 seconds following stimulus onset and relative to baseline, there was an interaction between familiarity and valence for the nose bridge region temperature: nasal temperature *increased* more strongly in the familiar distress condition compared to the familiar neutral condition, while in the unfamiliar condition, it increased more in the neutral condition compared to the distress condition (estimate ± se = 0.46 ± 0.17, t = 2.81, p = 0.004). There was no effect of participant age or sex (Table 5.7 and Figure 5.12).

Table 5.7 Results of the full model testing the effect of familiarity, valence, gender, and age on temperature change at the nose bridge region at 80 seconds

S.E.: standard error; LRT: Likelihood Ratio Test; P: p-value

Response variable (P = 0.083)	*Change in temperature relative to baseline in the nose bridge region at 80 sec*				
	Estimate	**S.E.**	**t value**	**LRT**	**P**
(Intercept)	0.290	0.422	0.689		
Familiarity(Unfamiliar) * Valence(Neutral)	0.464	0.165	2.808	8.087	**0.004**
Familiarity (Unfamiliar)	-0.059	0.095	-0.622	0.430	0.512
Valence (Neutral)	-0.139	0.124	-1.120	1.312	0.252
Age	0.010	0.231	0.044	0.002	0.962
Sex (Boy)	0.049	0.113	0.435	0.204	0.651

Significant values (P<0.05) are in **bold;** almost significant values are underlined (P < 0.9)

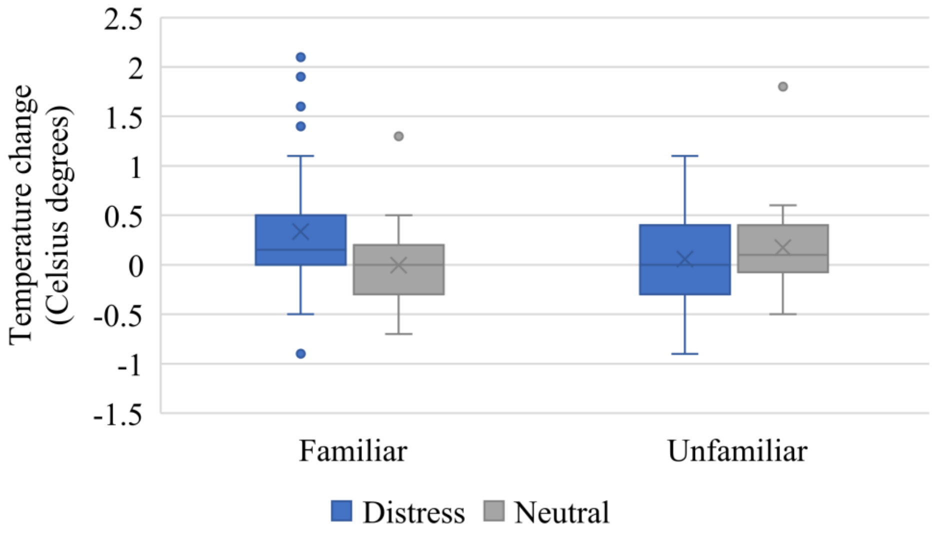

Figure 5.12 Nose bridge temperature change at 80 seconds as a function of familiarity of the model in the distress and neutral conditions. Crosses represent means. Dots represent outlier data that are outside the 1.5 times the interquartile range (IQR), up and down.

At 200 seconds following stimulus onset and relative to baseline, there was a main effect of valence and sex on nose bridge temperature: nasal bridge temperature increased more strongly in the distress condition compared to the neutral condition (estimate ± se = -0.58 ± 0.23, t = -2.56, p = 0.012 – Table 5.8 and Figure 5.13). It also increased more strongly in boys than girls (estimate ± se = 0.38 ± 0.17, t = 2.21, p = 0.024). There was no effect of familiarity nor participant age on the change of temperature.

Table 5.8 Results of the full model testing the effect of familiarity, valence, gender, and age on temperature change at the nose bridge at 200 seconds

S.E.: standard error; LRT: Likelihood Ratio Test; P: p-value

Response variable (**P < 0.05**)	*Change in temperature relative to baseline in the nose bridge region at 200 seconds*				
	Estimate	**S.E.**	**t value**	**LRT**	**P**
(Intercept)	0.866	0.632	1.371		
Familiarity (Unfamiliar)*	-0.203	0.207	-0.985	0.262	0.609
Valence (Neutral)	-0.581	0.227	-2.556	6.370	**0.012**
Age	-0.361	0.349	-1.034	1.161	1.161
Sex (Boy)	0.375	0.170	2.205	5.110	**0.024**

Significant values (P<0.05) are in **bold;** almost significant values are underlined (P < 0.9)

* The Familiarity*Valence interaction was not significant, therefore I removed it from the model and re-tested without it

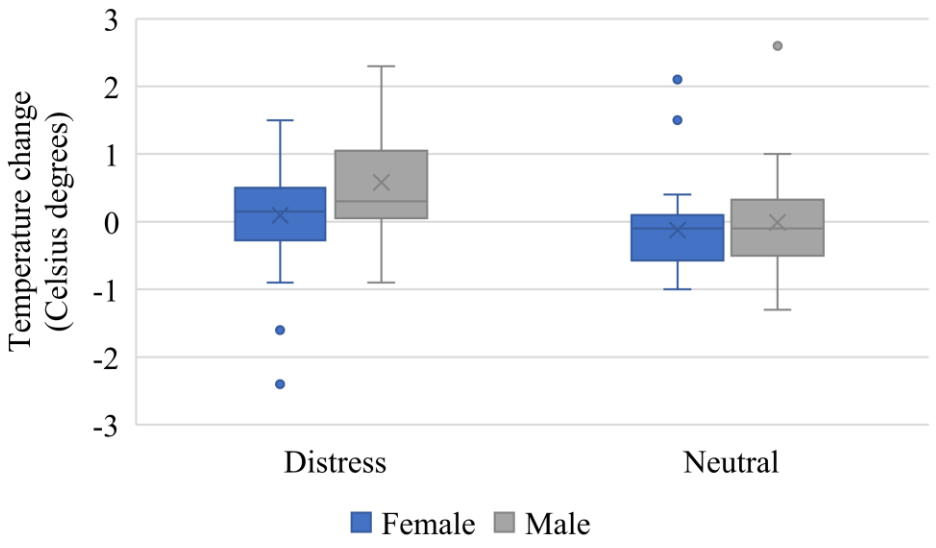

Figure 5.13 Nose bridge temperature change at 200 seconds as a function of sex of the participant in the distress and neutral conditions. Crosses represent means. Dots represent outlier data that are outside the 1.5 times the IQR, up and down.

At 200 seconds following stimulus onset and relative to baseline, there was a main effect of age on nose tip temperature: nose tip temperature increased more strongly in younger children than older children (estimate ± se = -0.83 ± 0.42, t = -1.98, p = 0.039 - Table 5.9 and Figure 5.14). It also tended to increase more strongly in the distress condition than the neutral condition (estimate ± se = -0.45 ± 0.24, t = -1.86, p = 0.063 – Figure 5.14), and more in boys than girls (estimate ± se = 0.38 ± 0.21, t = 1.87, p = 0.057). There was no effect of familiarity on the change of temperature.

Table 5.9 Results of the full model testing the effect of familiarity, valence, gender, and age on temperature change at the nose tip at 200 seconds

S.E.: standard error; LRT: Likelihood Ratio Test; P: p-value

Response variable (**P < 0.05**)	*Change in temperature relative to baseline in the nose tip region at 200 seconds*				
	Estimate	**S.E.**	**t value**	**LRT**	**P**
(Intercept)	*1.769*	*0.747*	*2.366*		
Familiarity (Unfamiliar)*	0.058	0.176	0.331	0.111	0.739
<u>Valence</u> (Neutral)	-0.451	0.242	-1.861	3.460	<u>0.063</u>
Age	-0.827	0.418	-1.978	4.264	**0.039**
<u>Sex</u> (Boy)	0.384	0.205	1.872	3.631	<u>0.057</u>

Significant values (P<0.05) are in **bold;** almost significant values are <u>underlined</u> (P < 0.9)

* The Familiarity*Valence interaction was not significant, therefore I removed it from the model and re-tested without it

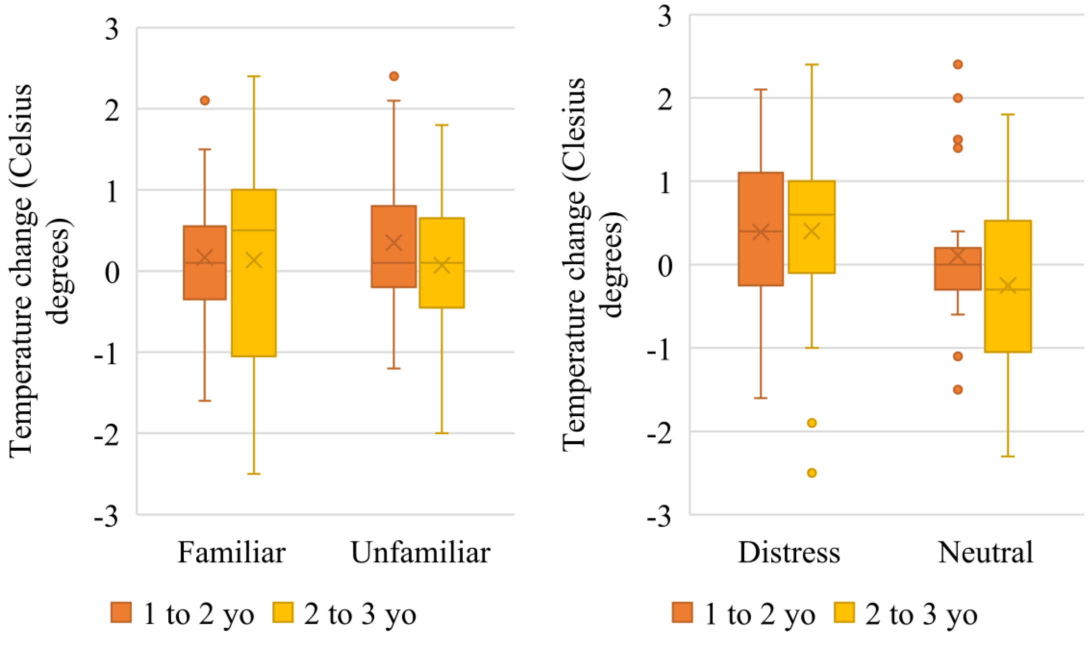

Figure 5.14 Nose tip temperature change at 200 seconds as a function of the age (yo = years old) of the participant and familiarity of the model (L) and as a function of the age of the participant and valence of the stimulus (R). Crosses represent means. Dots represent outlier data that are outside the 1.5 times the IQR, up and down.

Relative to baseline, the production of positive facial expressions increased more strongly in the neutral condition compared to the distress condition (estimate ± se = 2.43 ± 1.19, t = 2.04, p = 0.045). There was no effect of familiarity of the stimulus, nor age and sex of the participant (Table 5.10).

Table 5.10 Results of the full model testing the effect of familiarity, valence, gender, and age on the production of positive facial expressions

S.E.: standard error; LRT: Likelihood Ratio Test; P: p-value

Response variable (P = 0.080)	*Change in the duration of positive facial expressions relative to baseline*				
	Estimate	**S.E.**	**t value**	**LRT**	**P**
(Intercept)	5.707	4.605	1.239		
Familiarity (Unfamiliar)*	-1.274	0.794	-1.604	2.668	0.102
Valence (Neutral)	2.431	1.192	2.040	4.031	**0.045**
Age	-3.786	2.554	-1.482	2.367	0.124
Gender (Boy)	-0.006	1.258	-0.005	0.009	0.924

Significant values (P<0.05) are in **bold;** almost significant values are underlined (P < 0.9)

* The Familiarity*Valence interaction was not significant, therefore I removed it from the model and re-tested without it

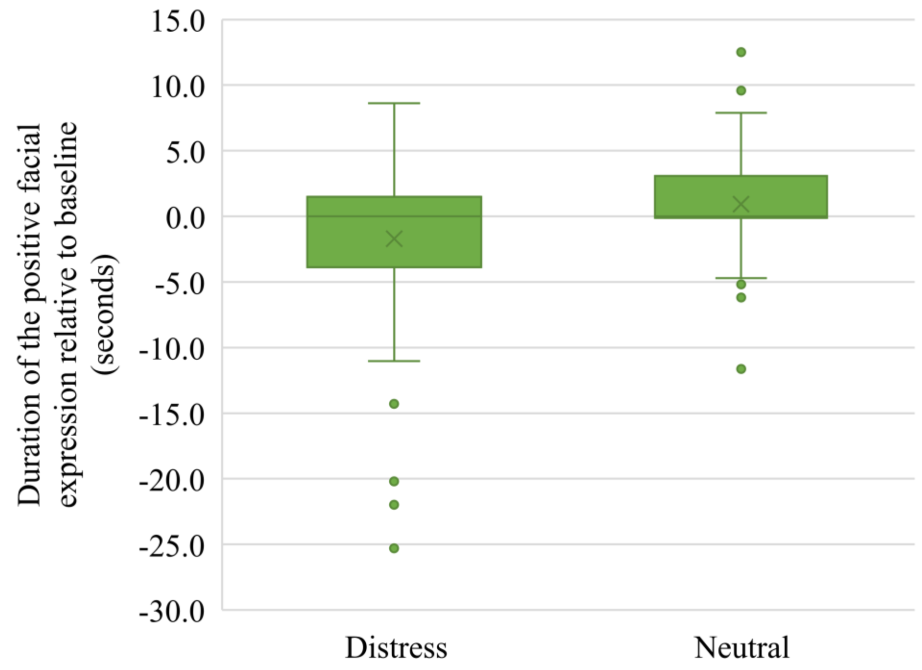

Figure 5.15 Production of positive facial expressions as a function of the valence of the stimulus. Crosses represent means. Dots represent outlier data that are outside the 1.5 times the IQR, up and down.

The full-null model comparisons did not reveal any effect of the room temperature and humidity variation (fixed effects), on the thermal response in the three regions of interest of the face at 80 or 200 seconds after onset stimulus (p > 0.05).

5.4.4 Results for the development of exploratory communicative responding and information seeking (Aim 2)

The full model for "attention to the stimulus" tended to explain the data significantly better than the null models (χ^2=8.245, d.f. = 4, p = 0.083). The other full-null model comparisons were nonsignificant (see Table 5.11) preventing further interpretation of the models. Over-dispersion was no issue, and no considerable collinearity was detected.

Table 5.11 Results of the comparison of the full models with the respective null model (R function 'anova' with argument test "Chisq")

Response variables	***χ2***	***d.f.***	***p***
Social referencing behaviour (duration)	8.237 (4.750)	5 (4)	0.144 (0.314)
Pointing behaviours (occurrences)	2.314 (2.234)	5 (4)	0.804 (0.693)
Focus to the stimulus (duration)	8.328 (8.245)	5 (4)	0.139 (0.083)

Significant values (P<0.05) are in **bold;** almost significant values are underlined (P < 0.9)

Values in brackets: full model without the interaction familiarity + valence, but only individual predictors.

For the full-null comparison that was approaching significance, I interpreted the model estimates. Relative to baseline, the participants looked at the screen more in the distress condition compared to the neutral condition (estimate ± se = -3.50 ± 1.72, t = -2.04, p = 0.046). There was no effect of familiarity of the stimulus, or age and sex of the participant (Table 5.12).

Table 5.12 Results of the full model testing the effect of familiarity, valence, gender, and age on temperature change at the nose bridge and nose tip

S.E.: standard error; LRT: Likelihood Ratio Test; P: p-value

Response variable (P = 0.083)	*Change in the duration of focus to the stimulus relative to baseline*				
	Estimate	**S.E.**	**t value**	**LRT**	**P**
(Intercept)	13.160	7.022	1.874		
Familiarity (Unfamiliar)	-0.277	1.295	-0.214	0.048	0.827
Valence (Neutral)	-3.500	1.719	-2.036	3.985	**0.046**
Age	-2.859	3.982	-0.718	0.565	0.452
Gender (Boy)	-3.063	1.962	-1.561	2.535	0.111

Significant values (P<0.05) are in **bold**

5.4.5 Results for the development of emotion regulation and coping strategies (Aim 3)

Given the correlation between the thermal measurements (see *Appendix 5.10*), I selected one of these measurements to test for the relationship between the thermal and behavioural response. The three full-null model comparisons were nonsignificant (see *Appendix 5.11*) preventing further interpretation. Over-dispersion was no issue, and no considerable collinearity was detected.

Bivariate Pearson correlations revealed that the change in facial skin temperature – for the three regions of interest at 80 and 200 seconds after the onset stimulus- did not significantly correlate with participant age, the production of self-directed behaviours (duration of self-directed behaviours), nor the length of time avoiding the stimulus (non-significant results are presented in *Appendix 5.12*).

The rate of social referencing (looking at the caregiver during the distress situation) correlated with the change of temperature in the peri-orbital region at 80 seconds (r = -0.52, p = 0.003, N

= 30). Partial bivariate Pearson correlations revealed this was mainly driven by the familiar condition (r = -0.42, p = 0.022, N = 30), not the unfamiliar condition (r = 0.037, p = 0.846, N = 30 - Figure 5.16).

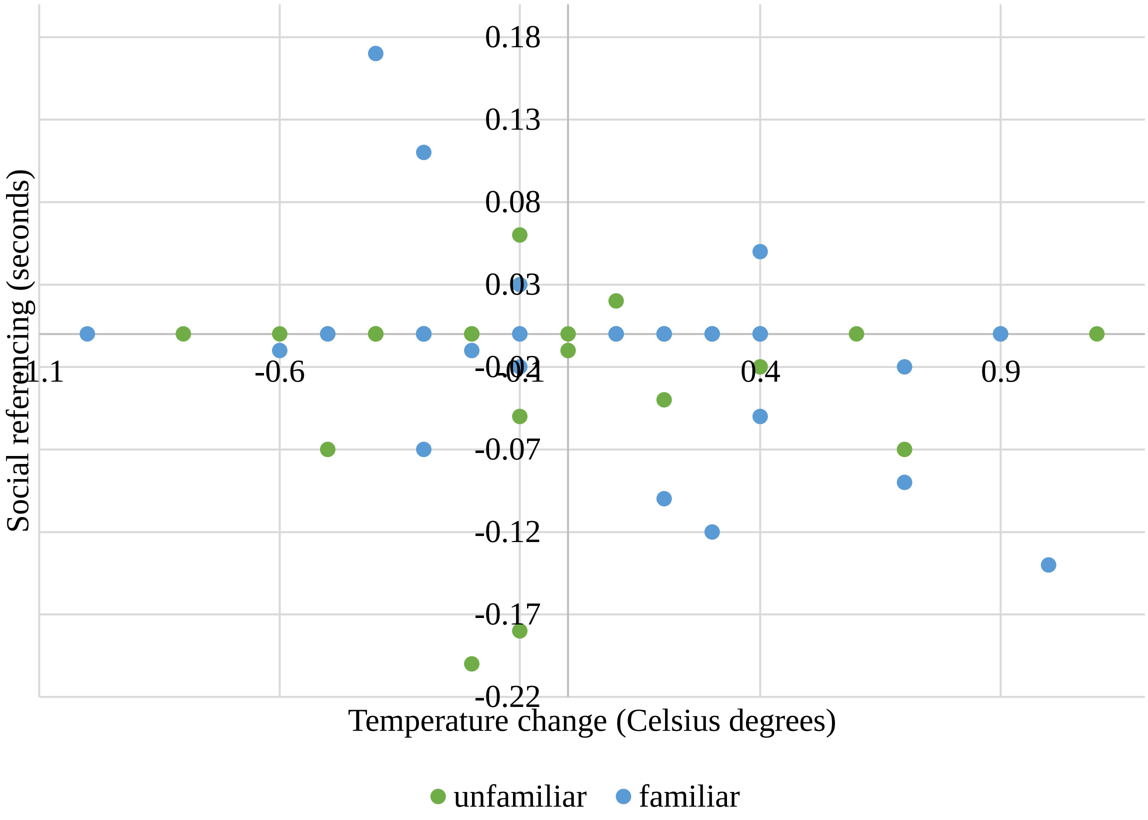

Figure 5.16 Rate of social referencing (relative to baseline) as a function of the change of temperature in the peri-orbital region at 80 seconds in familiar and unfamiliar conditions.

There was also a correlation between social referencing and the change of temperature in the peri-orbital region at 200 seconds (r = -0.40, p = 0.03, N = 30 – Figure 5.17) and in the nose bridge region at 80 seconds (r = -0.41, p = 0.03, N = 29 – Figure 5.18). However, it does not correlate with the change of temperature in the nose tip region at 80 seconds nor the nose bridge and nose tip regions at 200 seconds.

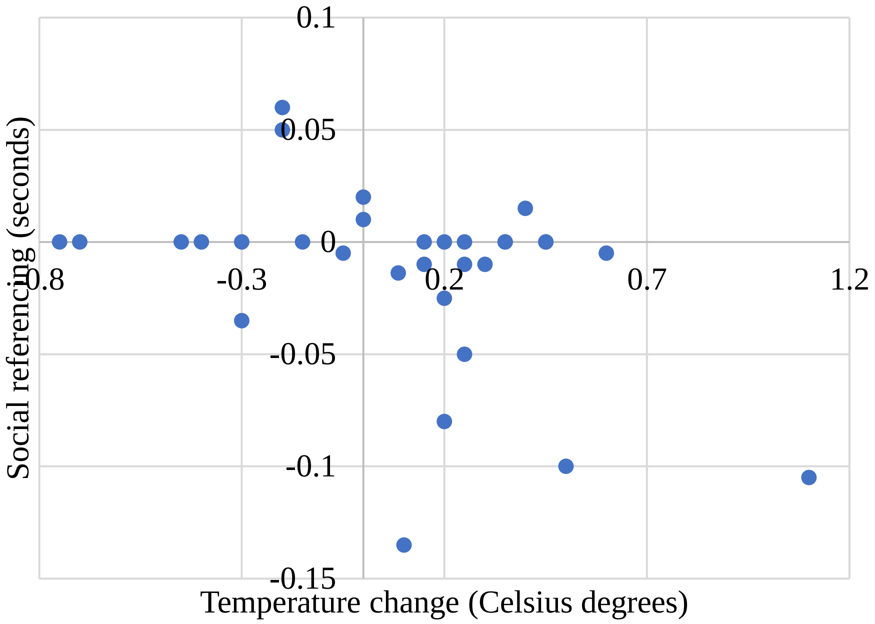

Figure 5.17 Rate of social referencing (relative to baseline) as a function of the change of temperature in the peri-orbital region at 200 seconds.

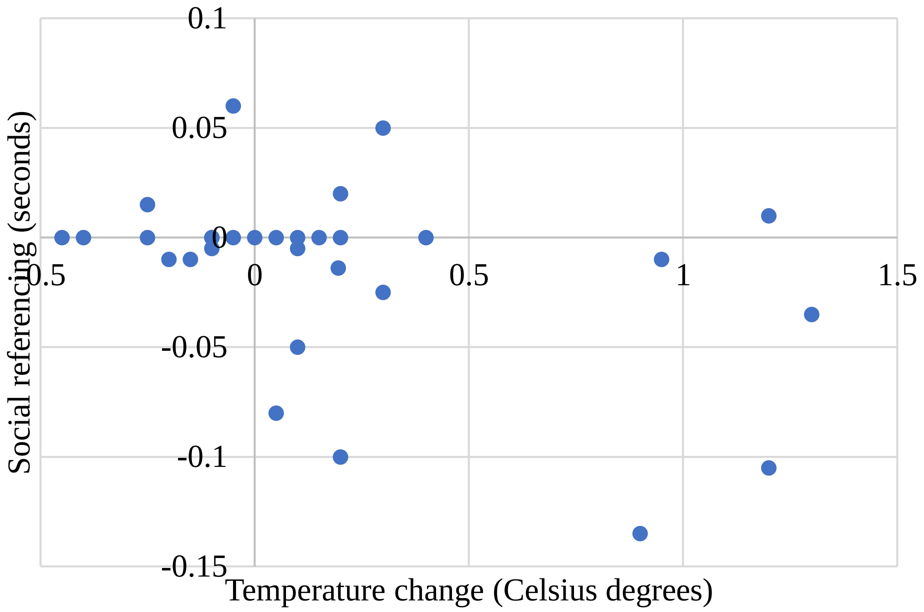

Figure 5.18 Rate of social referencing (relative to baseline) as a function of the change of temperature in the nose bridge region at 80 seconds.

The rate of social referencing behaviours also correlated with the production of positive facial expressions (r = 0.37, p = 0.047, N = 30). A partial bivariate Pearson correlation revealed that this tended to be driven by the familiar situation (r = 0.350, p = 0.058, N = 30 – Figure 5.19).

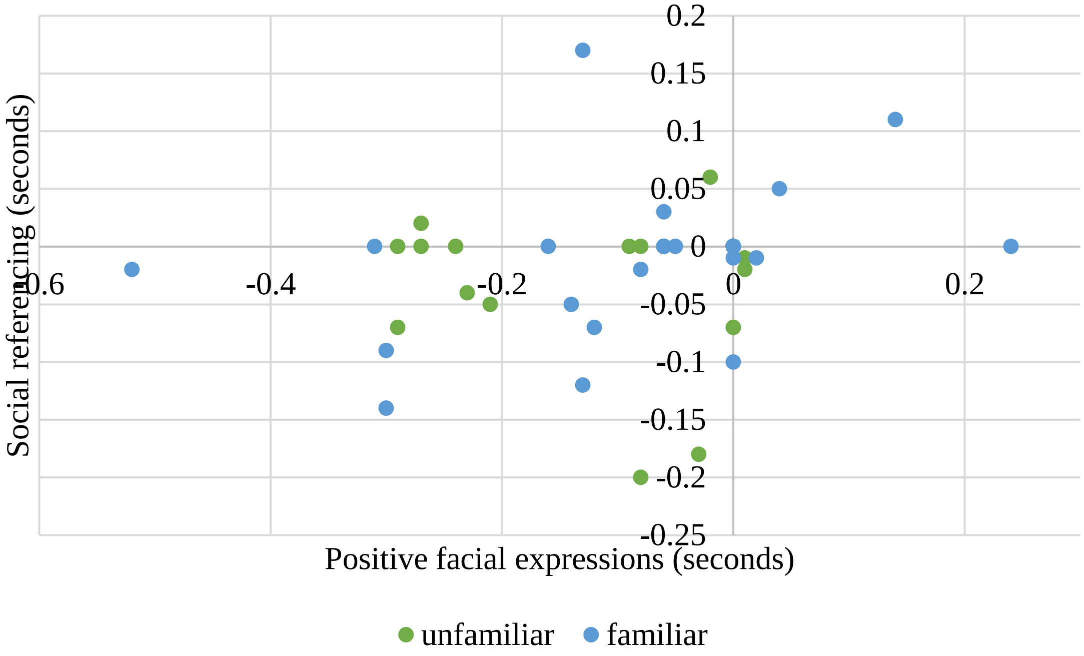

Figure 5.19 Rate of social referencing (relative to baseline) as a function of the production of positive facial expressions in familiar and unfamiliar conditions.

The rate of social referencing behaviours <u>tends</u> to correlate with the age of the participant (r = 0.33, p = 0.079, N = 30), with older children using more social referencing than younger ones, but not with the production of self-directed behaviours, the time spent avoiding the stimulus, or the age of the children (tendency: r = 0.326, p = 0.079, N = 30).

An overview of the Bivariate correlation results for the social referencing is provided in Table 5.13.

Table 5.13 Bivariate Pearson correlation results for social referencing

		Physiological responses at 80 seconds
Peri orbital region	Pearson correlation	**-0.524** (**-0.418**; 0.037)
	Sig. (2 tailed)	**0.003** (**0.022**; 0.846)
	N	30 (30; 30)
Nose bridge region	Pearson correlation	**-0.407** (-0.295; -0.048)
	Sig. (2 tailed)	**0.029** (0.128; 0.805)
	N	29 (28; 29)
Nose tip region	Pearson correlation	-0.167
	Sig. (2 tailed)	0.387
	N	29
		Physiological responses at 200 seconds
Peri orbital region	Pearson correlation	**-0.393** (-0.147; -0.112)
	Sig. (2 tailed)	**0.032** (0.446; 0.563)
	N	30 (29; 29)
Nose bridge region	Pearson correlation	-0.068
	Sig. (2 tailed)	0.719
	N	30
Nose tip region	Pearson correlation	-0.089
	Sig. (2 tailed)	0.638
	N	30
		Behavioural responses
Positive facial expressions	Pearson correlation	**0.365** (0.350; 0.088)
	Sig. (2 tailed)	**0.047** (0.058; 0.645)
	N	30 (30; 30)
Self-directed behaviours (occurrences)	Pearson correlation	0.036
	Sig. (2 tailed)	0.852
	N	30
Stimulus avoidance (duration)	Pearson correlation	-0.026
	Sig. (2 tailed)	0.893
	N	30
Age	Pearson correlation	0.326
	Sig. (2 tailed)	0.079
	N	30

Significant correlations are in **bold** (at the $P < 0.05$, 2 tailed); almost significant correlations are underlined ($P < 0.9$). Results of partial correlations for familiar and unfamiliar situations are indicated under brackets (familiar; unfamiliar)

5.5 Discussion

Responding appropriately to the distress of others is a crucial step in human development. Yet, very little is known about how underlying arousal links to external behaviours. In this study I aimed to investigate the development of emotional responding to other's distress through a multicomponent approach that includes both physiological and behavioural measures. To do this, I measured children's affective states in response to emotional video stimuli, using a combination of IRT and behavioural measures of their corresponding facial expressions and behaviours.

Overall, the findings confirmed a physiological reaction of children that was predicted by the age and sex of the child. Moreover, in line with the *empathy gradient,* this was predicted by the familiarity of the model for some measures. This is an important step towards the understanding of the underlying mechanisms of empathy. In contrast, I found no effect of sex, age nor familiarity on the corresponding behavioural responses. This suggests that the physiological and behavioural responses might be driven by different processes and cannot be assumed to be predictors of one another. When examining children's communicative responding and information seeking, although children paid greater attention to distress than control stimuli, there was no effect of age, sex, model familiarity, or stimulus type. Finally, some results also revealed a tenuous link between the behavioural responses of the children and their physiological response to the stimuli. These results are now discussed in more detail below in relation to the theoretical constructs of empathy.

5.5.1 Development of emotion contagion (Aim 1)

5.5.1.1 Physiological response

The results revealed that children’s physiological response (as measured in the nasal region: nose bridge and nose tip – 200 seconds) was stronger when in the distress condition than the neutral condition. In the nose bridge area (at 80 seconds), model familiarity and stimulus valence seemed to interact, whereby temperature increased more strongly in the familiar distress condition compared to the familiar neutral condition. However, it increased more strongly in the unfamiliar neutral condition compared to the unfamiliar distress condition. This finding partly challenges my prediction that the most emotionally intense situation would trigger more arousal. Because the neutral situation followed the distress situation, it is possible that the children were disturbed by seeing the unknown individual they had previously seen upset on screen again. The literature on the topic is very limited.

Overall, nasal skin temperature increased between baseline and the distress stimuli. This result contrasts with a child-mother empathy study in which the skin temperature decreased in the nasal region of children and mothers in a distress situation (Ebisch et al., 2012). However, the design of this study differed from ours where a toy broke when held by the child and triggered the emotional response in both the child and the mother. The non-human primate literature also indicates an overall decrease of the skin temperature in the nasal area (usually nose tip) in negative situations like fear (Kano et al., 2016; Kuraoka & Nakamura, 2011; Nakayama et al., 2005) or in association with the vocalisations of conspecifics (Dezecache et al., 2017). That being said, previous human studies on positive emotions highlighted contrasting/flexible results (decrease: Nakanishi and Imai-Matsumura 2008; Salazar-López et al. 2015; Cruz-Albarran et al. 2017; increase: Zenju et al. 2004; Robinson et al. 2012; Salazar-López et al. 2015), suggesting that the physiological reaction associated with a change in the facial skin temperature is complex and still difficult to understand. This is surely particularly challenging for complex emotions/reactions like empathic responding which is not binary (positive vs negative).

From a mechanistic perspective, this increase of temperature might result from vasodilatation leading to increased blood flow connected to an increase of the heart rate along with α- and β-adrenergic influences (Vella & Friedman, 2009). For instance, the immediate physiological and neural reaction that occurs in the face of danger, activates the body to confront or escape the threat, i.e., *flight* or *fight* response (Milosevic, 2015). In this situation, physiological changes like an increase in heart rate and shallow breathing prepare the individual for the emergency reaction, while diverting energy from other parts of the body, like the face or the digestive system (Milosevic, 2015). Such reactions could lead to a decrease in the temperature that would have resulted from the constriction of blood vessels that innervate a given facial region (e.g., arteriovenous anastomosis: Bergersen, 1993), resulting from the activity of the sympathetic postganglionic neurons (Hales, 1985).

Overall, the findings of the current study suggest that IRT might detect arousal, but not necessarily valence (also still a debated issue, see Adriaense et al., 2020 for a review; and *Chapter 4*). In particular, it is crucial to redefine the nature of the stimuli, as the binary valence does not seem to fit all situations. Future work should focus further on these components of emotions, i.e., arousal and valence, and untangle the thermal measurements with additional physiological and behavioural measures.

5.5.1.2 Sex differences

In line with the hypothesis that young boys show higher arousal levels and lower inhibitory control than girls (Brody, 1999; Chaplin, 2015), I found that boys showed a stronger physiological response than girls. Nevertheless, although I expected girls to be more emotionally expressive than boys (Zahn-Waxler et al., 1991, 2001), there were no sex differences in behavioural expressions. Aspects of study design and sample size may in part explain these mixed results. In the procedure, the children could look at the experimenter and the caregiver during the trial. However, as the caregivers were instructed to remain neutral throughout, an absence of reaction from the caregiver or the experimenter might have inhibited the children's expressiveness. In addition, as the video clips I used were posed, the children's responses may have been reduced (discussed below). Future work should be conducted in more ecologically valid settings to expand upon these findings.

5.5.1.3 Effect of age

The strength of the thermal response in the nose tip region decreased with age. This suggests that children gain control of the inner response, an indicator of their developing emotion regulation skills (Carlson, 2005; Cole et al., 2009). While emotion regulation develops with age, it is possible that the temperature difference could also be in part explained by the difference in skin physical characteristics, such as skin thickness and composition. Nevertheless, to my knowledge, there is no literature available to support this hypothesis.

5.5.1.4 Behavioural response

5.5.1.4.1 Positive facial expressions

The results indicated that children produce fewer positive facial expressions when watching the distress condition, which is congruent with what one would expect in a negative situation. However, children do show positive facial expressions in this context (in contrast to *not* producing any positive facial expressions when watching an individual in distress), which can also be a sign of discomfort, or a way to get emotional support and/or as a coping mechanism. Indeed, positive facial expressions are suggested to lower physiological arousal in negative situations (Levenson et al., 1990), with smiling helping the individual to engage with others, therefore preventing the increase of the negative arousal (Fredrickson & Levenson, 1998; McEwen, 1993) through the activation of specific facial nerves (Lang et al., 1991; Pressman et al., 2020).

5.5.1.4.2 Effect of age

Unlike age effects for the thermal response, no effect of age was highlighted for corresponding behaviours. However, the age range of our sample extended from 1 to 3, which includes the sensitive step of the 2 years (Roth-Hanania et al., 2011) that comes with the development of language and physical mobility. The development of these abilities impacts the regulating strategies, and so I expected to see a shift in the coping strategies employed by the children in the different situations. However, it may be that our age range is too restricted and our sample size is too limited to capture a developmental variation. Furthermore, the use of a non-contextual stimulus and video clips, as well as the presence of the caregiver and the experimenter in the room (*audience effect*, Zuberbuhler, 2008*; social facilitation*, Guerin & Innes, 2009; Mullen et al., 1997; Platania & Moran, 2001; Zajonc, 1965) might have biased the behavioural expression of emotions of the children (as described in the study limitation section below). Future work could expand the investigation to a broader age range to examine the use of smiling (and other positive facial expressions) as a coping mechanism to call for social support and lower the physiological arousal (Fredrickson & Levenson, 1998; Levenson et al., 1990; McEwen, 1993) across age. Furthermore, studies conducted in naturalistic conditions could help untangle these findings. Besides, our data set reveals an important individual variation.

5.5.2 Exploratory communicative responding and information seeking (Aim 2): Effect of stimulus valence and familiarity

In line with the hypothesis that children seek information to understand complex situations (Zahn-Waxler, Radke-Yarrow, et al., 1992; Zahn-Waxler, Robinson, et al., 1992b), I found that children focused more on distress stimuli than neutral stimuli. However, in contrast with my hypothesis that children should focus more on the socially relevant (i.e., familiar) individual in distress (Berlo et al., 2020; de Waal & Preston, 2017; Preston & de Waal, 2002), there was no effect of familiarity of the model on this attendance/focus. There are several possible explanations for this. First, although the social bond between the children and their primary caregiver at the nursery may be stronger than that of a stranger, it is not as strong as that with the mother used in previous studies (e.g., Davidov et al., 2020). Children might also have experience witnessing and responding to the distress of their mother or comforting her in various situations. By doing so, the child might have been rewarded with positive feedback and encouraged to repeat prosocial responses (Dahl, 2015; Davidov et al., 2020). In contrast, children do not have a similar experience with the nursery caregiver, who also has an authority role that might bias the social connection with the children. Finally, some children might have not been at the nursery for long enough to develop and strengthen this bond.

5.5.3 Development of emotional regulation and coping strategies (Aim 3)

5.5.3.1 Social referencing and physiological response

The results revealed that the more children looked at the caregiver present in the room, the weaker their physiological response (as measured in the peri-orbital region at 80 and 200 seconds, and nose bridge region at 80 seconds). Looking at the caregiver is a social referencing behaviour (McLellan et al., 2011; Walle et al., 2017) wherein children use the affective displays of an adult to get information about environmental objects, persons, and situations (Walle et al., 2017). The present finding suggests that children might use social referencing to regulate their arousal (McLellan et al. 2011).

In line with the *empathy gradient*, the temperature change recorded in the peri-orbital region was mainly observed when the children witness the distress of a familiar individual. Overall, the results of the present work are a bit mixed regarding the *empathy gradient* as some previous results were not supportive of it.

5.5.3.2 Social referencing and positive facial expressions

Findings show that the more children looked at the caregiver present in the room, the more positive facial expressions they produced and particularly when witnessing the distress of a familiar individual. This may highlight the attempt of the children to exchange information with the caregiver about someone they both know. The use of positive facial expressions may be an invitation from the child to seek emotional support from the caregiver in a situation that may be a bit disturbing. I also found that older children tended to use social referencing more than younger ones, which is in line with the notion that emotional communication improved with age (McLellan et al., 2011).

5.5.3.3 Self-directed behaviours and physiological response

Although I predicted self-directed behaviours would relate to stronger thermal responses, results did not reveal a relationship between the physiological response and self-directed behaviours. This was the case, even when taking into account that my ethogram included a broader range of self-directed behaviours (e.g., manipulation of one’s hair, clothing and/or accessories), in comparison to the non-human primate literature that usually focuses on self-scratching (Grolnick et al., 1996). It is possible that the sample size of this study did not allow for significant results. Future work should look closer into the self-directed behaviours to discriminate their exact function and/or significance.

5.5.3.4 Avoidance of the stimulus and physiological response

Although I predicted avoidance of the potentially disturbing stimulus (Kashdan et al., 2006) would be linked to the inner arousal of the children, results were inconclusive. Children develop new emotion regulation strategies with age, starting with simple ones like putting their hands in front of their eyes to stop seeing or physically leaving an emotional situation when they can. More advanced forms of regulation develop during the pre-school age along with the maturation of more complex mental processes (Altshuler & Ruble, 1989; Sala et al., 2014; Thompson, 1994). In the present study, although looking away from a negative stimulus may be a way to escape its negative impact (Sloan, 2004), the presence of the experimenter and/or the caregiver in the room may have disinhibited this behaviour, as the children may not have felt comfortable disobeying the instructions of being asked to watch the video. Follow up research could be conducted where children are left alone to engage with stimuli away from the direct observation of adults.

5.5.4 Study considerations and limitations

Although this study is an important first step in investigating the underlying mechanisms of empathy and its development, several limitations could have influenced the results and their generalisability. Some of these limitations echo the ones highlighted in the previous chapter with the chimpanzees (*Chapter 4*), and here I discuss how they might apply in the present experimental design and setting.

5.5.4.1 Experimental stimuli

5.5.4.1.1 Nature of the stimulus

Previous experimental studies conducted have used visual contextual cues, like pretend injuries (Davidov et al., 2020; Gill & Calkins, 2003; Zahn-Waxler, Radke-Yarrow, et al., 1992) and need for help (Hepach et al., 2016; Hepach, Vaish, Müller, et al., 2017a), to elicit emotional responses in children. However, the outputs of these studies are somewhat disputed as it is unclear whether the child reacts to the emotion of the individual or to the distressing situation itself. In the present study, the model simulates distress with non-contextual cues as to what caused the distress. By doing so, we exclude potential confounds that could trigger a response from the participant, other than the emotion of the model. Nonetheless, empathy is a complex phenomenon that is challenging to encapsulate within a single situation. Therefore, further work using various stimuli is valuable to identify the trigger of the behavioural and physiological response.

5.5.4.1.2 Posed versus spontaneous emotion demonstration

In this study, I used video clips of caregivers displaying posed emotional states. Previous studies have presented subjects with posed demonstrations (children: Gill & Calkins, 2003; Zahn-Waxler et al., 1992), video stimuli (Eisenberg et al., 1990, 1996; Hepach et al., 2013), or genuine audio stimuli (i.e., playback experiments, Gill & Calkins, 2003; Martin & Clark, 1982) to elicit emotions in the subjects. The interpretation of experiments using posed stimuli as opposed to genuinely expressed emotional states is challenging (Kret et al., 2020; Zuckerman et al., 1976). But despite the fact that actors tend to amplify stereotypical displays of emotions (Wallbott & Scherer, 1986), it seems that such stimuli constitute a good resemblance to genuine emotional displays (De Gelder & Van den Stock, 2011; Wallbott, 1990).

Previous attempts to use still images or video footage failed at eliciting physiological reactions in chimpanzees (Y. Sato et al., 2019), potentially because the visual stimulus was too weak. In the present study, the video clips included an auditory component that was successful at attracting the children's attention towards the screen, and also provided an auditory/vocal context to the emotional situation in contrast with images alone.

5.5.4.2 Experimental conditions

For practical and ethical reasons, it was necessary to have a nursery caregiver in the room during the experiment. However, the presence of others influences the behaviour of an individual (*social facilitation*, Guerin & Innes, 2009; Zajonc, 1965; *audience effect,* Zuberbuhler, 2008), so it is possible the presence of an audience influenced the children's responses (Mullen et al., 1997; Platania & Moran, 2001), potentially inhibiting their responses if children perceived them as authority figures (Choi & Loftness, 2012; Ioannou, Gallese, et al., 2014). Future work might consider isolating the child in a comfortable environment such as via one-way mirror. However, such settings present other limitations such as the potential stress induced by an isolation, that also has the potential to bias the results.

From more practical stances, the children who could sit down by themselves were asked to sit on a chair, while the younger ones were on the laps of their caregiver. It is conceivable that both the behavioural and physiological measurements had been impacted by these settings. Indeed, sitting on a chair may constitute a physical barrier to some behavioural responses such as approaching (Abramson et al., 2019). Also, the infants who were on the laps of their caregivers might have been impacted by the body heat of the caregiver, as well as by their movements. Future work should focus on designing experiments that allow for enough control to permit clear thermal measurement, while conveying as naturalistic conditions as possible to enable the children to express themselves with minimum constraints.

Although it is possible that the thermal results could have been impacted by the testing conditions, this testing environment was much more controlled than in *Chapter 4,* as temperature and humidity were constant, as well as the artificial lighting conditions (Ioannou, Gallese, et al., 2014; Kano et al., 2016). No significant changes in temperature and humidity were recorded during the trials.

5.5.4.3 Sample size

Overall, due to the challenges of conducting experimental work with small children and the major disruptions due to the Covid pandemic, the sample size of this study is relatively small. Larger sample sizes are needed to generalise the response patterns for social bias and response to negative emotional events investigated here, along with identifying individual differences, including the effect of social competence (Webb et al., 2017) and emotion regulation skills (Clay & de Waal, 2013a) on these mechanisms.

5.5.5 Conclusion

This mixed-methods study confirmed a physiological reaction of children when witnessing another's distress. I showed that this response matures across age along with social, cognitive, and emotional skills related to emotional responding. Intriguingly, the physiology results show a familiarity bias that contradicts the *empathy gradient*, suggesting that additional mechanisms might modulate the physiological response of children in this specific experimental situation. Sex differences in the physiological response confirm differences in emotion regulation skills present in young children, with boys showing stronger arousal than girls. When combining the behavioural and the physiological response, some results have revealed a tenuous link between behavioural responses of the children and their physiological response to the stimuli, contributing to new theoretical and methodological advances into how internal affective processes map onto external measures in early childhood. Overall, the results of this study highlight the complexity of measuring emotional responding. IRT provides complex data that can be difficult to interpret, particularly when combined with behavioural markers. It is crucial for future work to combine multiple measures, such as IRT, heart rate, pupil dilation and behavioural markers to improve our understanding of the underlying mechanisms of empathy.

Chapter 6 General discussion

In this last chapter, I discuss and reflect upon my empirical findings presented in this thesis in relation to the original research questions and discuss the contributions that my work has made. In particular, I discuss how my work contributes to the understanding of the behavioural and physiological markers of empathy in human children and great apes. I also discuss the relevance of the approaches and methods used, and re-assert the importance of taking a multi-methods approach. I also reflect on the broader implications of my work, including investigating the underlying physiological mechanisms of empathy. Finally, I consider more broadly the limitations and the main challenges that my own work and the field encounters. I consider how these could be addressed, and suggest future studies that could be conducted to advance our understanding of empathy in primates and other species.

6.1 Theoretical goals and summary of the thesis findings

6.1.1 Main theoretical goals

The overall goal of my thesis was to address fundamental questions about the evolutionary and developmental roots of empathy, along with its physiological mechanisms. In *Chapter 3*, I investigated the development of consolation in sanctuary-living bonobos, where I considered whether the effectiveness and selectivity of consolation varies across age, as well as the impact of rearing experiences. In *Chapter 4*, I investigated the physiological and emotional responses of sanctuary-living chimpanzees in response to other's distress and its relation to consolation, a putative behavioural marker of empathy. In *Chapter 5*, I experimentally investigated the development of emotion contagion and empathy, by exploring how young children (1-3 years) respond to others' distress – this included measuring their facial temperature responses and behavioural markers, including facial expressions of concern, exploratory communicative responding, information seeking and emotion regulation strategies.

To address these goals, I combined multiple approaches and methodologies. While naturalistic observations help to identify external markers of empathic behaviours like consolation (*Chapter 3*), controlled experiments are needed to identify the underlying physiological mechanisms (*Chapters 4* and *5*). In both human children and *Pan*, I investigated how these components develop across time using a cross-sectional design, to shed new light on their ontogenetic basis (*Chapters 3* and *Chapter 5*).

6.1.2 Consolation in sanctuary-housed bonobos

In contrast with my predictions, the ethological study conducted with the sanctuary-housed bonobos (*Chapter 3*) did not highlight significant developmental differences in bonobos' efficiency to alleviate another's distress, how socially discriminant they are in selecting the target of the consolation, and whether they tend to be first consoler or follower. Regarding the efficiency of consolation, results suggest that, regardless of who the consoler is, receiving the physical contact itself might provide emotional relief (Shamay-Tsoory & Eisenberger, 2021). Nonetheless, future work should combine behavioural metrics (e.g., self-directed behaviours) with physiological measurements (e.g., breathing rate; heart rate, Wascher et al., 2008), measured before and after a given consolation, to increase the understanding of the function and underlying mechanisms. Similar work has already been conducted in semi-tame free-roaming geese equipped with fully implanted transmitters (Wascher et al., 2008). These transmitters allowed for the recording of immediate physiological responses (heart rate) in response to a live naturalistic social event.

Regarding the selectivity, although social awareness and cognitive control develop over time (Clay & de Waal, 2013a, 2013b; Cordoni et al., 2006; Webb et al., 2017), the maturation of these abilities might not be crucial to the selectivity of empathic responding. Nonetheless, future work should focus on younger subjects than included in this study, in order to assess whether these abilities develop and mature earlier than what the current sample can discriminate. Altogether, these findings might suggest that although the cognitive components of empathy develop over time, advanced cognition may not be essential for the expression of concern, or at least such skills might not be necessary for a consolatory contact to serve its consolatory role, opening the way to more questions about the development of the mechanisms underlying the empathic response.

Results highlighted developmental and rearing differences in the speed and pattern of consolatory behaviours. Indeed, immature consolers were slower at offering consolation and more likely to offer non-sexual consolatory behaviours than socio-sexual ones, particularly embrace and play. Older subjects also use fewer consolatory behavioural categories than younger ones. Broader investigations of consolation across age, focusing on younger samples and different contexts, coupled with physiological measurements, are needed to further document its ontogenetic path.

Investigating the impact of rearing environments on the development of empathy (Leavens et al., 2019; Liebal & Haun, 2012; Nielsen & Haun, 2016), I showed that orphans were slower at offering consolation to a conspecific in distress compared to mother-reared individuals – as were younger individuals as compared to older ones. Mother-reared consolers tended to be more likely to offer non-sexual consolatory behaviours than socio-sexual ones, as compared to orphans. This might be explained by the fact that mother-reared consolers might also have been more likely to console their mothers with whom the exchange of socio-sexual contacts is limited (Hashimoto, 1997). Another possibility might be that it is more stressful for orphans to console, therefore they use socio-sexual contacts as a way for them to release stress. As the exception of these findings, this study did not highlight significant effects of rearing on the cognitive and socio-emotional skills of the bonobos, suggesting that adapted care and attention after an early trauma can alleviate its negative consequences on the development of the young individual (Hodges & Tizard, 1989). Future work should investigate whether the distress state of the consoling bystanders (assessed via behavioural measures such as self-scratching and/or physiological measures such as heart rate measures, e.g., Wascher et al., 2008) impact their consolatory strategies, in order to better understand the intrinsic motivations of consolation.

6.1.3 Relating external markers of empathy with underlying physiology in sanctuary-housed chimpanzees

In order to deepen our understanding of empathy, in *Chapter 4,* I integrated for the first-time behavioural data of empathic responding from naturalistic observations of consolation with physiological data from thermal-imaging experiments, in order to relate external and internal markers of empathy in chimpanzees. Given the complexity of empathy, combining measures is needed for a richer understanding of the different components underlying empathy (Russell 2003; Barrett et al. 2006; see section 6.2.2 below).

Results show that consolation was predicted by inner arousal, as measured in the temperature change in the periorbital region, upon seeing a conspecific in distress. However, due to a limited sample size, it was not possible to test whether inner arousal predicts subject anxiety behaviours. The social bias of empathy was supported by greater inner arousal in the nose tip region upon seeing a familiar human displaying positive emotion traits as compared to unfamiliar humans. Finally, the results contradict the hypothesis that IRT measurements translate both the *valence* and *arousal* dimensions of the emotional experience in the periorbital region, highlighting how complex measuring emotion is, and revealed and confirmed that IRT technology itself provides complex data that is challenging to interpret.

Overall, this study highlighted developmental differences in the physiological response to a human displaying positive affect, with the nose tip temperature increasing in younger subjects, while it decreased in older ones. This contrast suggests that the mechanisms at the base of the physiological process mature with age. Alternatively, this result might be explained by model familiarity, with older individuals reacting more negatively to a stranger, while the younger ones were more responsive to the positively valence stimuli. Future work could take a closer look at the dynamic of the response, in order to investigate whether and how emotion regulation processes differ according to valence. Overall, these results confirm the hypothesis that the *empathy gradient* finds its roots at the physiological level of the response to an emotional stimulus and develops with age, potentially alongside cognitive mechanisms.

6.1.4 Investigating the external and internal markers of empathy in human children

Results from *Chapter 5* confirmed a physiological reaction of children when witnessing another's distress as compared to control. There were effects of age and sex on thermal responses in the nasal region in response to distress stimuli: younger infants showed stronger thermal responses as compared to older children, suggesting that children gain control of the inner response, an indicator of their developing emotion regulation skills (Carlson, 2005; Cole et al., 2009). Boys showed a stronger thermal response than girls. This is in line with the theory that young boys show higher arousal levels than girls (Brody, 1999), and supports the proposal that boys show lower inhibitory control than girls (Chaplin, 2015).

Nevertheless, despite difference in thermal responses, there were no sex or age differences in behavioural responses. This finding goes against the hypothesis that girls are more emotionally expressive than young boys (Zahn-Waxler et al., 1991, 2001), and suggests that a direct relation between internal and external measures cannot be assumed. Against our hypothesis of an empathy bias based on familiarity, there was no effect of model familiarity on children's behavioural responses, but some effect was highlighted on their thermal response. It is possible that the age range in this study might be too restricted and our sample size too limited to capture this developmental variation. Future work should include a bigger sample of children from a broader age range (e.g., up to 5- or 6-year-old, when language is well developed), encouraging collaborations and standardisation of the methods.

In regard to communicative responding and information seeking, children paid greater attention to distress stimuli than control stimuli. This supports the hypothesis that children seek information to understand emotionally complex situations (Zahn-Waxler, Radke-Yarrow, et al., 1992; Zahn-Waxler, Robinson, et al., 1992b). However, there was no indication of enquiring behaviours (such as social referencing and pointing) being a function of age, sex, model familiarity or stimulus type.

In regard to emotion regulation, the more children looked at the caregiver present in the room, the weaker their physiological response was, suggesting that children might use social referencing to regulate their arousal (McLellan et al., 2011; Walle et al., 2017), wherein children use the affective displays of an adult to gain information about their environment (Walle et al., 2017).

Furthermore, the more children looked at the caregiver present in the room, the more positive facial expressions they produced, suggesting they sought comfort and/or information. There were no significant results on self-directed behaviours. Future work should look closer at self-directed behaviours (e.g., self-scratching, touch hair or face), to discriminate their exact function and/or significance, ideally with physiological correlates to look at their function (heart rate and breathing rate, using IRT).

6.2 Wider contribution and implications

In this section, I discuss the broader implications of my findings. I will place my work with respect to the classical, philosophical definition of empathy, and discuss whether our current conception of the evolution of empathy requires modification. To do so, I discuss five major points: 1/ what the findings tell us about the evolutionary roots of empathy; 2/ the need to move towards a multi-componential approach to empathy: 3/ whether the consolation is a valid marker for empathy; 4/ whether arousal can be considered a marker of empathy, and finally to discuss the challenges of 5/ disentangling the valence and arousal dimensions of animal emotions.

6.2.1 The value of the comparative/evolutionary approach

Comparing the capacities of humans with non-human animals, and particularly with *Pan* apes, our closest living relatives, allows us to identify the evolutionary roots of a capacity. Such comparison is also necessary to discriminate causal relationships between psychological phenomena and their underlying mechanisms that are interrelated in the development (Krupenye & Call, 2019; MacLean et al., 2012). Although valuable, directly comparing related species is also challenging, as it requires similar designs and methodologies that might not be adaptable from one species to another.

The three study populations of this thesis presented their specific set of limitations. Therefore, I optimised the data collection procedure for each study population, instead of compromising each of them to meet the criteria of a cross-species comparison (Bard et al., 2014; Bard & Leavens, 2014). For instance, my sample included apes are of all ages in sanctuary settings, where external conditions could not be controlled. In contrast, the children sample was composed of a narrow age range, tested in a more controlled environment, by a species-specific experimenter.

In this thesis, I conducted naturalistic observations of post-conflict and post-distress situations in nurseries with young children, following the same protocol as with the non-human apes studied in this thesis (see an example of consolation recorded at the nursery here[14]. The intention was to directly compare the ontogeny of empathy across species, to detect the extent to which its affective and cognitive sub-components are shared with our closest living relatives. However, due to circumstances detailed in *Chapter 2*, it was not possible to complete the planned data collection. Nonetheless, conducting naturalistic observations of different species is a valuable initial step towards better understanding the evolutionary roots of some behavioural markers of empathy (Leavens et al., 2019).

Finally, the rise of new techniques and technologies offers valuable opportunities for tackling the challenges of comparative research. In particular, non-invasive technologies (as detailed in the section below), have the potential for being adapted to several populations and species. Such methods used in (ecologically valid or relevant) settings, allow for the quantification and direct comparison of a given underlying mechanism measured via the same designs and methods. Future work should look at adapting the designs proposed in this thesis (i.e., naturalistic observations, experimental tasks, and physiological measurements), and systematically administer them in a standardised fashion to ape species, so as to develop a systematic investigation of empathy and its behavioural and physiological markers.

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[14] https://www.dropbox.com/s/7hygospll2ubdn7/Diane%20Austry%20PhDthesis_Chapter6_Naturalistic%20observation%20kids.mp4?dl=0

6.2.2 Towards a multi-componential approach to empathy and affective science

As a complex multi-componential phenomenon, empathy is challenging to measure. Therefore, empirical studies have mostly, thus far, focused on isolated components of empathy, and have investigated indirect or evasive processes that cannot be directly assessed from behavioural or physiological data alone (Adriaense et al., 2020). A multi-component approach is needed to assess the underlying mechanisms of empathy-related reactions and the complexity of its expression (see Adriaense et al. 2020).

This thesis combined, for the first time to my knowledge, observations and physiological measurements, to allow for a more integrated interpretation of the various measurements. These include *arousal* and *valence* – two crucial components of the emotional experience (Russell 2003; Barrett et al. 2006). Indeed, while it is challenging to access both arousal and valence by studying thermal profiles or observational data alone, combination across such data sets can enhance our global understanding of the emotional experience.

Nonetheless, there are limitations in using behaviour and thermal variability methods. Indeed, while non-invasive, conducting thermal measurements requires specific and controlled settings, including the subject being somehow restrained in their movements, a situation that might impact and condition the associated behavioural data collection. Furthermore, it is not always possible to conduct the physiological and behavioural measurement simultaneously. That is why, in this thesis (*Chapter 4*), the connection between the physiological and behavioural/prosocial responses was investigated indirectly in two different contexts, as used in previous empirical studies in children (Hastings et al., 2006). New designs that allow for more connected measurements of the physiological and behavioural responses such as pupil dilation (Hepach et al., 2012; Hepach, Vaish, & Tomasello, 2017), and heart rate modulation

(Wascher et al., 2008) are needed to understand the link between physiological responses and prosocial behaviours.

The past decade has seen the emergence of numerous powerful technologies and techniques that provide innovative ways to address or challenge critical questions on complex psychological mechanisms such as empathy. Non-invasive methods, (i.e. those that avoid "non-care-related insertions, injections or incisions", Ross & Leinwand, 2020), are of particular interest for studying humans and other animals in more ethically and ecologically valid settings (reviewed in Krupenye et al., In Prep.). Regarding physiological measures, methods such as IRT, pupillometry (Hepach & Westermann, 2016; Laeng et al., 2012; Sirois & Brisson, 2014), heart rate (e.g., Baciadonna et al., 2019), and electrodermal activity (Dawson et al., 2017) quantify the activity of the autonomic nervous system (ANS), thus providing information on the arousal and affect of the empathic experience. Facial action coding systems (FACs, Ekman & Rosenberg, 1997), and electromyography (Tassinary et al., 2007), track the activity of facial muscles connected to emotion facial expressions and internal emotional experiences; while other techniques such as gaze-tracking (Gredebäck et al., 2009; Hopper et al., 2021), can help investigate cognitive components (of empathy) through the study of active choices. Finally, advanced techniques such as electroencephalogram (EEG, Hirata et al., 2013) and functional Magnetic Resonance Imaging (fMRI, Karl et al., 2020; Wilson & Petkov, 2011) record neural activity. Although each of these individual techniques, along with behavioural observations, is valuable to investigate aspects of the emotional and cognitive–processing, combining them would allow for a richer interpretation of how the various components of empathy interact.

6.2.3 Consolation, a valid marker for empathy?

Like many behavioural studies, this thesis rested on the assumption that consolation is a putative marker of "other-oriented" concern (Pérez-Manrique & Gomila, 2018). Consolation has primarily been observed in the context of post-conflict and post-distress situations, when an uninvolved bystander offers an unsolicited affiliative contact to the individual in distress. However, there are numerous non-negligible potential confounds which might explain consolatory-like behaviours – also called “third-party affiliation,” (e.g., Call et al., 2002; Palagi & Cordoni, 2009)- that might be driven by different proximate mechanisms serving selfish adaptive functions without invoking an empathy-based explanation (e.g., Call et al., 2002; Schino & Marini, 2012). Below, I present some alternative explanations, and then discuss the importance of adding physiological measurements.

6.2.3.1 Self-oriented versus other-oriented behaviour

Many studies require that the uninvolved bystander witnesses the distressing element (e.g., a conflict between group members, e.g., Clay & de Waal, 2013a,b; de Waal & van Roosmalen, 1979; Palagi et al., 2004, and *Chapter 3*). However, witnessing a fight may trigger a physiological reaction (Dezecache et al., 2017; Kano et al., 2016) and personal distress, leading to the act of consolation to alleviate this distress (Adriaense et al., 2020). To determine the underlying motivations for consolation, it is crucial to directly investigate the arousal/distress level of the bystander before and after consolation, to establish whether consolation could be explained as being self-soothing rather than other-oriented, or potentially both.

In the absence of a suitable methodology, studies have relied on behavioural proxies for the measure of distress (e.g., self-directed behaviours, de Waal & Aureli, 1996, also used in *Chapter 3*) which might not be accurate. To control for this confound, the potential “consoler” could be ignorant of the stressor (Burkett et al., 2016; Li et al., 2019; Quervel-Chaumette et al., 2016). By introducing video clips of victims of a conflict in which only the victim was shown but not the conflict, *Chapter 4* initiates such a design, in which the subject is blind to the stressor, and combines the physiological measurements with the observation of naturalistic affiliations. Despite being an innovative design, the study is also limited by the disconnection between the physiological measurements and the spontaneous behavioural reaction to the distress of others (i.e., post-conflict affiliation tendencies, discussed in *Chapter 4*). A recent study on jackdaws offers a novel approach to overcome this confound in a naturalistic scenario, where the female experiences a stressor (playback stimuli), and the behavioural response of the mate to its female's state when coming back to the nest (i.e., the mate is assumed to be ignorant of the origin of the female's state) is recorded (Hooper et al., 2021). In that case, the adaptive value of responding to another individual's state directly incorporates ecologically relevant trade-offs, building the foundation of a new predictive framework for empathy in non-human animals.

6.2.3.2 Motivation for social contact

Helping behaviours, for example, when a subject releases a conspecific from a trap without obtaining a reward (Bartal et al., 2011), could be triggered by a motivation for social contact rather than empathy (Silberberg et al., 2014). In a series of studies, rats were shown to only help distressed individuals rather than non-distressed ones (Bartal et al., 2014; Sato et al., 2015), suggesting that the motivation to help and alleviate distress overrides the motivation for social contact. This result supports the hypothesis that helping is motivated by empathy rather than a selfish need for social contact. Nonetheless, it is important to consider this alternative explanation and control for it when possible, as it is challenging – even in controlled experimental settings- to ensure we test and interpret correctly what we observe.

6.2.3.3 Social benefits of consolation

Post-conflict affiliative contacts – rather than being other-oriented- could function to protect the bystander from becoming the target of redirected aggression (Fraser et al., 2009; Koski &

Sterck, 2009; Palagi & Cordoni, 2009; Schino & Marini, 2012). This is especially relevant for the orphans who might not benefit from the social support of their mothers (*Chapter 3*). In *Chapter 3*, results revealed that consolation is directed towards socially close individuals (in line with Clay & de Waal, 2013), but did not highlight that consolers became more selective towards closely bonded partners with age. Instead, the "self-protection" explanation is a relevant alternative to explore for consolation selectivity. Future research could focus on testing whether individuals who are less likely to be the target of redirected aggression respond more broadly and offer affiliative contacts more frequently because they face a lower risk of post-conflict attacks, while others offer consolation mainly to closely associated partners who are less likely to redirect aggression towards them. Other alternative explanations are that consolation may function as a form of third-party reconciliation between the aggressor and the victim (Wittig & Boesch, 2010), or to reinforce and promote social alliances (Das et al., 1998). Once again, although very similar to what has been defined as "consolation", these behaviours have different motivations and functions (Adriaense et al., 2020).

6.2.3.4 Protection of the victim

Another related function for post-conflict affiliative contact offered by a (likely closely bonded) bystander, could be to limit renewed aggression towards the distressed victim, a form of prosocial behaviour related to empathy. Indeed, the – often aversive- distress signalling, could lead other bystanders and/or the previous aggressor to act aggressively towards the victim to stop the screaming (Palagi et al., 2006). This time, the behaviour of protection is directed towards another individual, not the bystander (section above). In line with this theory, rhesus macaques' mothers consent more often to their infant's screaming when potentially aggressive individuals are close by (Semple et al., 2009), supposedly to protect their infants as well as themselves.

6.2.3.5 Stopping the aversive signalling

Another more proximate explanation for consolation may be that the victim's screaming is aversive to the receiver (Kitko et al., 1999; Rendall et al., 2009; Rendall & Owren, 2010), and consolation effectively stops it from continuing. Such alternative explanations can be applied to studies looking at the prosocial motivation to help – e,g., a study by Rice and Gainer (1962), in which the distressed rat could have triggered self-arousal in the subject that therefore "helped" bring the conspecific down to serve a selfish purpose rather than a prosocial one (Lavery & Foley, 1963).

6.2.3.6 Consolation: a spontaneous contact?

Consolation is said to occur when a bystander *spontaneously* approaches to comfort an individual in distress in order to alleviate their distress (de Waal & van Roosmalen, 1979). Following this definition, most studies on post-conflict affiliations and consolation have focused on *unsolicited* contacts, and have excluded cases where the victim approached the consoler. Nevertheless, the victim's communicative signalling before a physical approach takes place has generally been overlooked (but see de Waal & Aureli, 1996). However, during a post-conflict or post-distress situation, the distressed individual typically expresses a rich array of behaviours, such as screaming, whimpering and gestural signals. In *Chapter 3*, I recorded the duration of the distress based on observable behaviours and distress vocalisations. These signals can also serve to promote affiliation from bystanders (Heesen et al., 2022). But if the affiliation is indeed solicited by the individual in distress, the motivation of the bystander moves away from consolation being an "other-oriented" response. Finer grained analysis of victim signalling is needed in order to better identify what is solicited and what is not.

6.2.3.7 Looking at the physiological mechanisms of empathy

Given that external behaviours can be triggered by different motivations, it is also essential to investigate the underlying processes and determine how they relate to one another. In this study I addressed this by combining IRT and behavioural observations, combining more physiological measurements (e.g., hormones: Butovskaya et al., 2005; Hohmann et al., 2009), which would enhance our understanding of these motivations. In particular, measuring the physiological state of both the bystander and a distressed individual would identify whether their physiological responses match, to confirm the phenomenon of emotion contagion. Finally, looking at the underlying mechanisms can help to detect processes that are not associated with external markers, and therefore have been missed by observational studies. As such, the physiological investigation might detect mechanisms that predict behaviour, while also dissociating the behaviour from its underlying mechanism.

6.2.4 Arousal, a marker for empathy or a sign of self-distress?

As a measure of affective arousal, it is difficult to disentangle whether IRT is detecting empathic responding, as opposed to personal distress. For instance, in a study on chimpanzees, the nasal skin temperature decreased, regardless of whether a subject witnessed another chimpanzee receiving an injection with a needle or observed the needle alone (Parr, 2001). This suggests personal arousal in response to a familiar aversive situation from the individual's *own* experience (i.e., veterinary contacts), rather than an other-oriented response. In a more recent study, chimpanzees' nasal skin temperature likewise decreased upon witnessing the realistic injury (with blood) of a human experimenter, but not when the experimenter pierced their (fake) thumb with a needle with no external cues of pain or blood (Sato et al., 2019). This last situation might have been more difficult for the subjects to understand, but suggests that unambiguous and familiar signs of distress or pain are required to trigger the subject's physiological response to a negative situation. However, whether it relates to personal distress or empathy remains unclear. As highlighted in *Chapter 4*, it is challenging to disentangle the thermal response of personal distress and that of empathy. However, rather than being one or the other, future work should investigate the temporal physiological responses, in order to identify a potential *arousal threshold* that would discriminate between the affective arousal as a motivation to help and the over-arousal leading to self-distress.

6.3 Limitations and future directions

Whilst this work offers progress in our understanding of empathy, the three empirical studies each present some limitations which could form the basis for developing future studies. I will discuss these further below.

6.3.1 InfraRed Thermography

6.3.1.1 Data collection

A significant goal and challenge of this project was the use of IRT to non-invasively assess the physiological mechanisms of empathy. In *Chapter 4*, the sanctuary-housed chimpanzees participated in the experiment voluntarily, without being isolated from their conspecifics and in a familiar environment (incorporated within their daily routine). By testing the chimpanzees in their indoor facilities after being fed, I sought to maintain both ethical and empirical standards, by ensuring that the subjects were in a calm state and in a familiar environment, to minimise the impact of external conditions on a thermal response. Nevertheless, because testing was voluntary and contact-free, many trials were interrupted because the subjects lost interest, a peer intervened, or something out of our control happened that distracted the subject. The temperature and humidity variation were recorded, but themselves could not be manipulated in an open environment (although no significant variation in temperature and humidity have been detected through the experimental session).

Overall, IRT presents some practical limitations that are challenging to mitigate. First, external conditions can impact the measurements and the subject should be introduced to the testing space and allowed to acclimatise for at least 10 minutes before the commencement of recording (Kano et al., 2016), Such procedure requires advanced testing facilities and the manipulation of the subjects, which can be difficult when working with non-human animals or in naturalistic settings.

Variation in blood flow linked to physical activity can impact the measurement (Nakanishi & Imai-Matsumura, 2008). Therefore, developing means to minimise movement of unconstrained subjects is required; however, food consumption can lower the nasal skin temperature (Chotard et al., 2018; Ioannou et al., 2015; Kano et al., 2016; van Baak, 2008). Working with wild animals calls for close monitoring of environmental and social conditions (e.g., Dezecache et al., 2017). Compared to other measures of arousal, the facial temperature change is relatively slow to report, sometimes as long as 2 minutes following stimuli onset (Kano et al., 2016), which can add further practical constraints.

6.3.1.2 Data extraction and coding

The main method I used for coding the thermal data was manually selecting the ROIs (with FLIR Tools software) and extracting the associated temperature. This method, as well as being time-consuming and providing limited insights into the dynamics of the thermal change, might also lack uniformity between coders and between studies. Furthermore, studies tend to use minimal or average temperature which makes direct comparisons difficult.

To make this process more efficient and reliable, I worked on an automatised method of temperature extraction in collaboration with Prof Camila Caiado (detailed in *Chapter 2* and *Appendix 2.2*). While this automated tracker allows for the precise selection of a given ROI and its constant tracking for the duration of the trial, it also presents some practical limitations. Indeed, when the ROI selected disappears from the frame, for instance, when the subject turns their head, the tracker loses track of the ROI. Therefore, close monitoring and removal of the spoiled frames is required.

I also encountered many challenges in developing this method, that can limit its use to non-coding specialists. Therefore, such projects might rely on collaboration with experts in computer sciences. In the case of the present project, developing and maintaining such a collaboration, resulted in significant delays and uncertainties, to the extent that it was eventually not useable for my thesis. Future projects involving the extraction of IRT data should seek the assistance of analysts, at least while this technique is still at its early stage of development in affective science.

6.3.1.3 Output interpretation

As well as the technical challenges in successfully creating and running an automated tracker of thermal profiles, the eventual outputs were also challenging to interpret. In particular, the thermal profiles obtained from the automatic extraction were rather noisy (Figure 2.3; *Appendix 6.1*). The apparently cyclical pattern of temperature change occurring within seconds, leaves space for variations in the significance of the measurements aimed at assessing the impact of a stimulus when selecting a single measure within an arbitrary time window (usually within 5 to 10 seconds). This observation is based on the assessment of a single thermal profile. In order to confirm this tendency, future work should focus on testing this novel method on additional

IRT data. Furthermore, by working on an adult sample in more controlled conditions, we could create a *thermal profile baseline* to better understand the potential fluctuation of temperature.

IRT is a novel and exciting technique in the field of affective science. However, a deeper understanding of the mechanisms at the origin of the thermal skin response is needed to accurately use this technique and interpret the results, as well as a powerful and precise method to extract the relevant data. Future work should focus on systematically characterising thermal skin profiles for different ROIs under various circumstances, to build a baseline that would be crucial to better understand the nature of the mechanisms at the origin of skin temperature variation, along with their anatomical and physiological characteristics.

An aim and challenge of affective research is to map and disentangle the components of affect, particularly along valence and arousal dimensions. Moving beyond the context in which the behaviour is expressed (e.g., Church 1959) or behavioural indicators (e.g., Brosnan & de Waal 2003), IRT accesses the underlying emotional component of a response. The change in facial skin temperature has been suggested to map these components of affect, with negative emotional states translating into a drop in the facial skin temperature (e.g., Kano et al., 2016), and positive emotional states translating into a rise in the facial skin temperature (e.g., Chotard et al., 2018). However, IRT measurements might not provide the clear pattern expected (see *Chapter 4*). Future work using different emotional stimuli as well as combining IRT measures with other physiological measures (e.g., heart rate or pupil dilation) as well as behavioural markers, would help disentangle the components of the emotional experience (Huber et al., 2017; Mendl et al., 2009; Paul et al., 2005).

6.3.1.4 IRT for comparative affective research

Although I did not directly compare across species in this thesis, comparative analyses could be informative to identify similarities and differences in empathic responding in non-human and human apes. However, such a comparison requires strict similar testing conditions between the species, which is often logistically and practically challenging to achieve (see 6.2.1). IRT provides a relevant technique for measuring arousal and affect in a wide range of species, even in the wild (Dezecache et al., 2017). In the following sections, I address the main testing differences and challenges between the experimental design and stimuli used with the sanctuary-house chimpanzees (*Chapter 4*) and the young children (*Chapter 5*) of this thesis. Other challenges faced have been discussed in *Chapters 4* and 5.

6.3.1.4.1 Experimental design

In *Chapter 4*, the chimpanzees were tested voluntarily in their familiar environment and with their conspecifics in proximity. While this provides ethical benefits, it meant that environmental and social conditions were difficult to control for. In contrast, the children tested in *Chapter 5* were isolated from their conspecifics and could be tested in a more controlled environment. Such a controlled environment is less natural, thus promoting reactions that might lack ecological validity. Therefore, a direct comparison between the two data sets was not possible. However, the creation of strictly similar designs between non-human and human primates could be useful for studying the evolution of empathy and associated skills, particularly when using physiological measurements like IRT.

6.3.1.4.2 Experimental stimuli

In *Chapter 4*, chimpanzees watched videos of conspecifics in distress and humans expressing sadness and happiness. By comparison, children (*Chapter 5*) watched videos of familiar and unfamiliar nursery caregivers in distress. The use of videos instead of live-actors allowed for consistency across trials and replicated the familiar and unfamiliar conditions efficiently. However, children (Song et al., 2016) and – presumably - other great apes can detect between real and fake emotional facial expressions, therefore potentially compromising the validity of the stimuli. Indeed, the interpretation of experiments using posed stimuli as opposed to genuinely expressed emotional states is challenging (Kret et al., 2020; Zuckerman et al., 1976). But despite the fact that actors tend to amplify stereotypical displays of emotions (Wallbott & Scherer, 1986), it seems that such stimuli constitute a good resemblance to genuine emotional displays (De Gelder & Van den Stock, 2011; Wallbott, 1990).

6.3.2 Studying empathy beyond post-conflict and post-distress contexts

Most of the studies investigating consolation and empathy focus on post-conflict and post-distress contexts (e.g., Clay & de Waal, 2013; Cordoni et al., 2006; de Waal & van Roosmalen, 1979). However, different environmental, social, and ecological contexts result in contrasting costs/benefits balance at both the individual and species levels when it comes to offering consolation and acting empathetically. By enlarging the scope of the contexts in which we investigate consolation and other-oriented behaviours for a given species, we can build a systematic quantitative approach of the behaviour based on the cost-benefit trade-off. Furthermore, the study of empathy itself would benefit from expanding towards the investigation of contexts other than post-conflict situations and negative valence contexts. This would be beneficial for grasping the complexity of consolation, and for understanding its ultimate and proximate levels (McAuliffe & Thornton, 2015; McNamara, 2013).

6.3.3 Kinship, social bonds, and familiarity to assess the empathy gradient

Considered as an extension of the mother-offspring bond shared across mammalian species (MacLean, 1985), empathy is biased towards socially close or familiar individuals (Preston & de Waal, 2002). In this thesis, I investigated different levels of familiarity and kinship to investigate this social bias of empathy, known as *empathy gradient* (Preston & de Waal, 2002). In primates, consolation is predicted by social closeness, being strongest among kin, followed by socially close partners, and weakest among socially-distant and/or unfamiliar individuals

(Fraser et al., 2008a; Romero et al., 2010; Clay & de Waal, 2013b; Palagi & Norscia, 2013). Therefore, in *Chapters 3* and *4*, I considered kin relations between mother-offspring (and offspring-mother) as well as social bonds: I calculated close bonds per dyad with dyadic affiliation scores relative to group levels (*Chapters 3* and *4*).

In *Chapters 3* and *4*, I treated mother-offspring versus offspring-mother links in the same way. However, from a functional stance, there are crucial difference to consider. Indeed, mothers responding to their offspring states implies direct fitness benefit, while offspring responding to their mother's states would be indirect fitness. Future work should thus focus on these differences to investigate the link between fitness and empathic responding, which in turn could improve our understanding of the mechanisms underlying the empathy gradient.

In contrast, I investigated the impact of non-kin familiarity of human stimuli on chimpanzees (familiar keeper *vs* unfamiliar villager, *Chapter 4*) and young children (familiar vs unfamiliar caregiver, *Chapter 5*). The two approaches – based on 1/ kinship and social bond or 2/ familiarity- rely on subjects being able to identify relevant social partners with whom a strong relationship bond had been developed, therefore being relevant when investigating empathy. Nonetheless, considering kin relations in contrast to social bonds in assessing the empathy gradient brings the concept of selection for close kin that can imply indirect fitness – if from offspring to mother- or direct fitness – if from mother to offspring- and not as much an other-oriented behaviour as the subject then as a direct benefit in protecting their genes (selfish gene theory, Dawkins & Davis, 2017).

6.3.4 Moving beyond WEIRD and BIZARRE/STRANGE populations

The interpretations and assumptions drawn from the studies of this thesis are biased to the populations studied. The understanding of species' continuity and cross-population differences in empathic abilities and empathic behaviours (in humans and other animals) remains a central breach in the comparative emotion literature (Adriaense et al., 2020; Nielsen & Haun, 2016). Nevertheless, the expansion of field sites across the world, along with progress in experimental methodologies (including field experiments) create and encourage prospects to transfer lab-based work to a wide scope of populations, from wild populations of nonhuman primates to remote human populations for cross-cultural human research.

6.3.4.1 BIZARRE (STRANGE) ape populations and cross-group comparison

Chapter 3 and *Chapter 4* rely on the observation and testing of bonobos and chimpanzees housed in sanctuary settings. A large proportion of these apes were orphans saved from the illicit bush-meat and pet trades and were integrated into a large mixed-age social group after a period of rehabilitation. Others were born at the sanctuaries. Therefore, although the study of apes living in semi-wild environments might approach the behaviour of their wild conspecifics (André et al., 2008), we are restricted in the interpretations of such studies. Apes raised in Barren, Institutional, Zoo, And other Rare Rearing Environments ("BIZARRE") have been judged as mediocre characterisations of the chimpanzee species (Leavens et al., 2010; also see Webster & Rutz, 2020). For instance, evidence suggests that captive animals execute cognitive tasks differently compared to their wild counterparts ("captivity bias", Haslam, 2013).

Most of the other-oriented affiliation and consolation studies are based on captive and semi-wild populations. However, wild populations develop in a more hazardous and ecologically complex environment than captive or sanctuary-housed individuals (Pritsch et al., 2017), leading to variations in the behavioural repertoire and cognitive skills of wild and captive animals (Boesch, 2020; Cauchoix et al., 2020; Thornton & Lukas, 2012; Webster & Rutz, 2020). Regarding consolation and consolatory behaviours, results seem to vary in wild ape populations as compared to captive ones (Cordoni et al., 2006; Pérez-Manrique & Gomila, 2018). Such variation suggests that the (selective) advantages and disadvantages of offering consolatory behaviours depend on various ecological factors (for example in corvids: Sima et al., 2016), that impact – among other things- the activity budget of the individuals of a given species (e.g., in chimpanzees: Inoue & Shimada, 2020). Thus, it is crucial to also conduct studies in the wild to gain insights into the true adaptive value and ultimate function(s) of consolatory behaviours (Pritchard et al., 2016; Thornton & Lukas, 2012).

Studying apes in a semi-wild environment such as sanctuaries seems like an acceptable threshold to enable the use of experimental designs and technology such as IRT. Furthermore, studying these populations offers the unique opportunity to ethically investigate the effect of early deprivation on emotional and cognitive skills, moving away from the early deprivation experiments conducted 50 years ago (Seay et al., 1962; Suomi et al., 1975, 1976). Nonetheless, controlled experiments remain challenging to run in field settings, and access to a large number of subjects is often difficult, particularly when measurements rely on voluntary participation. Finally, whether wild or captive, there might be a significant inter-individual variation when it comes to empathic tendencies.

6.3.4.2 WEIRD children and the importance of the cross-cultural approach

Thus far, empirical research has largely focused on western societies for understanding how empathy develops (Zahn-Waxler et al., 1985; Eisenberg & Fabes, 1990; Zahn-Waxler, Robinson, et al., 1992a; Roth-Hanania et al., 2011). Nevertheless, the Western model of development– defined as WEIRD, i.e., Western, Educated, Industrialised, Rich, and Democratic- may not be representative of human development (Henrich et al., 2010, but see Ghai, 2021). Therefore, it is crucial to study variability across cultures to understand the diversity and continuity in human empathy development (e.g., Madsen, 1971; Borke, 1973; Friedlmeier & Trommsdorff, 1999). The conclusions drawn in this thesis are limited to UK children. Further studies should focus on extending our understanding of empathy across a variety of cultures and social environments.

6.4 Concluding remarks: new insights into empathy and its development

In conclusion, the evidence presented within this thesis revealed that inner arousal – as measured with facial temperature change – might provide the underlying motivation of great apes to respond empathically to others in distress. Furthermore, my research highlighted developmental trends in the physiological and behavioural empathic response of human children and non-human apes, along with connections between the physiological and behavioural markers of empathy. These results further our understanding of how the different components of empathy develop, interact, and what their underlying mechanisms are. By combining several and new experimental designs, the empirical work within this thesis provided new insights into the connection between the behavioural and physiological markers of empathy. Empathy is a complex multi-componential phenomenon. This thesis emphasises the need to continue to increase our focus on disentangling its nature and underlying mechanisms, along with its developmental and evolutionary roots.

There is no perfect study that would control for all confounds and grasp the full complexity of empathy and other-oriented behaviours. But I hope that by approaching this topic from various complementary angles, this thesis improves our understanding of empathy and raises many more questions for further exploration and research.

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Appendices

Appendix 2.1 Specifications of the Temperature and Humidity Meter

Preciva LCD Digital Psychrometer Mini Temperature and Humidity Meter with Dew Point and Wet Bulb Temperature Hygrometer - Specifications

- Display: Large 4-1/2 dual digital LCD display
- Sensor Type: A single chip relative humidity and temperature muti sensor module comprising a calibrated digital output
- Response Time: %RH: 10S (90% at +25 °C still air)
- Accuracy Note: Accuracy is specified for the following ambient temperature range: 64°F to 82°F (18°C to 28°C)
- Sampling Rate: 2.5 samples per second
- Polarity: Automatic, (-) negative polarity indication
- Dewpoint Temperature: -20 °C~80 °C (-4 °F~176 °F)
- Wet Bulb Temperature: 0 °C~80 °C (32 °F~176 °F)
- Operating Conditions: 32°F to 104°F (0°C to 40°C); < 80% RH non-condensing
- Storage Conditions: 14°F to 140°F (-10°C to 60°C); < 80% RH non-condensing
- Power: One standard 9V, NEDA 1604 or 6F22 battery
- Dimensions: 175 x 58 x 35 mm
- Weight: 143g
- Humidity/ Temperature Measurement Range:
  - Humidity: 0%~100%RH
  - Temperature: -20 °C~80 °C (-4 °F~176 °F)
  - Resolution: 0.01%RH, 0.01°C/0.01°F
  - Humidity Accuracy: ±3%RH (at 25°C, 20%~80% RH); ±3.5%RH (At other ranges)
  - Air Temperature Accuracy: ±0.5°C/±0.9°F (at 25°C); 0.8°C/±1.5°F (all other ranges)

Appendix 2.2 A new data extraction method for Infrared Thermography data

For this part, I collaborated with Prof C. Caiado (CC) from the Mathematical Sciences department at Durham University. Prof Caido created the R and Python codes to extract the IRT data collected with an IR camera by continuously tracking a selected set of pixels for each ROI and extracting the temperature data for every frame. Here, I detail the main programming functions/algorithms (i.e., trackers) used, as well as the main steps of the methodology.

Multiple Object Tracking

The code created for this project included various functions/algorithms from **OpenCV** (Open-Source Computer Vision). OpenCV is a library of programming functions mainly aimed at real-time computer vision.

The Multiple Object Tracking class (MultiTracker[15]) in OpenCV provides an implementation of multi-object tracking. It processes the tracked objects independently without any optimization across the tracked objects. For this project, we used several trackers, including BOOSTING, Multiple Instance Learning (MIL), Kernelized Correlation Filters (KCF), Tracking, Learning and Detection (TLD), as well as MEDIANFLOW, GOTURN, and Minimum Output Sum of Squared Error (MOSSE).

Main steps

Step 1 - CSQ to CSV with FLIR Tools: The videos collected with the thermal camera (FLIR T series) are under the Compressed SeQuence *file (*CSQ) format used by FLIR which is not the easiest or common format to work with. Although not fully standardised, the Comma-Separated Values (CSV) format is a common data exchange format. There is an option in FLIR

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[15] https://github.com/ehsangazar/OpenCV-Object-Tracking

Tools to convert the CSQ files to CSV files. After opening the video, right-click on a video to export it as a CSV and its properties. The CSV files contain the temperature information for each pixel. Note that the CSV files are also very large and require a lot of memory.

Step 2 - CSV to PNG with R: At this stage, the CSV files are not formatted sensibly. We use the package ‘av’ to work with videos in R and extract frames information as needed (e.g., location) from the CSV file.

Step 3 - PNG to AVI with R: From the pictures extracted (PNG), we create a video (AVI) with R. Note that working with such heavy files can require a fair amount of physical memory.

Step 4 - Extract data from the areas of interest (AVI) with Spyder (Python): Once the video output (AVI) created, we use Python to select the area of interest in the AVI file.

Step 5 - Get the data for each region of interest converted in Celsius degrees with R

The codes

Final codes are available upon request from Prof. Caiado.

Appendix 4.1 Examining the temporal dynamics of the chimpanzee thermal response

The use of infrared thermography technology for comparative affective science is still at its infancy (see *Chapter 2*). Most of the studies conducted so far have focused on a single region of interest: the nose tip, for thermal measurements extraction in human (e.g., Nakanishi and Imai-Matsumura 2008; Vinkers et al. 2013; Ioannou et al. 2013) and non-human primates (Kano et al., 2016; Kuraoka & Nakamura, 2011; Nakayama et al., 2005). However, it is unclear whether the temperature of different facial regions varies independently depending on the stimulus valence or intensity (Chotard et al., 2018). Differences in blood supply could result in specific variations for different facial regions. It is thus crucial to explore these patterns to understand the mechanisms and the implications that might have for interpreting the findings.

Therefore, in Part One, I examined the dynamics of the chimpanzee thermal response by looking at facial skin temperature changes in four facial regions of interest (ROI) that have been used in two previous studies (Chotard et al., 2018; Ioannou, Gallese, et al., 2014) at four experimental time points. Knowledge about the underlying physiological processes resulting in the thermal changes is still limited, thus I used an exploratory approach. I hypothesised that the physiological response (see *Chapter 2*) in a given ROI would be consistent over a given period (**hypothesis 0.1**). Therefore, for a given ROI, I predicted that facial skin temperature changes will predict temperature changes and direction at the four key experimental time points.

Also, I hypothesised that anatomically close regions of interest (i.e., nose bridge and nose tip regions) which are irrigated by the same or close vessel networks will show similar physiological reactions, as compared to more distant regions (i.e., peri-orbital and upper lip regions; **hypothesis 0.2**). Therefore, I expected the temperature changes in the nasal regions, i.e., nose bridge and nose tip, to correlate at the four time points, while the temperature changes in the periorbital and upper lip regions will vary independently from the other ROIs.

Methods

Pearson Bivariate correlations

I examined correlations between the temperature change of the four regions of interest (i.e., PO: Peri-orbital, NB: Nose bridge, NT: Nose tip, UL: Upper lip) at the four time points (i.e., ES: Early Stimulus, LS: Late Stimulus, ER: Early Recuperation; LR: Late Recuperation) during my experimental presentations using Bivariate Pearson correlations. Before doing so, I checked for normal distribution, linearity and homoscedasticity which were assumed. All measurements for all conditions were included.

GLMMs

To analyse whether the regions of interest and the time points predict the temperature change during the experiment, I fitted a GLMM. The dependent variable was the temperature change (in Celsius degrees, Model 1 from *Chapter 4*). The predictors in the model were the ROI (PO, NB, NT, UL) and the time points (ES, LS, ER, LR). I also included an interaction between the ROI and the time points. Control effects were the characteristics of the stimulus: the species (conspecifics; human), familiarity (familiar; unfamiliar), valence (positive; negative; neutral). I could not include an interaction between these factors because the fixed-effect model matrix was rank deficient so I had to drop coefficients. Random effects were the ID of the subject and the testing event. Here, the data set included all measurements for all conditions for a total of N = 728 measurement.

Results

Statistically significant positive linear relationships exist between the temperature changes at the four time points for the four areas of interest with the strength of the association being moderate to strong ($0.45 < \rho < 0.83$, see Table A. cells highlighted in green). Such relationships also exist between the temperature changes at the four time points for the nose bridge and the nose tip regions with the strength of the correlation being moderate to strong ($0.34 < \rho < 0.79$, see Table A. cells highlighted in yellow) – except for the temperature change in the nose tip region at the early stimulus point and the temperature change in the nose bridge region at the early recuperation point that only show a *tendency* for a statistically significant positive correlation ($\rho = 0.28$, $p = 0.083$). The results do not reveal a statistically significant correlation between the temperature changes in the peri-orbital region at the four time points and any of the other regions of interest at any measured time points. In contrast, there are statistically significant positive linear relationships between the temperature changes in the upper lip and the two nasal regions, and particularly with the nose bridge region at the four time points – although there is only a *tendency* for the temperature change in the upper lip area taken at the start of the stimulus display and the temperature change in the nose bridge region taken during the recuperation phase (early recuperation phase $p = 0.061$; late recuperation phase, $p = 0.076$). Regarding the relationship between the change of temperature in the upper lip and the nose tip, there are statistically significant positive linear relationships between different time points (see Table A, highlighted in blue).

Table A Bivariate Pearson correlation results between the four ROIs and the four time points - Matrix

		PO				**NB**				**NT**				**UL**			
		PO _ES	PO _LS	PO_ ER	PO_ LR	NB _ES	NB _LS	NB _ER	NB _LR	NT _ES	NT _LS	NT_ ER	NT_ LR	UL_ ES	UL _LS	UL_ ER	UL_ LR
PO	PO_ ES	/	x	x	x												
	PO_ LS	/	/	x	x												
	PO_ ER	/	/	/	x												
	PO_ LR	/	/	/	/												
NB	NB _ES	/	/	/	/	/	x	x	x	x	x	x	x	x	x	x	x
	NB _LS	/	/	/	/	/	/	x	x	x	x	x	x	x	x	x	x
	NB _ER	/	/	/	/	/	/	/	x		x	x	x		x	x	x
	NB _LR	/	/	/	/	/	/	/	/	x	x	x	x		x	x	x
NT	NT_ ES	/	/	/	/	/	/	/	/	/	x	x	x	x			
	NT_ LS	/	/	/	/	/	/	/	/	/	/	x	x	x		x	x
	NT_ ER	/	/	/	/	/	/	/	/	/	/	/	x		x	x	x
	NT_ LR	/	/	/	/	/	/	/	/	/	/	/	/			x	x
UL	UL_ ES	/	/	/	/	/	/	/	/	/	/	/	/	/	x	x	x
	UL_ LS	/	/	/	/	/	/	/	/	/	/	/	/	/	/	x	x
	UL_ ER	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	x
	UL_ LR	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/

Strong statistically significant positive linear relationships exist between the temperature changes at the four experimental time points for three of the four areas of interest, i.e., nose bridge, nose tip, and upper lip. Detailed results are provided in Table B.

Table B Bivariate Pearson correlation results between the four ROIs and time points - Matrix

			PO				NB				NT				UL			
			PO_ES	PO_LS	PO_ER	PO_LR	NB_ES	NB_LS	NB_ER	NB_LR	NT_ES	NT_LS	NT_ER	NT_LR	UL_ES	UL_LS	UL_ER	UL_LR
PO	PO_ES	Pearson Correlation	1	0.792	0.662	0.735	0.063	0.120	-0.069	-0.031	-0.014	0.177	0.129	0.095	-0.081	0.186	0.037	-0.120
		Sig. (2-tailed)		**<0.001**	**<0.001**	**<0.001**	0.672	0.437	0.676	0.867	0.920	0.219	0.398	0.572	0.574	0.201	0.816	0.478
		N	55	50	43	35	48	44	39	31	52	50	45	38	50	49	41	37
	PO_LS	Pearson Correlation	.792**	1	0.581	0.665	0.186	0.142	-0.008	-0.074	0.059	0.266	0.108	0.051	-0.077	0.133	0.104	-0.132
		Sig. (2-tailed)	0.000		**<0.001**	**<0.001**	0.221	0.353	0.960	0.699	0.688	0.065	0.497	0.772	0.613	0.367	0.530	0.449
		N	50	53	42	34	45	45	39	30	49	49	42	35	46	48	39	35
	PO_ER	Pearson Correlation	.662**	.581**	1	0.701	0.119	0.234	0.083	0.072	0.189	0.120	0.208	0.304	-0.140	0.239	0.238	0.108
		Sig. (2-tailed)	<0.001	<0.001		**<0.001**	0.472	0.152	0.618	0.710	0.224	0.449	0.186	0.080	0.382	0.118	0.145	0.530
		N	43	42	46	34	39	39	38	29	43	42	42	34	41	44	39	36
	PO_LR	Pearson Correlation	.735**	.665**	.701**	1	0.007	0.045	-0.083	-0.013	-0.067	-0.029	0.071	0.182	-0.185	0.066	-0.100	0.101
		Sig. (2-tailed)	<0.001	<0.001	<0.001		0.971	0.817	0.663	0.947	0.706	0.873	0.695	0.303	0.310	0.711	0.591	0.568
		N	35	34	34	36	29	29	30	27	34	33	33	34	32	34	31	34
NB	NB_ES	Pearson Correlation	0.063	0.186	0.119	0.007	1	0.749	0.566	0.622	0.533	0.667	0.34	0.403	0.52	0.382	0.563	0.585
		Sig. (2-tailed)	0.672	0.221	0.472	0.971		**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**0.036**	**0.022**	**<0.001**	**0.011**	**<0.001**	**<0.001**
		N	48	45	39	29	49	41	37	30	48	44	38	32	44	43	35	33
	NB_LS	Pearson Correlation	0.120	0.142	0.234	0.045	.749**	1	0.682	0.694	0.482	0.788	0.712	0.741	0.423	0.492	0.415	0.677
		Sig. (2-tailed)	0.437	0.353	0.152	0.817	<0.001		**<0.001**	**<0.001**	**0.001**	**<0.001**	**<0.001**	**<0.001**	**0.005**	**0.001**	**0.008**	**<0.001**
		N	44	45	39	29	41	48	37	31	43	46	39	32	43	44	40	34
	NB_ER	Pearson Correlation	-0.069	-0.008	0.083	-0.083	.566**	.682**	1	0.617	0.278	0.413	0.709	0.553	0.311	0.537	0.785	0.517
		Sig. (2-tailed)	0.676	0.960	0.618	0.663	<0.001	<0.001		**<0.001**	0.083	**0.009**	**<0.001**	**0.001**	0.061	**0.001**	**<0.001**	**0.002**
		N	39	39	38	30	37	37	42	30	40	39	39	33	37	37	38	33
	NB_LR	Pearson Correlation	-0.031	-0.074	0.072	-0.013	.622**	.694**	.617**	1	0.376	0.546	0.541	0.725	0.334	0.413	0.507	0.572
		Sig. (2-tailed)	0.867	0.699	0.710	0.947	<0.001	<0.001	<0.001		**0.034**	**0.002**	**0.002**	**<0.001**	0.076	**0.021**	**0.004**	**0.001**
		N	31	30	29	27	30	31	30	33	32	31	30	31	29	31	30	30
NT	NT_ES	Pearson Correlation	-0.014	0.059	0.189	-0.067	.533**	.482**	0.278	.376*	1	0.589	0.453	0.481	0.342	0.213	0.168	0.263
		Sig. (2-tailed)	0.920	0.688	0.224	0.706	<0.001	0.001	0.083	0.034		**<0.001**	**0.002**	**0.003**	**0.017**	0.146	0.293	0.121
		N	52	49	43	34	48	43	40	32	55	49	44	37	48	48	41	36
	NT_LS	Pearson Correlation	0.177	0.266	0.120	-0.029	.667**	.788**	.413**	.546**	.589**	1	0.51	0.586	0.314	0.245	0.392	0.388
		Sig. (2-tailed)	0.219	0.065	0.449	0.873	<0.001	<0.001	0.009	0.002	<0.001		**<0.001**	**<0.001**	**0.034**	0.093	**0.010**	**0.021**
		N	50	49	42	33	44	46	39	31	49	53	45	37	46	48	42	35
	NT_ER	Pearson Correlation	0.129	0.108	0.208	0.071	.340*	.712**	.709**	.541**	.453**	.510**	1	.826	0.290	0.472	0.52	0.54
		Sig. (2-tailed)	0.398	0.497	0.186	0.695	0.036	<0.001	<0.001	0.002	0.002	<0.001		**<0.001**	0.065	**0.001**	**<0.001**	**0.001**
		N	45	42	42	33	38	39	39	30	44	45	47	37	41	43	41	35
	NT_LR	Pearson Correlation	0.095	0.051	0.304	0.182	.403*	.741**	.553**	.725**	.481**	.586**	.826**	1	0.233	0.329	0.372	0.6
		Sig. (2-tailed)	0.572	0.772	0.080	0.303	0.022	<0.001	0.001	<0.001	0.003	<0.001	<0.001		0.192	0.050	**0.028**	**<0.001**
		N	38	35	34	34	32	32	33	31	37	37	37	39	33	36	35	36
UL	UL_ES	Pearson Correlation	-0.081	-0.077	-0.140	-0.185	.520**	.423**	0.311	0.334	.342*	.314*	0.290	0.233	1	0.542	0.478	0.583
		Sig. (2-tailed)	0.574	0.613	0.382	0.310	<0.001	0.005	0.061	0.076	0.017	0.034	0.065	0.192		**<0.001**	**0.002**	**<0.001**
		N	50	46	41	32	44	43	37	29	48	46	41	33	51	46	39	34
	UL_LS	Pearson Correlation	0.186	0.133	0.239	0.066	.382*	.492**	.537**	.413*	0.213	0.245	.472**	0.329	.542**	1	0.611	0.717
		Sig. (2-tailed)	0.201	0.367	0.118	0.711	0.011	0.001	0.001	0.021	0.146	0.093	0.001	0.050	<0.001		**<0.001**	**<0.001**
		N	49	48	44	34	43	44	37	31	48	48	43	36	46	52	41	36
	UL_ER	Pearson Correlation	0.037	0.104	0.238	-0.100	.563**	.415**	.785**	.507**	0.168	.392*	.520**	.372*	.478**	.611**	1	0.54
		Sig. (2-tailed)	0.816	0.530	0.145	0.591	<0.001	0.008	<0.001	0.004	0.293	0.010	0.000	0.028	0.002	<0.001		**0.001**
		N	41	39	39	31	35	40	38	30	41	42	41	35	39	41	45	34
	UL_LR	Pearson Correlation	-0.120	-0.132	0.108	0.101	.585**	.677**	.517**	.572**	0.263	.388*	.540**	.600**	.583**	.717**	.540**	1
		Sig. (2-tailed)	0.478	0.449	0.530	0.568	<0.001	<0.001	0.002	0.001	0.121	0.021	0.001	<0.001	<0.001	<0.001	0.001	
		N	37	35	36	34	33	34	33	30	36	35	35	36	34	36	34	39

Significant values (P<0.05) are in **bold;** almost significant values are underlined (P < 0.09)

The full model did not explain the data significantly better than the null model – which only contained the intercept, control and random effect ($\chi2 = 13.54$, d.f. = 15, $p = 0.561$).

Discussion

In line with the predictions, strong statistically significant positive linear relationships were highlighted between the temperature changes in the anatomically close regions of interest – which included the ROIs of the nasal area as well as the upper lip. This result suggests that the physiological response resulting in vasodilatation or vasoconstriction in anatomically close ROIs is similar/dependent. This can be explained as these close ROI are irrigated by the same or close vessel networks. Therefore, it is important to take into account such dependence in physiological responses when selecting ROIs for psycho-affective studies. In contrast, the temperature change in the peri-orbital region varies independently as it is irrigated by more distant vessel networks. At this stage of the use of IRT in emotion research, it is crucial to explore these patterns further to understand better the mechanisms involved and the implications that might have for the interpretation of the findings.

Appendix 4.2 Ethogram depicting the behavioural coding system during the IRT experiment *(Table C)*

Attention towards the emotional display

Screen	The subject looks at the screen, i.e., sustained attention towards a direction that is likely to be the screen (the camera is usually not strictly facing the chimp)
Chimpanzee	The subject looks at another chimpanzee
Away	The subject does not look at the screen or another chimp
The emotional reaction towards the emotional display	
Presence of facial expressions	The subject produces any other facial expression that is not neutral (i.e., relaxed face with a close mouth)
Presence of vocalisations	The subject produces a vocalisation
Presence of self-directed behaviours	The subject touches/inspects its own body
Movement	
Sitting there	The subject seats, potential slight movements
Move	The subject is up and moving
Audience	
Alone	No chimpanzee within the subject’s arm reach
Arm reach	There is one or several chimpanzees within arms reach of the subject, without contact
Contact	A part of the subject’s body touches a part of another chimpanzee’s body

Appendix 4.3 Kappa coefficients between the main coder and the two extra coders (A and B) for the coding of the occurrence of an interaction, the identity of the interaction bystander, the initiator of the first behaviour in an interaction, and the occurrence of a consolation *(Table D)*

Kappa coefficients	Interaction	ID	Initiator	Consolation	Self-directed behaviours
Main coder vs Coder A	0.95	0.94	1.00	0.88	0.84
Main coder vs Coder B	0.85	0.96	0.92	0.81	0.74
Overall agreement between the main coder and Coder A and Coder B	0.91	0.95	0.97	0.85	0.80

Appendix 4.4 **Intraclass correlations coefficients (ICC) for absolute agreement using the two-way random effect models (minimum skin temperature for the four regions of interest –** ***Table E)***

Average measures for the regions of interest	**Intraclass Correlation**	**95% Confidence Interval**		**F Test with True Value**			
		Lower Bound	*Upper Bound*	*Value*	*df1*	*df2*	*Sig*
Peri orbital	0.878	0.835	0.909	8.173	173	173	<0.001
Nose bridge	0.982	0.972	0.988	55.885	81	81	<0.001
Nose tip	0.991	0.988	0.993	110.904	179	179	<0.001
Upper lip	0.727	0.604	0.811	3.658	113	113	<0.001

Appendix 4.5 Self-directed behaviour data for the N = 13 subjects tested *(Table F)*

ID code	Number of bouts/instances	Total duration of all SDBs (seconds)	Total observed time (seconds)	Rate: SDB/observed time
DA	N/A	N/A	0	NA
DV	14	24.1	1500	0.016
DI	0	0	900	0
DR	N/A	N/A	0	NA
JA	6	71.9	3300	0.022
JO	N/A	N/A	0	NA
MG	1	0.1	300	< 0.001
MS	N/A	N/A	0	NA
ME	N/A	N/A	0	NA
MM	N/A	N/A	0	NA
NO	N/A	N/A	0	NA
TR	4	9.7	300	0.032
ZS	N/A	N/A	0	NA

Appendix 5.1 Access to Nursery resources for the purpose of conducting research

Durham University
Legal Services

Shaped by the past, creating the future

[redacted]

5th of November 2018

Re: Access to Nursery resources for the purposes of conducting research associated with the project *"Development of Empathy in Young Children"* (the "Project")

Dear [redacted],

Thank you for enabling researchers from the University of Durham (the "University") to come to the Durham University Day Nursery (the "Nursery") to allow them to undertake research contributing to the above noted Project as further described in the attached outline (the "Research").

This letter sets out the understanding of the Parties in regards to the performance of the research, and the responsibilities of each party to ensure that all data collected in the course of the Research is collected lawfully and in accordance with all relevant Data Protection Legislation which means the Data Protection Act 1998, the Regulation EU/2016/679 of the European Parliament and of the Council of 27 April 2016 (the General Data Protection Regulation) and all applicable laws and regulations relating to processing of personal data and privacy including where applicable the guidance and codes of practice issued by the Information Commissioner.

Therefore, it is hereby agreed as follows:

1. The Research shall take place over a period of approx. 10 months, commencing on the 1st of June 2018. The Nursery shall allow the University access for the purposes of undertaking the Research as set out in the attached outline.
2. At least 30 days prior to commencement of the Research, the University shall provide to the Nursery with copies of all necessary Privacy Notices.
3. The Nursery shall be responsible for, and hereby warrants to the University that such Privacy Notices shall be promptly distributed to all children and/or their parents (as appropriate), and consent shall be fully and properly collected in respect of each Data Subject from whom Personal Data shall be collected in the course of the Research in accordance with the relevant Privacy Notice.
4. The Nursery shall be responsible for, and shall ensure that no child from whom full consent has not been collected is permitted to participate in the Research or to provide any data or information to the University.
5. The University hereby warrants to the Nursery that any and all data collected in the course of the research shall be handled and processed strictly in accordance with the Privacy Notice

supplied to the Nursery in accordance with Clause 3 above, and at all times in accordance the Data Protection Legislation.

6. Each Party warrants to the other that it holds all necessary insurances and has conducted all necessary ethical and risk assessments in order for the research to take place.
7. The Nursery shall ensure that all researchers are made aware of any relevant Health and Safety policies applicable to the areas accessible to researchers.
8. Nothing in this Agreement shall create, imply or evidence any partnership or joint venture between the Parties or the relationship between them of principal and agent or employers and employee.
9. Any amendment to the terms of this Letter of Agreement shall be made in writing and signed by both Parties.
10. This Letter of Agreement shall be governed by English Law. The English Courts shall have exclusive jurisdiction to deal with any dispute which may arise out of or in connection with this Agreement.

The University thanks you once again for the participation of your Nursery and the children in your care in this valuable area of research. I would appreciate it if on behalf of the Nursery l, you could confirm your agreement to participate in the research as outlined herein, and your acceptance of the terms and conditions of participation as set out above, by signing and returning one copy of this letter of agreement to: Legal Services, University of Durham, Mountjoy Centre, Stockton Road, Durham DH1 3LE.

Yours sincerely,

Sally McGill / Denise McConnell
(Interim) Chief Financial Officer
The University of Durham

Appendix 5.2 Parent information sheet

Parent information sheet

Why is this research study being conducted? What is its purpose?

Although empathy is an important part of what it means to be human, we know little about how empathy develops in early life. Here, we are interested in understanding how empathy develops in early childhood. To do this, we would like to involve your child in our research. As part of this project, we are interested in how children experience emotions internally (at a physiological level). To look at how children experience emotions internally, we would like to use a new contact-free method, known as an infrared thermal imaging camera, to measure children's facial temperatures during empathy-inducing short video clips. By investigating how children experience empathy, we hope to extend our knowledge of how emotions are experienced and how these processes develop.

Who is conducting this research study?

This research is being conducted by Diane Austry, a PhD student at Durham University (UK), under the supervision of Dr Zanna Clay, a developmental and comparative psychologist in the Department of Psychology. Both researchers have full DBS clearance to conduct this research.

How many children will participate in the study?

We hope that approximately 30-50 children aged 0.5-3 years will participate in the study.

What will my child and myself need to do to be a part of this research study?

Before starting the task, your child will be involved in quiet and funny activities (e.g., colour pictures, look at a book of birds, play a quiet game) that will help him/her feeling comfortable with us and the settings. Then your child will be sat on a chair adapted to his/her age, facing a laptop displaying two videos of a familiar caregiver and two videos of an unfamiliar caregiver. The videos have been recorded with the caregivers of your nursery and the caregivers of another nursery that collaborates in our project, under the supervision and approval of the nursery managers. In a first set of videos a caregiver pretends to be sad for 50 sec before feeling better, and in a second set of videos the caregiver pretends to read a leaflet. This paradigm has been widely used in developmental research. All scenes (and the overall session) will end on a positive note for your child. A thermal camera will be set on a tripod to measure the physiological reaction of your child, along with a normal camcorder. This phase will last about 15-20 minutes.

As a complement to this research, we would like to ask you to complete a short questionnaire about your child's social and emotional development. If you have any questions about the questionnaire, please refer to Diane Austry, who will assist you.

Your involvement in this study is entirely voluntary.

What are the benefits of taking part in this research? Are there any disadvantages?

By participating in the current research, you are enabling scientists to better understand how children experience emotion and empathy. These findings are very useful for both scientific research as well as for practical application in educational and care-giving settings. We will always ask children if they would like to participate and no child will ever be forced into participating or continuing in a task. However, we find that children are interested in taking part and we always reward any child taking part. We hope that there are no disadvantages to you or your child, and we always provide lots of positive reassurance to the children about their participation. We would always terminate the trial if we see any signs of distress or discomfort. Having conducted developmental research in British nurseries over the past year, Diane Austry has acquired substantial experience in monitoring child wellbeing and we take the conservative approach to terminate trials in any case where a child shows signs of discomfort (i.e., we monitor their behaviour, as well as asking them how they are feeling).

Upon completion of the study, you and your child will be asked if you have any questions. If there is anything you or your child wish to discuss further, please contact us.

Do I have to take part?

Participation in this study is entirely voluntary and you will be free to withdraw your consent at any time after participation. Please note that after six (6) months, all data will be anonymised.

What will happen to the data?

All data will be kept strictly confidential and secure in accordance with Data Protection Legislation. If we seek to publish the paper, the results from each participant will remain entirely anonymous and no individually identifiable information would be published. We will retain the research data for a period of 15 years after any publication.

Who can I contact about this research study?

If you have any questions about this study please contact **Diane Austry** at diane.a.austry@durham.ac.uk;
or contact **Zanna Clay** on 0191 334 9114 or at zanna.e.clay@durham.ac.uk

We would greatly appreciate your support with our research.
If you do wish to take part, please sign and return the privacy notice and consent form provided, as well as the child information form and questionnaire.

With thanks,
Dr Zanna Clay and Diane Austry
Department of Psychology
Durham University Science Site
South Road


Zanna


Diane

Appendix 5.3 Privacy notice

Privacy Notice - Psychology Department

Durham University

Durham University's responsibilities under data protection legislation include the duty to ensure that we provide individuals with information about how we process personal data. We do this in a number of ways, one of which is the publication of privacy notices. Our privacy notices comprise two parts – a generic part and a part tailored to the specific processing activity being undertaken.

Data Controller

The Data Controller is Durham University. If you would like more information about how the University uses your personal data, please see the University's Information Governance webpages or contact:

Information Governance Unit.
Telephone: (0191 33) 46246 or 46103
E-mail: info.access@durham.ac.uk

Data Protection Officer

The Data Protection Officer is responsible for advising the University on compliance with Data Protection legislation and monitoring its performance against it. If you have any concerns regarding the way in which the University is processing your personal data, please contact the Data Protection Officer:

Jennifer Sewel
University Secretary
Telephone: (0191 33) 46144
E-mail: jennifer.sewel@durham.ac.uk

Retention

The University keeps personal data for as long as it is needed for the purpose for which it was originally collected. Most of these time periods are set out in the University Records Retention Schedule.

Your rights in relation to your personal data

Privacy notices and/or consent

You have the right to be provided with information about how and why we process your personal data. Where you have the choice to determine how your personal data will be used, we will ask you for consent. Where you do not have a choice (for example, where we have a legal obligation to process the personal data), we will provide you with a privacy notice. A privacy notice is a verbal or written statement that explains how we use personal data.

Whenever you give your consent for the processing of your personal data, you receive the right to withdraw that consent at any time. Where withdrawal of consent will have an impact on the services we are able to provide, this will be explained to you, so that you can determine whether it is the right decision for you.

Accessing your personal data

You have the right to be told whether we are processing your personal data and, if so, to be given a copy of it. This is known as the right of subject access. You can find out more about this right on the University's Subject Access Requests webpage[16].

Right to rectification

If you believe that personal data we hold about you is inaccurate, please contact us and we will investigate. You can also request that we complete any incomplete data. Once we have determined what we are going to do, we will contact you to let you know.

Right to erasure

You can ask us to erase your personal data in any of the following circumstances:

- We no longer need the personal data for the purpose it was originally collected
- You withdraw your consent and there is no other legal basis for the processing
- You object to the processing and there are no overriding legitimate grounds for the processing
- The personal data have been unlawfully processed
- The personal data have to be erased for compliance with a legal obligation
- The personal data have been collected in relation to the offer of information society services (information society services are online services such as banking or social media sites).

Once we have determined whether we will erase the personal data, we will contact you to let you know.

Right to restriction of processing

You can ask us to restrict the processing of your personal data in the following circumstances:

- You believe that the data is inaccurate and you want us to restrict processing until we determine whether it is indeed inaccurate

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[16] https://www.dur.ac.uk/ig/dp/sar/

- The processing is unlawful and you want us to restrict processing rather than erase it
- We no longer need the data for the purpose we originally collected it but you need it in order to establish, exercise or defend a legal claim and
- You have objected to the processing and you want us to restrict processing until we determine whether our legitimate interests in processing the data override your objection.

Once we have determined how we propose to restrict processing of the data, we will contact you to discuss and, where possible, agree this with you.

Making a complaint

If you are unsatisfied with the way in which we process your personal data, we ask that you let us know so that we can try and put things right. If we are not able to resolve issues to your satisfaction, you can refer the matter to the Information Commissioner's Office (ICO). The ICO can be contacted at:
Information Commissioner's Office
Wycliffe House, Water Lane, Wilmslow
Cheshire, SK9 5AF
Telephone: 0303 123 1113, Website: Information Commissioner's Office[17]

PART 2 – TAILORED PRIVACY NOTICE

This section of the Privacy Notice provides you with the privacy information that you need to know before you provide personal data to the University for the particular purpose(s) stated below.

Type(s) of personal data collected and held by the Department of Psychology and method of collection:

We will collect personal data on your child through the "Child Information Form" (date of birth, sex, nursery, diagnostic information). Video footage will be collected using both a normal video camera and a thermal camera.

How personal data is stored by Department of Psychology:

The records of this study will be kept privately and securely, which includes your child's name and the information you provide. Computer files will be stored on password-secured computers at the University of Durham. Paper copies will be stored in locked filing cabinets securely in the Department of Psychology. Only researches directly involved in this study will have access to the information collected.

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[17] https://ico.org.uk/

How personal data is processed by Department of Psychology:

Within 6 months of completing data collection, we will anonymise all personal (non-video) data and the original participant details sheet ("Child Information Form" following this notice) will be destroyed. It means that your child will only be identified by participant number; so individual identity cannot be determined. After which we won't be able to identify (nor exclude) your child's data from the complete data set. If you decide to withdraw your child information and footage, please contact us within two months after the end of the data collection. In order to retain consent form for your participation, the consent form you will sign if you agree to take part in this study will be kept for up to 15 years following completion of this study, including your contact details (email address) which we may use to contact you for additional consent. In any publication, we will not include any information that will make it possible to identify any participant. Nonetheless, with your consent, we would like extracts from recordings to be included in publications, presentations and teaching materials. If we seek to publish the paper, the results from each participant will remain entirely anonymous and no individually identifiable information would be published.

How long personal data is held by Department of Psychology?

The personal data that we will collect through the "child's details form" will be will be anonymised, i.e., name will be translated as participant number, gender will be translated as 1 or 2, date-of-birth will be translated into age in days/months, names of the nurseries will be encoded into number (e.g., nursery 1), any diagnosis of developmental disorder will be coded as present or absent – and subject with developmental disorder will be excluded from the data set and the associated data will be destroyed within 6 months. The original document will be hold for 6 months, after which it will be destroyed. All **video footage** will be securely stored at the University for up to 15 years following completion of this study and accessed only by investigators. After this retention period, all personal video data -as well as the consent form with your contact details- will be deleted (unless we get in touch to request additional consent from you). By its nature, it is not possible to make video footage fully anonymous (e.g. the face of your child needs to be visible in order for us to make the thermal imaging recordings). For this reason, we maintain the strictest data protection policies in safeguarding this data, in line with new GDPR policies. We are committed to following the strict ethical protocols in place at Durham University to ensure data is fully protected and not viewed by anyone other than the investigators. This means that video data will be security and only accessible by identified researchers directly involved in the project. Personal information pertaining to child name/gender will not be directly recorded in association with the video file, but associated to an anonymous code that would allow us identify and destruct the data if you require us to do so. You are entitled to request destruction of this data at any time by contacting us.

How to object to Department of Psychology processing your personal data:

If you have any issues with the processing of your personal data, please contact **Zanna Clay** on 0191 334 9114 or at zanna.e.clay@durham.ac.uk ; or **Diane Austry** at diane.a.austry@durham.ac.uk

Appendix 5.4 Informed consent form for parents

Informed consent form

Durham
University

Please read each of the following statements, and sign your initials after each to indicate that you have read and understood each one:

I have read and understood the attached Information Sheet and Privacy Notice.	
I have been given full information regarding the aims of the research and have been provided with contact details should I require further information.	
I understand that any written responses provided by me or my child will be anonymized and confidential.	
I understand that data from this study may be published in a scientific journal, or presented at a conference, but that **no individually identifiable information** will be revealed through these processes.	
I give consent for my child to participate in the above project.	

Video footages:

I consent to my infant and I being **videoed** and the videos to be seen by the investigators.	
I consent for **extracts from the recordings** to be included in publications, presentations and teaching materials.	

Withdrawing:

I understand that both myself and my child are free to withdraw from this without having to give a reason to withdraw, and without any adverse result of any kind, up until the point at which the data are anonymized (within 6 months). If so, I understand that unless I agree otherwise, any recordings that I have provided as part of the study will be destroyed.	

Parent/Caregiver's name and signature:…………………………………………………
Date:…………………

Please tick the boxes appropriately:

- I agree for the researchers to retain my contact details (email address) in case they need to contact me for any reason relating to the study. [ ]
- I am interested in receiving an overview of the results of this study by email [ ]

Email address: ………………………………………………………………………

Our contact details: diane.a.austry@durham.ac.uk ; zanna.e.clay@durham.ac.uk, Phone: 0191 334 9114

Appendix 5.5 Child information form

Child Information Form

Please provide in block capitals

Name of Child: ....

Gender: M / F Date of Birth (dd/mm/yyyy):….………………………

Nursery: ….……………………………………………………………………………….

Room at the Nursery: ………………………………………………………………………

Usual days of attendance:
…………………………………………………………………………………………………
…………………………………………………………………………………………………
…………………………………………………………………………………………………
…………………………………………………………………………………………………

Has your child received a formal diagnosis of any developmental disorders? (e.g., Autism Spectrum Disorder, ADHD, dyslexia…)? Y / N

Parent's (or guardian's) name: .………………………………………………………………..

PLEASE RETURN WITH CONSENT FORM

Thank you for completing this information sheet. The information you provide on this sheet will be collected and disclosed in accordance with Data Protection Legislation. We will anonymise this information within 6 months of the date of collection, and destroy this sheet thereafter.

Appendix 5.6 Informed consent form for caregivers (stimuli recording)

Informed consent form for caregivers

As part of our project on the development of empathy, we are interested in the physiological reaction of children when they witness the distress of somebody else. This experiment is based on the idea that children would react more strongly when seeing somebody they know in distress in contrast to a stranger. You are familiar to the children in your nursery, but non-familiar to the children in the other nursery we are collaborating with. That is why we asked you / would like to ask you if you would be willing to take part in quick acting acts (1 min) in which you would pretend to (1) be very sad and (2) read a leaflet. This act will be recorded and use to test the empathic reaction of children in your nursery and a second nursery collaborating in the project. Note that other than the children, the footages will only be seen by the principal investigators of the project.

Please read each of the following statements, and sign your initials after each to indicate that you have read and understood each one:

I am happy with the information I have been given regarding the aims of the research. I also have been provided with contact details should I require further information.	
I consent to be recorded for this experiment, and I agree for the researcher to keep this footage (that will not be identified with my name) for the duration of the project.	
I consent for the video clips to be played to the children in my "home nursery" and in the other nursery that collaborates on the project.	
I understand that if I change my mind after agreeing for the researcher to record, keep and use the footage I must inform the researcher of my decision before the start of the data collection with the children (i.e., within 5 days).	

Name:…………………………………………………………………………........

Nursery and Room: ……………………………………………………………………

Signature: ………………………………………...………. Date:…………………

Please tick the boxes appropriately:

- I agree for the researchers to retain my contact details (email address) in case they need to contact me for any reason relating to the study. [ ]
- I am interested in receiving an overview of the results of this study by email [ ]

Email address: ……………………………………………………………………

Our contact details: diane.a.austry@durham.ac.uk ; zanna.e.clay@durham.ac.uk, Phone: 0191 334 9114

Appendix 5.7 Durham City, demographics information

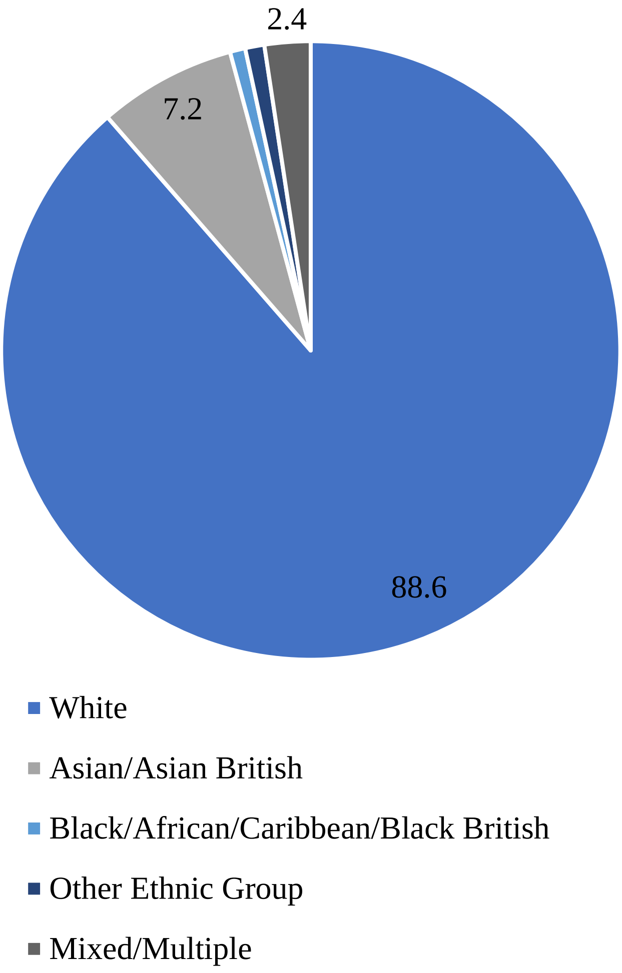

Figure A Ethnicity representation for Durham City, Office for national statistics (ONS, 2011 Census)**[18]**

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[18] Source: https://www.durhaminsight.info/population/report/view/1a2cb68561014660afe0338e7d550ac6/E02004314/

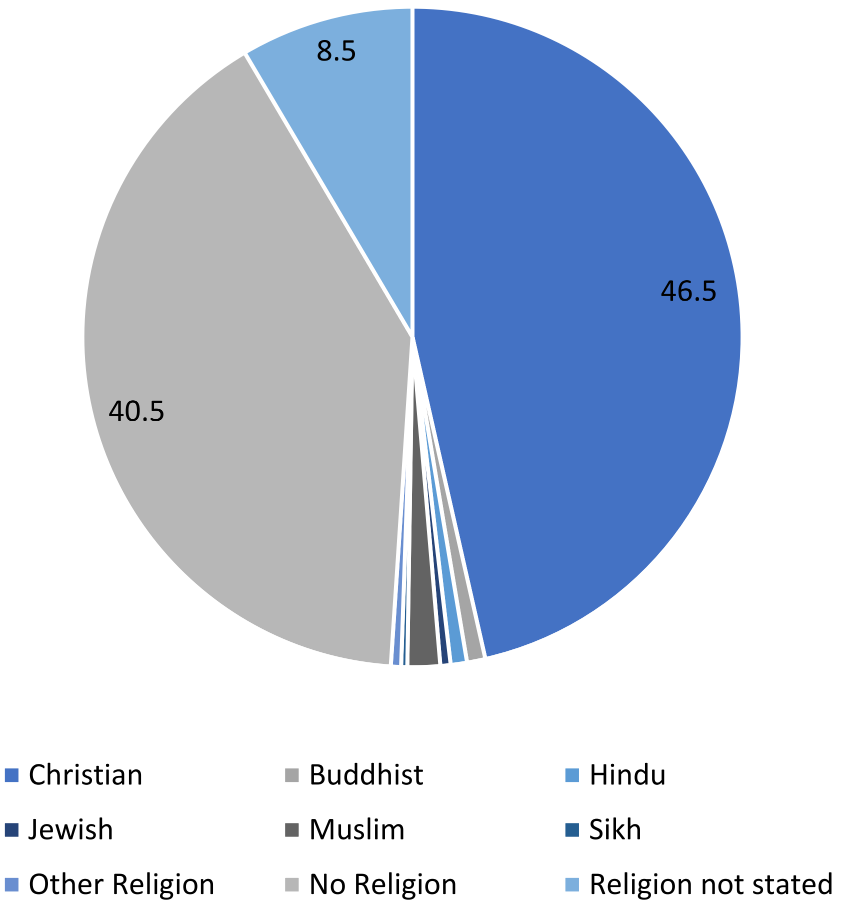

Figure B Resident population by Religion in the Durham City (Middle Layer Super Output Areas, MSOA)[19]

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[19] Source: https://www.durhaminsight.info/population/report/view/1a2cb68561014660afe0338e7d550ac6/E02004314/

Table G Summary of key economic indicators for County Durham, UK[20]

	Data	**Source**
Economic Activity Rate (16 - 64 yrs old)	76.30%	ONS APS (2020-06)
Employment Rate (16 - 64 yrs old)	72.10%	ONS APS (2020-06)
Disabled Employment Rate	50.90%	ONS IDBR (2020-06)
Economic Inactivity Rate (16 - 64 yrs old)	23.70%	ONS APS (2020-06)
Unemployment Rate (16 - 64 yrs old)	5.50%	ONS APS (2020-06)
Business Enterprises in 2020	14,105	ONS IDBR
Total GVA (£millions) in 2018	£8,834m	ONS GVA
Total GVA per Head in 2018	£16,763	ONS GVA
Total GDHI (£millions) in 2018	£8,717m	ONS GVA
Total GDHI per Head in 2018	£16,542	ONS GVA
Total Annual Gross Earnings in 2020	£22,188	ONS ASHE
Total Weekly Gross Earnings in 2020	£406	ONS ASHE

Source abbreviations:
ONS APS = Office for National Statistics Annual Population Survey
ONS IDBR = Office for National Statistics Inter Departmental Business Register
ONS BRES = Office for National Statistics Business Register Employment Survey
ONS GVA = Office for National Statistics Gross Value Added
ONS GDHI = Office for National Statistics Gross Domestic Household Income
ONS ASHE = Office for National Statistics Annual Survey of Hours and Earnings

Source: https://www.durhaminsight.info/economy-and-employment/

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[20] Source: https://www.durhaminsight.info/economy-and-employment/

Appendix 5.8 Ethogram for children’s behaviour in the IRT experiment

Facial expressions

To code for the facial expression of concern, the participant’s facial expression included sobering, sad expression with corners of the mouth turned down, or ‘sympathy face’ with brow furrow, or lips tight together (Davidov et al., 2020).

Regarding other negative facial expressions, the child could also show distress facial expressions which were defined as eyes wide and mouth open as signs of wariness or fear or discomfort facial expression.

Other less frequent expressions of negative emotion were sadness (inner corners of brows raised, outer corners lowered, eyes narrowed or squinted, corners of the mouth pulled down and out), fear (brows straight or normal, slightly raised or drawn together, eyelids raised and tense, mouth open and corners straight back) or anger (brows down straight or slanting down toward the centre, brows often drawn together, cheek raised) facial expressions (Izard, 1979).

Participants could also produce expressions of positive affect which includes expressions of amusement, happiness or excitement, e.g., mouth smiling and cheeks raised (Dimberg & Thunberg, 2012).

Self-directed behaviours

Self-directed behaviours were defined as when the participant made soft repeated scratching movements or a sharp single movement with their fingertips (with or without the use of nails) on their own body, as coded in the non-human primate literature (Castles & Whiten, 1998; Koski et al., 2007). It also included the manipulation of one’s hair, clothing and/or accessories.

Social referencing and information seeking/sharing

I coded the participant as "looking at the caregiver" when the face of the child was oriented towards the caregiver (± 20-degree angle) for at least 1 second. This behaviour involves a rotation of the head of more than a 35-degree angle from the screen after looking at the stimulus, suggesting that child seek visual comfort/support and/or social referencing (i.e., contingency of looking at the stimuli and then looking at the caregiver in the room).

Similarly, I coded when the participant was "looking at the experimenter (me)" following the same criteria. However, I did not analyse the time spent by the child looking at the experimenter because I tended to move around to deal with the equipment. When the child raised and extended their arm, hand and at least one finger towards the screen, I coded it as "pointing behaviour". During this behaviour, the child could have been looking toward the direction of their arm/hand/finger or not.

Appendix 5.9 IRT data description

For the 360 measurements, I extracted the ideal frames on average at ±2.4 seconds (SD = 2.8 seconds; minimum = 0 seconds; maximum = 9 seconds around 80 and 200 seconds after the onset of the stimulus). See below the mean skin temperatures of the three measured facial areas of the children when tested for distress and neutral situations (Table X).

Table H Mean (±SD) skin temperatures (Celsius degrees) of the three measured facial areas of the children when tested for the distress and neutral situations

		Familiar		**Unfamiliar**	
Time points	Region of interest	*Distress*	*Neutral*	*Distress*	*Neutral*
Baseline	*Peri orbital*	35.0 (±0.7)	35.0 (±0.7)	35.0 (±0.6)	35.1 (±0.7)
	Nose bridge	33.5 (±1.8)	33.9 (±1.6)	33.6 (±1.8)	33.7 (±2.0)
	Nose tip	32.8 (±2.1)	33.3 (±1.9)	32.8 (±2.0)	33.1 (±2.1)
80 sec (Test)	*Peri orbital*	35.0 (±0.5)	35.1 (±0.7)	35.0 (±0.7)	35.1 (±0.5)
	Nose bridge	33.8 (±1.7)	33.9 (±1.7)	33.6 (±1.9)	33.8 (±1.9)
	Nose tip	33.3 (±2.1)	33.3 (±2.0)	33.0 (±2.1)	33.3 (±2.0)
200 sec (Recuperation)	*Peri orbital*	35.0 (±0.7)	35.0 (±0.5)	35.1 (±0.6)	35.0 (±0.7)
	Nose bridge	34.0 (±1.4)	33.6 (±1.8)	33.8 (±2.0)	33.5 (±1.7)
	Nose tip	33.2 (±1.9)	33.0 (±2.0)	33.2 (±2.2)	33.0 (±2.1)

Appendix 5.10 **Correlations between the change of temperature in the different regions of interest at 80- and 200-seconds following stimulus onset**

To instigate the correlation between the change of temperature in the different regions of interest at the two time points, I ran bivariate Pearson correlations

The change of temperature in the nose bridge and the nose tip at 200 second were strongly correlated ($r = 0.810$, $p < 0.001$, $N = 110$), so were the change of temperature in the peri-orbital and the nose tip areas at 200 seconds ($r = 0.214$, $p < 0.05$, $N = 104$). The change of temperature of the three regions of interest correlated at the two time points: peri-orbital at 80 and 200 seconds ($r = 0.467$, $p < 0.001$, $N = 106$), nose bridge ($r = 0.709$, $p < 0.001$, $N = 108$), and nose tip ($r = 0.552$, $p < 0.001$, $N = 108$). Given the correlation between the thermal measurements, I selected a single of these measurements to test for the relationship between the thermal and behavioural response.

Appendix 5.11 Results of the comparison of the full models with the respective null model (R function 'anova' with argument test "Chisq" – _Table I_)

Response variables	***χ2***	***d.f.***	***p***
Self-directed behaviours (occurrences)	0.492	3	0.921
Social referencing behaviours (duration)	0.653	3	0.884
Avoidance behaviours (duration)	2.019	3	0.568

Appendix 5.12 Bivariate Pearson correlation results for the change in facial skin temperature for the three regions of interest at 80 and 200 seconds after the onset stimulus – with participant age, the production of self-directed behaviours (duration of self-directed behaviours), and the time avoiding the stimulus *(Table J)*

Region of interest		**Peri orbital**	**Nose bridge**	**Nose tip**
		80 seconds after stimulus onset		
Age (continuous)	Pearson correlation	-0.215	0.077	0.047
	Sig. (2 tailed)	0.255	0.691	0.807
	N	30	29	29
Self-directed behaviours (occurrences)	Pearson correlation	0.028	0.116	0.227
	Sig. (2 tailed)	0.881	0.549	0.236
	N	30	29	29
Time avoiding the stimulus (duration)	Pearson correlation	0.069	-0.285	-0.275
	Sig. (2 tailed)	0.717	0.134	0.148
	N	30	29	29
		200 seconds after stimulus onset		
Age (continuous)	Pearson correlation	-0.057	-0.093	-0.086
	Sig. (2 tailed)	0.765	0.626	0.650
	N	30	30	30
Self-directed behaviours (occurrences)	Pearson correlation	0.184	0.130	0.268
	Sig. (2 tailed)	0.331	0.494	0.152
	N	30	30	30
Time avoiding the stimulus (duration)	Pearson correlation	0.075	-0.158	-0.281
	Sig. (2 tailed)	0.695	0.404	0.133
	N	30	30	30

Appendix 6.1 Temperature variation of the nasal facial skin

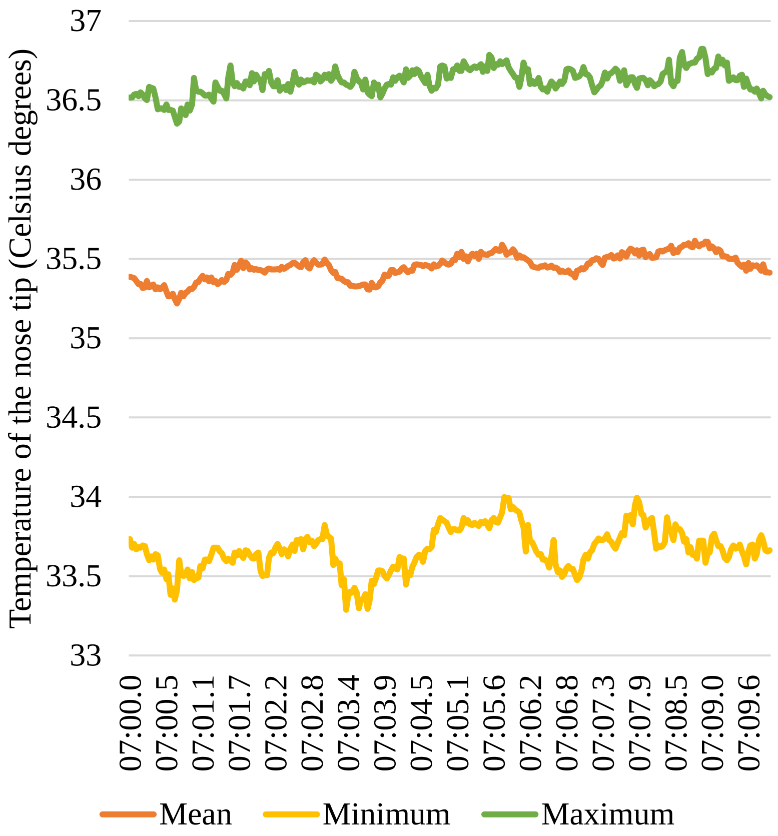

Figure C Visual representation of the temperature variation of the nasal facial skin within 10 seconds (mean, minimum, and maximum, in Celsius degrees)

Table K Quantification of the temperature variation of the nasal facial skin within 10 seconds (from 07:00 to 07:10; mean, minimum, and maximum, in Celsius degrees)

	Temperature extracted		
	Mean	Minimum	Maximum
Min	35.2	33.3	36.4
Max	35.6	34.0	36.8
S.D.	0.08	0.14	0.08