

Challenges in the comparative study of empathy and related phenomena in animals

J.E.C. Adriaense^{a,b,c,*}, S.E. Koski^d, L. Huber^e, C. Lamm^{a,c,*}

^aSocial, Cognitive and Affective Neuroscience Unit, Department of Cognition, Emotion, and Methods in Psychology, Faculty of Psychology, University of Vienna, Vienna, Austria ^bDepartment of Cognitive Biology, Faculty of Life Sciences, University of Vienna, Vienna, Austria ^cVienna Cognitive Science Hub, University of Vienna, Vienna, Austria ^dFaculty of Social Sciences, University of Helsinki, Unioninkatu 35, 00014 Helsinki, Finland

^eComparative Cognition, Messerli Research Institute, University of Veterinary Medicine Vienna, Medical University of Vienna, University of Vienna, Vienna, Austria

*Corresponding authors at: jessie.adriaense@univie.ac.at (J.E.C. Adriaense), claus.lamm@univie.ac.at (C. Lamm).

Received 1 April 2019; Received in revised form 6 December 2019; Accepted 18 January 2020; Available online 27 January 2020

ABSTRACT

The aim of this review is to discuss recent arguments and findings in the comparative study of empathy. Based on a multidisciplinary approach including psychology and ethology, we review the non-human animal literature concerning theoretical frameworks, methodology, and research outcomes. One specific objective is to highlight discrepancies between theory and empirical findings, and to discuss ambiguities present in current data and their interpretation. In particular, we focus on emotional contagion and its experimental investigation, and on consolation and targeted helping as measures for sympathy. Additionally, we address the feasibility of comparing across species with behavioural data alone. One main conclusion of our review is that animal research on empathy still faces the challenge of closing the gap between theoretical concepts and empirical evidence. To advance our knowledge, we propose to focus more on the emotional basis of empathy, rather than on possibly ambiguous behavioural indicators, and we provide suggestions to overcome the limitations of previous research.

Keywords: Comparative research, Empathy, Affect, Emotions, Animal, Emotional contagion, Consolation, Sympathy, Prosociality

1. Introduction

There is wide agreement in both scientific and folk conceptions that empathy is a skill of central importance for human sociality and group cohesion (Decety, 2015). Broadly speaking, empathy allows us to respond to and even experientially share the feelings of others, and thus to better understand and relate to their inner emotional and mental states (Singer and Lamm, 2009). Apart from fostering smooth and efficient coordination and communication, empathy has a strong impact on prosocial behaviour, such as when we help and support others whose suffering and needs we resonate with (Decety, 2015; Lamm et al., 2019). In these ways, empathy may act as a social glue that not only ties us together as individuals, but also is essential for building and maintaining the complex societies that humans have evolved to live in. Naturally, if this claim is correct, it raises the questions of where this complex skill comes from (in evolutionary terms), and whether other species, who also rely to a great extent on living and cooperating in large groups of individuals, possess empathic skills similar to those ascribed to humans. By pursuing a comparative approach, through investigating empathy's related phenomena in different species, the major aim of the present review and opinion paper is to shed some light on these questions. We begin our review with an overview of the definitions of human empathy, and how these may relate to and inform comparative research on empathy. In that section, we also discuss current theoretical frameworks of animal empathy and their applicability for interpreting empirical data. This is followed by extensive discussions of three major empathy-related phenomena, namely emotional contagion, consolation, and targeted helping (see Table 1 for definitions used in this paper, terminology often used in other literature, and empirical examples of the phenomena). Each of these phenomena will be introduced by their definitions and theoretical foundations, followed by an examination of empirical approaches used to investigate them. We build our discussion of these approaches on specific conceptual issues, and we draw upon selected empirical examples to support our arguments. Hence, the reviewed literature is not exhaustive, and the cases used intend to include diverse species, methods, and paradigms. For each phenomenon, we consider the question whether the empirical data may indeed

reflect the existence of the particular phenomenon in the respective species, or whether a more parsimonious alternative explanation should be considered. As will become clear throughout the paper, we would like to argue that in some empirical cases there may be an oversimplification of the discussed phenomenon, and that interpretations sometimes lack conclusive validation (methodologically as well as conceptually), being based on rather indirect or ambiguous evidence. With this review and opinion paper, we want to raise awareness of how and when the label empathy is used, and how empathy-related phenomena are currently being investigated in comparative research.

1.1. Human empathy

Historically, empathy research has been driven by two related questions, "How do we understand others' feelings?" and "How does that knowledge lead to actions of care for the other?" (e.g. Batson, 2009). The first question concerns the experience of empathy itself and the second focuses on the behaviour that follows from that experience. Many scholars have come up with their own definition, by putting emphasis on both or either one of these questions. This has led to ongoing disagreement on how to best define and measure this complex and multi-faceted construct, and its numerous sub-concepts and their complex interlinkages (e.g. Batson, 2009; Singer and Lamm, 2009; Yamamoto, 2017). One of the major challenges hampering scientific progress in empathy research is this conceptual and empirical elusiveness, which does not only concern research on humans but also on nonhuman animals (henceforth animals). In the human literature, Daniel Batson critically reviewed eight empathy related phenomena (2009) (see Box 1 for all phenomena and their description). While these phenomena, ranging from emotional contagion to sympathy, carry distinct definitions, he outlines that researchers in various fields have repeatedly referred to "these things" as empathy. In a similar vein, a recent review uncovered 43 distinct definitions of empathy in human research alone (see Cuff et al., 2016, for a discussion of the definitions).

Term	Definition	Other used terminology	Empirical examples
Mimicry	A copying of another's physical appearance (Zentall, 2001). The copying is an involuntary, automatic and fast response of the physical or behavioural traits of others (Chartrand and Bargh, 1999)	Motor mimicry ¹ (= Body posture mimicry + Facial mimicry); Synchronization (of expressions, movements, postures, or vocalizations)	Batesian mimicry (Ohsaki, 1995); Rapid facial mimicry (Palagi et al., 2019a, 2019b)
Behavioural Contagion	Two or more animals show similar, species-typical (unlearned) behaviour (Thorpe, 1963). The behaviour in one animal is automatically triggered by the similar behaviour of others (Zentall, 2001)	Motor contagion ¹	Contagious stretching (Gallup et al., 2017); Contagious scent-marking (Massen et al., 2016); Yawn contagion (Massen and Gallup, 2017); Coordinated movements in courtship displays (Tinbergen, 1960); Coordinated movements in antipredator behaviour, such as seen in flocking or herding (Zentall, 2001), or mobbing (Hoogland and Sherman, 1976)
Emotional Contagion	Emotional state-matching of a subject with an object (de Waal, 2008)	Vicarious emotion; Emotional transfer; Emotion transmission; Affect matching; Affective empathy; Emotional replication	Contagious laughter (Provine, 1992); Positive emotional contagion (Reimert et al., 2017); Negative emotional contagion (Adriaense et al., 2019a)
Personal distress	A self-oriented, aversive emotional response (Lamm et al., 2007)	Vicarious aversive or negative arousal	Spread of distress in infant monkeys (de Waal, 2008)
Empathy	The ability to respond to and experientially share the feelings of others, which eventually leads to a better understanding of their inner emotional and mental states (Singer and Lamm, 2009). See also Box 1 and Box 2.	Often described as feeling with or feeling as the other (distinct from the feeling for, which defines sympathy or compassion)	Empathy for pain (Singer et al., 2004; Rütgen et al., 2015)
Sympathy	An emotional response and concern about another's state, including attempts to ameliorate this state (de Waal, 2008)	Sympathetic concern; Empathic concern; Compassion; Consolation. Often described as feeling for the other.	Consolation (Burkett et al., 2016; Quervel-Chaumette et al., 2016)
Perspective Taking	A mental process that enables to take another's perspective and relate to other's emotions, thoughts and intentions (Decety and Svetlova, 2012)	Cognitive empathy; Theory of Mind	See Massen et al., 2019 (This special issue)
Targeted helping	Help based on the cognitive appreciation of the situation or needs of others (de Waal, 2008)	Prosocial behaviour	Giving access to food (Warneken and Tomasello, 2006); Handing a tool (Yamamoto et al., 2009); Rescue behaviour (Bartal et al., 2011; Hollis and Nowbahari, 2013)

Definitions of empathy related phenomena as we use them in text. Other used terminology refers to other terms researchers have used as synonyms or closely related phenomena. Empirical examples are selected studies on the topic. ¹ The terms motor mimicry, motor contagion and behavioural contagion are often intermittently used (e.g. Hess and Fischer, 2014), though by definition mimicry and contagion are different.

Within this set of definitions, the authors identified eight themes that form the major distinctions between these definitions, and propose an updated definition of empathy (see Box 2). Hence, somewhat ironically, human empathy research is now facing (at least) 44 different definitions and 8 distinct conceptual themes. These complexities in theoretical and methodological understanding naturally translate to the animal domain. There, on top of the challenges in human research, most measures of emotion and cognition are indirect and have to rely predominantly on behaviours observed in animals - while research in humans benefits from potential disambiguation via self-report (although not without its own issues, see e.g. limitations in self-report in Winkelman and Berridge, 2004). These intricacies not only apply to empathy defined as an umbrella term, but also to its subcomponents, such as seen for instance in self-other distinction. Self-Other (S-O) distinction (also labelled 'S-O recognition') is the ability, and awareness, to differentiate between one's own feelings and the other's (Lamm et al., 2019), which for example is important to decrease personal distress in order to help others. The Mirror-Self-Recognition (MSR) test has been suggested as a way to test S-O distinction in animals (Gallup, 1970), with evidence of MSR in humans and great apes (Anderson and Gallup, 2015), yet, further demonstration in other species has been proven challenging. For example, despite advanced cognitive skills, many animals do not show MSR, such as Goffin's cockatoos (*Cacatua goffiniana*, van Buuren et al., 2018), some methodological approaches to test MSR have been found questionable (see Anderson and Gallup, 2015, for a critical review on MSR in primates), and evidence in non-primate species (e.g. elephants) is often based on single individual findings (see Gallup and Anderson, 2018, for a review on MSR in non-primates). Moreover, it remains unresolved whether MSR in animals demonstrates S-O distinction or whether

MSR can be explained alternatively, and whether S-O distinction automatically implies self-awareness, as disputed in a recent paper on MSR in cleaner fish (*Labroides dimidiatus*) (Kohda et al., 2019; but see de Waal, 2019, for a critical discussion of Kohda et al., 2019, and the application of a gradual perspective on MSR, rather than the current binary one). Accordingly, important distinctions between notions of awareness should be considered, such as the difference between one's physical awareness (where one is located in space) versus one's mental awareness (of one's self as an entity) (Vonk, 2019a).

Considering the disagreement on the empirical evidence for S-O distinction in animals, the presence of this distinction in a social or emotional setting seems an even more challenging hypothesis to test. Moreover, human empathy requires a flexible regulation between self and other (affective and cognitive) representations, which then again may not always be accompanied by congruent and overt emotional responses. All these elements remain a major challenge to demonstrate in animals (e.g. see for dogs, *Canis familiaris*, Boch and Lamm, 2017, as commentary on Kujala, 2017, 2018) and we propose that investigating whether 'animals show empathy' within the framework of a human definition is too restricted. This stance is well in line with a recent opinion article, proposing that holding the investigation of (animal) empathy up to the strict criteria of a (human) definition limits the findings in animal research, which then again "might not be constructive when investigating the evolution of empathy from comparative viewpoints." (Yamamoto, 2017, p. 2). While some scholars argue that research has already provided sufficient evidence for animal empathy (e.g. Sivaselvachandran et al., 2018), we propose based on our review that this is not the case, or at least not sufficiently so to exclude alternative hypotheses, and that we should seek to re-orient our perspective of investigating empathy to a more systematic comparative approach.

Box 1: Batson's eight empathy-related phenomena, or "These things called empathy" (Batson, 2009, p. 3).

Daniel Batson, a social psychologist who has devoted most of his career to empathy research, describes eight empathy-related concepts or phenomena based on a broad multidisciplinary review of the literature. Importantly, he considers these related concepts not as components or elements of empathy, but phenomena that are stand-alone and psychologically distinct. The phenomena are therefore different psychological states one may experience in social interactions with another (e.g. such as when talking to a friend who went through a negative experience), and these different states correspond to the eight empathy-related phenomena. Notably, in the literature reviewed, each of these phenomena is often referred to as being “empathy itself”, adding to the confusion to what empathy “really is”. Though, according to Batson, these phenomena are conceptually distinct, and although they are related to empathy, they should be labelled by their own conceptual name.

Concept 1: “Knowing Another Person’s Internal State, Including His or Her Thoughts and Feelings” (Batson, 2009, p. 4). Concept 1 is the general knowledge about somebody’s internal state. This concept has also been labelled empathy (e.g. Preston and de Waal, 2002) or cognitive empathy (e.g. Zahn-Waxler et al., 1992a, 1992b).

Concept 2: “Adopting the Posture or Matching the Neural Responses of an Observed Other” (Batson, 2009, p. 4). Concept 2 refers to mimicking the posture or expression of the other, and is also generally labelled as motor mimicry (e.g. Hoffman, 2000) or imitation. Batson argues that this concept may contribute to eventually understanding the other’s feelings and thoughts, yet, he also argues that neither neural response matching (such as seen in the PAM, Preston and de Waal, 2002) or motor mimicry are sufficient sources or cues for empathic feelings for the other.

Concept 3: “Coming to Feel as Another Person Feels” (Batson, 2009, p. 5). Concept 3 is feeling as the other, though Batson mentions that it is not clear from research whether these feelings should be exactly the same emotion or could be a similar emotion. This concept is often also commonly referred to as emotional contagion, in which both emotional matching and catching are important (Hatfield et al., 1994). Emotional matching means that two subjects experience the same emotional state, which is in contrast to for example physiological matching, in which two subjects show a similar physiological profile, yet, this profile or arousal might be associated with different emotions (see also our discussion in Chapter 2.2.2.). Emotional catching refers to the source from where the emotional state is ‘caught’, which can be either from observing the other subject’s state (i.e. emotional contagion), or can originate from the shared situation (i.e. the source which originally changed the other subject’s state) (see also our discussion in Chapter 2.2.2.1.).

Aside from emotional contagion, this concept has in the contemporary literature also been labelled affective empathy (e.g. Zahn-Waxler et al., 1992a, 1992b), and automatic emotional empathy (e.g. Hodges and Wegner, 1997).

Concept 4: “Intuiting or Projecting Oneself into Another’s Situation” (Batson, 2009, p. 6). Concept 4 relates to for example the process a writer or painter goes through when depicting a character or object, and was described by Lipps (1903) as “Einfühlung” (“feeling into”), and named empathy (Titchener, 1909). Batson refers to this definition of empathy as an “aesthetic projection” (p. 6), yet, this definition is in contrast to the contemporary descriptions in the scientific literature of empathy.

Concept 5: “Imagining How Another Is Thinking and Feeling” (Batson, 2009, p. 7). Concept 5 entails that you imagine how the other feels and thinks (based on how they act, what they say, and your knowledge of the situation). This concept is also labelled perspective taking (Ruby and Decety, 2004), psychological empathy (in contrast to aesthetic empathy from Concept 4, Wispé, 1968), and empathy or projection (Adolphs, 1999).

Concept 6: “Imagining How One Would Think and Feel in the Other’s Place” (Batson, 2009, p. 7). Concept 6 refers to how you would feel and think if you were the other, and so, the focus is here on the self, whereas in Concept 5 the focus is on the other. This concept is also called cognitive empathy (Povinelli, 1993), projective empathy (Darwall, 1998), and perspective taking (Piaget, 1953).

Concept 7: “Feeling Distress at Witnessing Another Person’s Suffering” (Batson, 2009, p. 7). Concept 7 refers to feeling distress by seeing the other in distress, which is in contrast to feeling distress for the other (Concept 8) and feeling distress as the other (Concept 3). This concept is also named personal distress (Batson, 1991), empathic distress (Hoffman, 2000), or empathy (Krebs, 1975).

Concept 8: “Feeling for Another Person Who Is Suffering” (Batson, 2009, p. 8). Concept 8 is an other-oriented emotional response, implying that the emotion is felt for the other. This emotional response for the other is elicited by perceiving the state of the other, in which both the other-oriented emotional response and other’s state are congruent in their valence (a negative state in the other elicits a negative response, and vice versa for positive state). This means that you may feel negatively for the other when they feel sad, but you don’t need to feel exactly the same emotional state (such as in Concept 3). This concept is also labeled empathic concern (Batson, 1991), sympathetic distress (Hoffman, 2000), or sympathy (Darwall, 1998; Preston and de Waal, 2002; Wispé, 1986).

Batson discusses that each of the eight phenomena (may) serve as answer to either one or both of empathy’s important research questions, “How do we understand others’ feelings?” and “How does that knowledge lead to actions of care for the other?”. Question 1 relates to Concept 1 and Concepts 2–6 have been proposed as potential answers to this question. Batson argues that Concept 7 and 8 do not provide insight into another’s state, but they are reactions to that insight or state. Additionally, some have argued that Concepts 1–7 may serve as antecedents of Concept 8. Furthermore, Batson discusses that the second question taps into empathy for the other, such as feelings of sympathy, which may eventually motivate to act and relieve another’s suffering. Therefore, question 2 may be answered by Concepts 7 and 8, with Concept 7 involving a motivation coming from self-concern, and Concept 8 entailing motivation based on other-oriented concern. See Batson (2009) for further extensive discussion of the empathy-related concepts.

Box 2: Eight major themes underlying the difference in 43 distinct empathy definitions (Cuff et al., 2016)

In a recent review paper, Cuff et al. (2016) uncovered 43 distinct definitions of empathy in human research. The major distinctions between these definitions can be summarized in eight themes.

- The 1st theme concerns the distinction between empathy and its related concepts. Some view empathy as the overarching category (e.g. Preston and de Waal, 2002) while others argue for a more distinct approach (e.g. Batson, 2009, see also Box 1). For instance, in particular concerning sympathy, some have argued that this concept should not be merged with empathy (as agreed upon by e.g. Decety and Michalska, 2010; Eisenberg et al., 1991; Hein and Singer, 2008; Singer and Lamm, 2009; but see for other viewpoints e.g. Davis, 1996; Hoffman, 2000).
- The 2nd theme entails the question whether empathy is cognitive or affective, which refers to either understanding another's feelings versus experiencing another's feelings, and some definitions argue to include both as cognition and affect can occur in interaction (e.g. Lamm et al., 2007).
- The 3rd theme concerns the difference between experiencing congruent or incongruent emotional states with the other. Congruent experiences between observer and target are also referred to as shared or vicarious experiences, and some consider such emotional congruency as necessary in order to be related to empathy (e.g. Decety and Lamm, 2009; Hein and Singer, 2008; Lamm et al., 2019), though others disagree, or even argue that measuring exact emotional matching is almost impossible (Preston, 2007). In line with the 1st theme, it has been argued that emotional congruency is essential to separate empathy from sympathy, in which the latter relates to one's own feelings for the other, and may therefore be incongruent with the other's state (Hein and Singer, 2008).
- The 4th theme relates to empathy needing a direct perception of (the emotional state of) the other versus other stimuli being sufficient to lead to empathy (e.g. Blair, 2005). Such is the case when the target does not show emotional cues but the observer infers the emotional state through imagination or perspective taking, or for instance when dealing with a fictional character (Singer and Lamm, 2009).
- The 5th theme concerns whether empathy involves self-other distinction (e.g. De Vignemont and Singer, 2006) or involves a merging with the other, and others add that a merging with the other is important to eventually understand the other (e.g. Decety and Sommerville, 2003). Self-other distinction has also been argued to be important to differentiate empathy from other concepts such as emotional contagion (Decety and Lamm, 2009; Lamm et al., 2016).
- The 6th theme entails whether empathy is a trait (i.e. ability, capacity) or a state (and thus, context dependent). Here some argue that individuals can be more empathic than others with empathy being stable over time (e.g. Oliveira-Silva and Gonçalves, 2011), though situational factors may also influence empathy such as similarity between observer and target.
- The 7th theme relates to empathy having a behavioural outcome or not, in which it is argued that sometimes empathy is followed with a response, though not always (e.g. de Vignemont & Singer, 2006; Eisenberg et al., 1994), or even never in an immediate manner. Some scholars say that empathy only has a behavioural response when it is mediated through sympathy (e.g. De Vignemont and Singer, 2006; Eisenberg et al., 1994, but see for other viewpoint e.g. Oliveira-Silva and Gonçalves, 2011).
- The 8th theme refers to empathy being automatic or under control. While initial neuroscience research seemed to suggest that empathy may be automatically elicited upon perceiving the emotional state of the other (Singer et al., 2004; though this study did not directly study automaticity), later and more systematic work has questioned this assumption (Gu and Han, 2007), and it is now widely accepted that empathy may be controlled, modified, reframed, or suppressed by cognitive processing or other factors (Hodges and Biswas-Diener, 2007; Hein and Singer, 2008)

Based on these eight themes Cuff and colleagues have proposed an updated definition of empathy, namely "Empathy is an emotional response (affective), dependent upon the interaction between trait capacities and state influences. Empathic processes are automatically elicited but are also shaped by top-down control processes. The resulting emotion is similar to one's perception (directly experienced or imagined) and understanding (cognitive empathy) of the stimulus emotion, with recognition that the source of the emotion is not one's own."

1.2. Comparing empathy across species

Research on animal empathy has generally embraced the investigation of different empathy-related phenomena (of which some appear in the overview by Batson, 2009, see Box 1). In a highly influential paper setting the stage for the comparative study of empathy, Preston and de Waal proposed the Russian doll model which organizes these phenomena in a unified design (Preston and de Waal, 2002; de Waal and Preston, 2017). At the model's foundation is the Perception Action model (PAM), which has been proposed as the main mechanism of empathy in both humans and animals. This mechanism is described as the "Spontaneous activation of an individual's own personal representations for a target, their state and their situation when perceiving the target's state" (de Waal and Preston, 2017, p. 4). In other words, the perception of the other leads to matching neural responses, which in turn leads to either an experiencing or understanding of the other's emotional state. Mirror neurons have been proposed to serve as neurobiological evidence for the PAM (Gallese et al., 1996; Rizzolatti et al., 1996; de Waal and Preston, 2017; but see Rizzolatti and Caruana, 2017). These neurons engage both when seeing an action and when performing that action oneself, and recent suggestions propose a similar mechanism for perceiving and feeling an emotion as well (e.g. Carr et al., 2003). Yet, to date there is no overall consensus on mirror neuron function and a potential role in understanding emotions or empathy (Decety, 2010; Baird et al., 2011), and disagreement exists about whether mirror neuron activation only reflects, in the sense of correlation, or indeed suggests understanding of an action (e.g. Molenberghs et al., 2009; Hickok, 2009). Consequently, whether mirror neurons are causally related to our empathic responses remains a matter of debate (see Lamm and Majdandžić, 2015, for review; Bekkali et al., 2019).

With the PAM at its foundation, the Russian doll model comprises different evolutionary layers of empathy, which contain gradually more complex concepts that are built upon each other and which are functionally connected with each surrounding layer (see Fig. 1). At the basic layer and its perception-action mechanism are the resulting phenomena of emotional contagion and motor mimicry. These concepts are the inner core that forms the foundation of all other, higher-placed concepts. From that base onwards, the sequential and vertically aligned layers are related to increasing development of cognitive complexity, emotional regulation, and self-other distinction. The latter plays an important role in differentiating the basic layers from the upper layers, often referred to as self- versus other-oriented concern (de Waal, 2008). The remaining surrounding layers represent other empathic phenomena such as sympathetic concern and consolation, and perspective taking and targeted helping. In the Russian doll model, empathy is considered an umbrella term for all the phenomena and is defined as the "emotional and mental sensitivity to another's state, from being affected by and sharing in this state to assessing the reasons for it and adopting the other's point of view" (de Waal and Preston, 2017, p. 1).

The doll model has greatly motivated the investigation of animal empathy and inspired many scholars to embrace the notion of animals experiencing (self- and other-focused) emotions. Yet, its proposed structure inherently generates some limitations, which we believe deserve attention when using the model as a theoretical framework of animal empathy. The main restriction concerns the linear composition, which proposes a contingency between the model's layers (and thus, its phenomena). By claiming linearity and contingency, the model assumes that certain phenomena serve as prerequisite for other concepts (Hollis and Nowbahari, 2013; Yamamoto, 2017). This contradicts several findings in the literature, such as, e.g., evidence for helping without (evidence of) perspective taking (in tufted capuchin monkeys, *Cebus apella*, as discussed in Yamamoto, 2017; in laboratory rats, *Rattus norvegicus*, Bartal et al., 2011; in ants, *Cataglyphis cursor*, Hollis and Nowbahari, 2013), or perspective taking without helping (e.g. in chimpanzees, *Pan troglodytes*, Yamamoto et al., 2009; see Yamamoto, 2017, for a discussion on the difference between helping through cues versus pro-active helping).

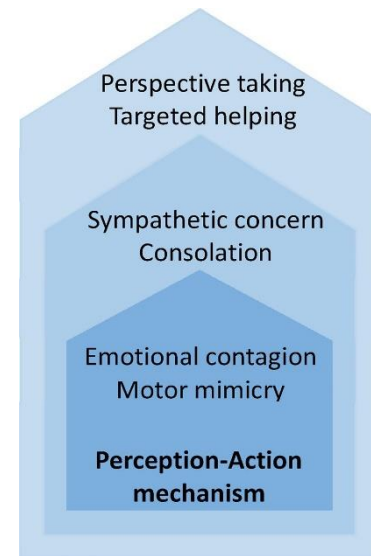


Fig. 1. Russian doll model of empathy.

At the doll model's foundation is the perception-action mechanism, which leads to a similar emotional state in observer and target. From this mechanism result the two concepts motor mimicry and emotional contagion. The next concepts sympathetic concern and consolation are built further upon this core, and so are perspective taking and targeted helping. (Adapted by permission from Springer Nature Customer Service Centre GmbH: Springer Nature, *Nature Reviews Neuroscience, Mammalian empathy: Behavioural manifestations and neural basis*, de Waal and Preston, Copyright 2017).

In addition, the assumption of linearity also implies a dependency between the inner and the outer cores – therefore assuming that consolation, perspective taking, and helping, must contain elements of emotion sharing (at least in the context of an empathy based framework) (de Waal, 2008). Emotional contagion, for instance, is regularly labelled as a basic building block of empathy (e.g. Palagi et al., 2015). Yet, emotional contagion is often not empirically confirmed or even assessed when studying 'higher up' concepts such as consolation or targeted helping (see Chapter 3, for more detailed discussion). Moreover, rigorous empirical evidence for emotional contagion is still lacking in a great number of species (Edgar et al., 2012, for review, and see Chapter 2), which is in contrast to some scholars arguing otherwise (e.g. Sümeği et al., 2014; de Waal and Preston, 2017).

Though the Russian doll model has received acclaim for its elegant simplicity (e.g. Sivaselvachandran et al., 2018), this simplicity may not sufficiently reflect empathy's complexity (Hollis and Nowbahari, 2013; Yamamoto, 2017). Its broad approach in which every concept flows into the other and in which any higher up concepts encompass all the lower ones, may furthermore hinder an exhaustive grasping of each individual concept (Coplan, 2011). We argue that all phenomena related to empathy are equally relevant for our understanding of animal empathy. By systematically disentangling each of them, their definition (s), underlying mechanism(s), and potential interactions with other concepts, we hope to reduce confusion and facilitate the interpretation and comparison of results (see also Cuff et al., 2016; but see also de Waal and Preston, 2017, for an argument against such a "dissected" approach as, "There exists a tendency to treat each aspect separately and dwell on the distinctions, but in doing so we lose sight of the functionally integrated whole", p. 1). A similar argument has also been made in the human empathy field, such as that confusion may be reduced by acknowledging empathy's complexity, and that "The best one can do is recognize the different phenomena, make clear the labelling scheme one is adopting, and use that scheme consistently" (Batson, 2009, p. 8).

As an alternative to the Russian doll model, Yamamoto suggested a combination model of empathy (2017) which allows for the study of the

independent emergence of each phenomenon, as well as its interactions (see Fig. 2). In particular, the combination model consists of three organizing factors of empathy: matching with others (e.g. emotional contagion), understanding of others (e.g. perspective taking), and prosociality (e.g. food sharing). The three factors, also labelled components or mechanisms of empathy (Yamamoto, 2017), can exist independently on their own, or with potential combinations between them. Unlike the Russian doll model, they do not require a sequential dependence on each other. For example, the combination model suggests that phenomena under 'prosociality' do not necessarily require an emotional matching. In addition, the concepts in the combination model are not linked to an increase in cognitive complexity (with the exception of the centre concepts, see Chapter 3.2.3.). This decoupling may motivate researchers to investigate a concept in a given species due to the concept being relevant for the species' ecology, rather than due to a general idea of more or less cognitive capacity (Hollis and Nowbahari, 2013). Overall, the combination model allows to focus on each phenomenon, how it (mechanistically) works, why it is (functionally) relevant to the studied species, and how it interacts with other phenomena (Coplan, 2011). By focusing on the phenomena first in an independent fashion, research might resolve ambiguous conceptual and empirical boundaries.

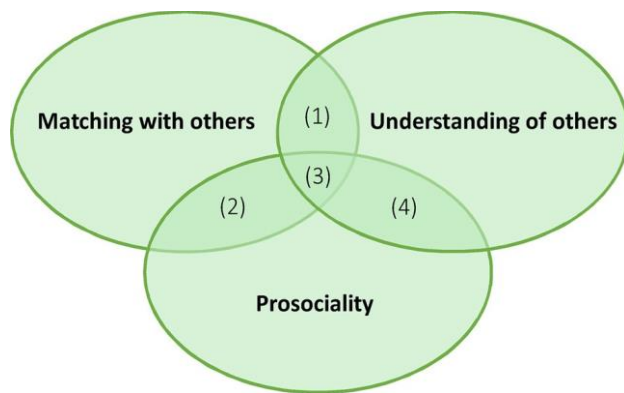


Fig. 2. Combination model of empathy

The combination model is divided into three organizing factors of empathy, namely Matching with others, Understanding of others, and Prosociality. Each factor contains a set of phenomena. Matching with others includes synchrony, mimicry, emotional contagion; Understanding of others includes perspective taking, Machiavellian intelligence, Schadenfreude; Prosociality includes food sharing, prosocial choice. The combination section (1) includes Cognitive contagion, Envy or disadvantageous inequity aversion; (2) includes Pre-concern, Chameleon effect, Collaboration; (3) includes Sympathy or consolation, Calculated reciprocity, Advantageous inequity aversion; (4) includes Targeted helping. (Adapted by permission from John Wiley and Sons: *Wiley Interdisciplinary Reviews: Cognitive Science, Primate empathy: three factors and their combinations for empathy-related phenomena*, Yamamoto, Copyright 2017).

This initial review of the use of the term empathy and of two prominent, yet, rather distinct models of animal empathy make us propose that as long as there is disagreement on what empathy "really" is, the field should probably refrain from using observations of related concepts as evidence for empathy (e.g. Batson, 2009). Interestingly, the challenges outlined for the comparative investigation of empathy resemble those faced for other complex cognitive abilities, such as the evolution of language. Instead of favouring a specific factor of language (e.g. speech), and consequently a devaluation of the other components (e.g. syntax), Fitch (2017) advocates for acknowledging the complexity of language and its multi-componential nature in order to progress comparative research. Similarly, the combination model (Yamamoto, 2017) argues for a multi-component approach to recognize empathy's complexity. As such, despite the confusing terminological and empirical history of animal (and human) empathy, many researchers will agree that empathy is a complex construct composed of a multiplicity of distinct concepts, overlapping components and different mechanisms within these. We are convinced that this

complexity needs to be acknowledged more systematically, both in theoretical and empirical work.

In conclusion of this first section of our review, we would like to emphasize that a human driven definition of empathy has a set of strict (yet, debated) requirements for a behaviour to be considered empathy. Therefore, comparing animal research against this human reference may inhibit the progress of animal empathy research. In addition, the established Russian doll model of empathy (Preston and de Waal, 2002) may, due to its linear structure, confine the complex nature of empathy. For this reason, the combination model has been proposed as alternative (Yamamoto, 2017), which prompts to investigate the distinct empathy-related phenomena independently. In our discussion of the three phenomena emotional contagion, consolation, and targeted helping, we now review the feasibility of the two frameworks, and how they guide the interpretation of empirical evidence.

2. Emotional contagion

2.1. Definitions and terminology

In the human literature, emotional contagion was originally defined by Hatfield et al. (1994) as "The tendency to automatically mimic and synchronize facial expressions, vocalizations, postures, and movements with those of another person's and, consequently, to converge emotionally" (pp. 153–154). Together with the PAM (see Chapter 1.2.), human research has proposed mimicry as a potential mechanism for emotional contagion (Hatfield et al., 1994). This hypothesis suggests that upon mimicking another's facial expression or body posture, the mimicker receives emotional feedback from those expressions, consequently leading to a convergence with the other's emotional state. Yet, current evidence in human research does not fully support the mimicry hypothesis (see e.g. Hess and Blairy, 2001, and see Chapter 2.2.1. below), and which other mechanisms underlie emotional contagion is still undetermined (an overview of the different proposed mechanisms is outside the scope of this review but see e.g. Deng and Hu, 2018; IsernMas and Gomila, 2019, for an extensive discussion of the mimicry hypothesis). Earlier work on animal behaviour may have hinted at emotional contagion between animals, although without necessarily labelling it so (e.g. rats refrain from pressing a lever to avoid conspecifics receiving an electric shock, Church, 1959; rats relieve a suspending rat in the air, Rice and Gainer, 1962; rhesus monkeys avoid pulling a chain which delivers an electric shock to their conspecific, Masserman et al., 1964; rats alarm the rest of their colony by means of "Stimmungsübertragung" (translated as "mood transmission"), Lorenz, 1966). The term 'emotional contagion' was eventually brought into the animal research limelight by de Waal's pioneering work on animal empathy (e.g. 2002; 2008; see Chapter 1.2. and Fig. 1 in our paper). He defines emotional contagion as "an emotional state-matching of a subject with an object" (2008, p. 282; see also Table 1). Importantly, emotional contagion does not differentiate between the emotional state of the self and the other, as the subject takes on the other's emotional state as if it were its own state. In addition, the concept does not require or address whether, or how, this relates to concern for the other (Singer and Lamm, 2009). We now review two key issues that we believe require more consideration in current emotional contagion research, and make suggestions for future investigations.

2.2. Measuring emotional contagion

2.2.1. Mimicry does not equal emotional contagion

In its original definition by Hatfield et al. (1994), mimicry is incorporated in the definition of emotional contagion, with the suggestion that mimicry mechanistically underpins emotional contagion. The mimicry hypothesis as underlying driver has been embraced by many in both the human and animal research world (e.g. Preston and de Waal, 2002; McIntosh, 2006; Palagi et al., 2015). Yet, the first arising problem is that the exact relation between mimicry and emotional contagion remains a matter of debate (Isern-Mas and Gomila,

2019). In the human literature there is an ongoing examination of this relation and its potential causal direction (Hess and Fischer, 2014; Prochazkova and Kret, 2017), showing that research on this topic often involves other concepts such as emotion recognition (Olszanowski et al., 2019), and until recently the majority of human studies failed to demonstrate a direct and strict link between mimicking facial expressions and experiencing those feelings subsequently (e.g. Hess and Blairy, 2001; Van Der Schalk et al., 2011; but see Olszanowski et al., 2019, for recent evidence of mimicry as potential mediator). Moreover, though they often occur simultaneously, emotional contagion has been shown to occur without co-occurrence of mimicry (e.g., Isern-Mas and Gomila, 2019), and mimicry (e.g. body posture) may occur as a means to, for example, establish affiliative bonds, without the immediate need for, or consequence of, emotional contagion (Chartrand and Bargh, 1999; Lakin and Chartrand, 2003a; though note that it seems plausible that affiliative bonding, due to mimicry, may be enhanced through an affective mechanism such as emotional contagion (Lakin et al., 2003b)). Due to the question of their putative connection, some scholars have argued for the theoretical and empirical separation of emotional contagion and mimicry (Hess and Fischer, 2014; Nakahashi and Ohtsuki, 2015). In this context, it seems important to note that conceptually, mimicry and emotional contagion have indeed been regarded as distinct terms by many scholars (see also Table 1). Emotional contagion, on the one hand, is the copying of another's emotional state (Nakahashi and Ohtsuki, 2015) or, put in human-oriented terms, "the matching of a subjective emotional experience" (Hess and Fischer, 2014, p. 47). Mimicry, on the other hand, is the copying of another's appearance and motor display, such as facial expressions (Nakahashi and Ohtsuki, 2015), and mostly concerns "the matching of nonverbal displays" (Hess and Fischer, 2014, p. 47) without necessarily implying emotion matching.

This conceptual difference and the debated validation of the mimicry hypothesis are relevant to our review, as they highlight the second problem, namely, that emotional contagion in animals is often inferred from the presence of mimicry. In other words, the (putative, though not sufficiently confirmed) mechanism of a phenomenon is taken as evidence for the phenomenon itself. Moreover, emotional contagion necessarily includes an emotional experience, which is not included in the definition of mimicry. Consequently, for some phenomenon to be labelled as emotional contagion, one needs to provide evidence for an emotional response (Isern-Mas and Gomila, 2019; but see Lahvis, 2016, who argues for a behavioural basis), rather than providing evidence for one putative mechanism leading to, or is correlated with, such a response. Yet, a large part of the published work on emotional contagion in animals shows a blurring of the two concepts, which is why the observation of overt mimicry is often interpreted as evidence for the presence of emotional contagion. For instance, studies on rapid facial mimicry during play (e.g. in orangutans, Pongo pygmaeus, Davila-Ross et al., 2007; in dogs, Palagi et al., 2015; in meerkats, *Suricata suricatta*, Palagi et al., 2019a, 2019b), or contagious yawning (e.g. in dogs, Joly-Mascheroni et al., 2008, but see e.g. Harr et al., 2009, for no evidence of contagious yawning in dogs) have argued to provide evidence for emotional contagion. Nonetheless, as also discussed in human research (e.g. Hess and Fischer, 2014), the presence of congruent motor action does not automatically imply congruent emotional states (e.g. O'Hara and Reeve, 2011, who show no evidence of a connection between emotional contagion and contagious yawning in dogs), and congruent emotional states have been observed without congruent motor action (e.g. in dogs, who show a matching of distress with their owners, Sümegi et al., 2014; in ravens, *Corvus corax*, who show affect matching with a conspecific, Adriaense et al., 2019a). Regarding facial expressions, it is important to point out the variation in intentionality of facial expression production, and its interaction with context and affect. Human facial expressions and mimicry may be under more volitional control than expressions demonstrated by animals. For instance, it is assumed that playface in animals occurs as a spontaneous expression and for that reason its relation to underlying affect may be more reliable. Although in the mentioned human research participants were not explicitly asked to mimic facial expressions, and the research goal was masked by a cover story (e.g. Hess and Blairy, 2001), the

notion of intentional production of facial mimicry remains an important concept to consider when comparing human and animal research literature.

Based on our discussion of the distinction between mimicry and emotional contagion, we cannot conclude with confidence that all animals that exhibit some form of mimicry are also susceptible to emotional contagion, and even less so that their mimicry responses are evidence for emotional contagion. However, we find little mention of this distinction in the animal research literature (but see e.g. Edgar and Nicol, 2018; Nakahashi and Ohtsuki, 2015; and Isern-Mas and Gomila, 2019). Therefore, in the next chapters, we attend to yawn and play contagion in more detail. In regards to the theoretical frameworks, emotional contagion in the Russian doll model (Preston and de Waal, 2002) assumes to be tightly linked to motor mimicry. In contrast, in the combination model (Yamamoto, 2017), this link is not necessarily a prerequisite for either concept. According to our discussion of the mimicry hypothesis of emotional contagion, it seems commendable for future research to carefully interpret collected empirical data in light of both models, and to compare them accordingly.

2.2.1.1. Yawn contagion. Contagious yawning has been taken as indicative of empathy, or at the very least as evidence for emotional contagion (e.g. Palagi et al., 2014a, 2014b; Norscia and Palagi, 2011; Clay et al., 2018). In a broad sense, yawn contagion is considered as a form of mimicry (Yoon and Tennie, 2010; see Table 1 for definitions of mimicry and behavioural contagion). Therefore, the notion of linking yawn contagion to emotional contagion partially developed from the rationale that mimicry is, to some degree, linked to emotional contagion (see Chapter 2.2.1). Yet, as discussed, the (causal) relation between mimicry and emotional contagion remains debated. Hence, this limitation also extends to the domain of yawn contagion, and the conclusion of yawn contagion as an indicator of emotional contagion, or empathy (broadly defined), seems premature on several accounts (see also Massen and Gallup, 2017, for a review). First, the connection between yawn contagion and empathy is often based on observations of a familiarity bias (i.e. increased response toward familiar vs. unfamiliar conspecifics). Though this bias indeed exists in humans (Palagi et al., 2014a), as well as for example in primates (Campbell and de Waal, 2011; Demuru and Palagi, 2012) and in dogs (Silva et al., 2012), this bias could be caused by increased attention to familiar individuals, rather than by a higher propensity to mimic their behaviour (e.g. Yoon and Tennie, 2010; see for further discussion on familiarity bias Chapter 3.2.1.). Second, developmental research in humans is not congruent with a simple, mechanistic connection between emotional contagion and yawn contagion. For instance, infants are susceptible to surrounding emotions from the moment they are born, and self-regulatory skills start to control the contagion during the first year of life (Hay et al., 1981; Hatfield et al., 1994; Davidov et al., 2013). If yawn contagion were linked to the root mechanism of near-automatic mimicry of movements and emotions, it should also appear very early in development and show a decline in frequency and/or susceptibility to the yawn stimulus as self-regulation of emotional states improves. However, children begin to show contagious yawning only at the age of four to five years, after the stages of unregulated mimicry and emotional contagion have passed, and during the development of more cognitively oriented processes of empathy (Millen and Anderson, 2010; note that the parallel development does not necessarily imply an explicit connection, Massen and Gallup, 2017). Third, emotional contagion necessarily includes an emotional experience, which is questionable in regards of yawning. It remains unclear which emotional state would be present, and transferred, during yawn contagion, and the literature does not present a consistent hypothesis on such a state (Massen and Gallup, 2017). For example, researchers have suggested that yawning is a sign of boredom (Lehmann, 1979; Toohey, 2011, as discussed in Burn, 2017) and thus, following this statement, yawn contagion should reflect the transfer of boredom. To test this hypothesis, (behavioural and physiological) parameters should be assessed, such as disrupted sleep and abnormal behaviour, and then combined to establish a potential boredom state (see Burn, 2017, for a review on boredom). To our knowledge, these particular parameters have not been reported in the literature, and for this reason, the collection of (long-term) behavioural data of other expressions together with observations of yawn

contagion could be interesting to further investigate the boredom hypothesis. Others have claimed a connection between contagious yawning and (mild) stress. For instance, when stump-tailed macaques (*Macaca arctoides*) observe conspecifics yawning, the subjects demonstrate contagious yawning and self-scratching (which is often observed in a stress context) (Paukner and Anderson, 2005). Several studies in dogs have aimed at testing the stress hypothesis, but their results are ambiguous. In one study, dogs who performed contagious yawning had no increase in heart rate (Romero et al., 2013), but another study showed that dogs who yawn in response to human yawns have elevated cortisol levels (though only on the individual level of 12 out of 60 subjects) (Buttner and Strasser, 2014). Interestingly, a recent study did not find contagious yawning in dogs, but did demonstrate that oxytocin administration decreases yawning (Kiss et al., 2019). Based on the hypothesis of oxytocin having a stress relieving effect, the authors propose that contagious yawning is a social stress response and suggest that there is no relation with an empathy related concept. Similarly, in lowland gorillas (*Gorilla gorilla gorilla*), researchers found no observations of yawn contagion but did report an increase in self-directed behaviour, which in turn may be stress related (Palagi et al., 2019a, 2019b). In contrast to hypotheses of negative states, some argue that yawning might relate to a relaxed state, or at least might serve to signal the absence of danger, which is assumed to reduce tension in a group (e.g. in the South African ostrich, *Struthio camelus australis*, Sauer and Sauer, 1967). A relaxed state is defined as a positive state (Mendl et al., 2010), and, thus, researchers should aim at assessing additional, positive related parameters to test this hypothesis. Finally, contrary to claims of emotional contagion, others have suggested that yawn contagion may be arousal related (e.g. contagious yawning and stretching in budgerigars, Miller et al., 2012), and some scholars argue that yawn contagion (merely) reflects an example of behavioural contagion (Yoon and Tennie, 2010; see Table 1). In the latter case, yawning and its contagious expression are an indicator of a neutral state and, therefore, contagious yawning might not reflect any emotional state (see also Guggisberg et al., 2010; Massen and Gallup, 2017; for extensive reviews of contagious yawning).

In conclusion, at present, yawn contagion does not provide clear and convincing evidence of emotional contagion, and even less so of empathy, irrespective of its specific definition. We argue that to further validate claims such as “yawn contagion is a form of emotional contagion” (Palagi et al., 2014a, 2014b, p. 2), research should continue to focus on assessing additional parameters and emotional states during events of yawn contagion, systematically record the social context in which contagion occurs, and add observations of long-term behavioural data. If yawn contagion is indeed related to the transfer of either a negative or positive state, then it is important to measure negative or positive related parameters, respectively, such as avoidance or approach behaviour, and physiological changes. In addition, it remains important to specify which empathic phenomena could be related to, or facilitated by, contagious yawning. Recent research in humans shows that subjects who score higher on an implicit test of empathy (i.e. the Interpersonal Reactivity Index) also demonstrate higher frequency of contagious yawning (Franzen et al., 2018). This is an interesting addition to the current literature, still, in light of our previous discussion on empathy defined from a human perspective (Chapter 1), and in order to benefit comparative research, studies should aim to disentangle the different empathy-related phenomena in the study of yawn contagion.

2.2.1.2. Play contagion. Play behaviour has been observed in a large range of species (Burghardt, 1998) and there is ample evidence of play behaviour having both short- and long-term beneficial consequences for motor, brain, and behavioural development (see Held and Špinková, 2011, for an extensive review). For that reason, play has been proposed to facilitate group life by reducing aggression and increasing social harmony (see e.g. Sharpe and Cherry, 2003). Still, this hypothesis remains unconfirmed and research shows contrasting results. For instance, social play in meerkats does not reduce aggressive interactions (Sharpe and Cherry, 2003) or improve social cohesion (Sharpe, 2005), though, it does improve social cohesion in dogs (Sommerville et al.,

2017), and improves future social bonding in juvenile macaques (*Macaca fuscata*, Shimada and Sueur, 2018). Under the assumption that play has positive effects on social relations, researchers have proposed a connection between the spread of play (i.e. play contagion), and the presence of positive emotional contagion. Upon seeing a conspecific perform object play (e.g. in common ravens, Osvath and Sima, 2014), and upon hearing a playback of a conspecific’s play-call (e.g. in kea, *Nestor notabilis*, Schwing et al., 2017), the respective observing animals began performing play behaviour themselves (see also Briefer, 2018, for a review of vocal contagion, including laughter contagion). In both studies, the authors suggest this to be evidence for positive emotional contagion. Yet, this conclusion seems insufficiently substantiated. In a similar vein as in our previous discussion of mimicry, it is important to consider that the occurrence of similar behaviours between animals does not necessarily allow researchers to infer the presence of the same (or any) contagiously transferred emotional state (Briefer, 2018). For this inference, researchers would need to show whether observed play behaviour remains on the level of (motor) mimicry, or whether it is also accompanied by a matching affective state. Furthermore, if emotional responding does occur, the question remains which emotion that would be, and whether play always and indisputably carries a matching (presumably positive) state. If it is assumed that play behaviour correlates with a positively valenced state, studies should expect to find a variety of positive behavioural expressions (Briefer, 2018) – but such indicators were not reported in either study (Osvath and Sima, 2014; Schwing et al., 2017). In fact, a recent review shows that a direct scientific investigation of the relationship between positive affect and play is still missing (Ahloy-Dallaire et al., 2018).

Additionally, a review on the function of play (in dogs) shows that social play appears in a range of different positive and negative contexts, that play is modulated by different factors such as early-life experience and the context of interaction, and that play may serve different functions such as motor skill development and social cohesion (see Sommerville et al., 2017, for a review of different theories). However, the beneficial outcome of play, such as social cohesion, does not necessarily imply that play itself is positive in the moment it occurs. Research shows that adult male chimpanzees use social play as a means to reduce social tension in all-male groups, which confirms the positive outcome of play (Yamanashi et al., 2018). Yet, play bouts tend to be increased before feeding (which is often perceived as stress inducing due to the anticipation of food, see also Palagi et al., 2009, for bonobo play before feeding), and though social grooming (which is known to reduce anxiety, see e.g. Russell and Phelps, 2013) correlates negatively with aggressive encounters, play behaviour shows no correlation with aggression. Moreover, social grooming and social play are negatively correlated in these chimpanzee groups. This conclusion does not diminish the positive outcome of play on social group life, yet, it does put the interpretation of play as a global indicator of positive emotional state, or positive contagion, into question.

Taken all these factors into account, it seems more plausible that the emotional state during play and the social consequences of play depend greatly on the species and their social system, and the individual’s own experiences and contexts during which play occurs. Therefore, implying that contagious play is related to experiencing a positive emotional state, and thus interpreting social play as an indicator of positive emotional contagion, seems not warranted at present (which contrasts to what is often assumed, e.g. Palagi et al., 2019a, 2019b). Unquestionably, the empirical demonstration of emotions in animals is challenging in general. Such demonstration requires a focus on both the arousal and valence component of an emotional state (see below), and the observation of synchronised changes in behaviour, physiology, and cognition (i.e. the multi-component nature of an emotion, see Chapter 2.2.2., and Paul et al., 2020). We are positive about play contagion as a valuable approach to investigate emotional contagion in animals, under the condition that its empirical investigation is approached from an emotional, and thus multi-componential, perspective. Considering the beneficial outcomes of play and the large body of research in an extensive range of species, we encourage researchers to continue using play as a model to test novel paradigms of assessing (positive) emotions and, subsequently, emotional contagion.

2.2.2. The importance of valence and arousal

Overall, human and animal emotion researchers agree that emotions are multi-componential, in which changes in behavioural, physiological, and cognitive components occur in a coordinated manner (see for reviews Mendl et al., 2010; Paul et al., 2005 on the relevance of measuring cognitive components; see Anderson and Adolphs, 2014, for a discussion on the multi-componential nature of emotions; and see Fig. 3). An additional component in humans is the subjective (conscious) feeling, which is currently considered unmeasurable in animals. Nevertheless, some scholars argue this should not restrict research on animal emotions (see for a discussion e.g. LeDoux, 1996; Berridge, 2018; Rolls, 2013; Mendl et al., 2010; de Waal, 2010). Thus, the multicomponent model allows for a systematic study of the coordinated changes of each of the (measurable) components, which further permits to study animal emotions comparatively. Additionally, these components can be classified according to two dimensions of an emotional experience, namely valence (positive or negative) and arousal (low or high intensity) (commonly referred to as ‘core affect’ in human psychology, see e.g. Russell, 2003; Barrett et al., 2007).

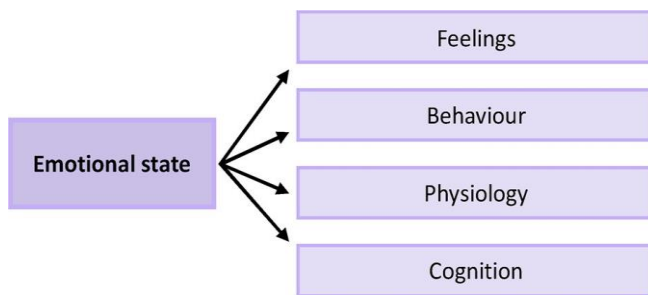


Fig. 3. Multi-component model of an emotion

Changes in emotional states can be observed through changes in feelings (i.e. subjective experience), behaviour, physiology, and cognition. Importantly, these changes in different components occur in a coordinated or parallel manner. Depending on the scholar the direction of causality between emotional state and components differs (see Anderson and Adolphs, 2014, for a discussion) (Adapted from Cell, 157, Anderson and Adolphs, A framework for studying emotions across phylogeny, 187-200, Copyright (2014), with permission from Elsevier)

Generally, notable contributions have been made to study social emotions through their different components, with the majority of empathy research being done on rodent models (e.g. see Panksepp, 1991, 2004). Regarding the behavioural component, studies on pain contagion show social modulation of pain expression in mice (*Mus musculus*, Langford et al., 2006; a full review on rodent empathy is outside the scope of this review, thus see for extensive reviews e.g. Keum and Shin, 2016; Sivaselvachandran et al., 2018; Meyza et al., 2017). In the same behavioural domain, but on fear contagion, naïve pigs (*Sus scrofa*) that are put together with experienced pigs, after the latter underwent negative treatment (i.e. restraint and isolation), show (negative related) behavioural changes 2 days and 18 days after placement with the experienced animals. Likewise, after observing demonstrator pigs coming from positive situations (i.e. enriched environment and food rewards), naïve pigs show positive behavioural parameters, again 2 and 18 days after observation, hinting at emotional contagion (Reimert et al., 2017). Some authors argue that, rather than observing emotional contagion, the exhibited behaviour reflects social learning that is potentially facilitated by emotional contagion. After being placed together with conspecifics coming from a fearful environment, naïve observer rats show an increase in exploratory behaviour and acoustic startle response, which the authors label as emotional arousal (Knapaska et al., 2010; Meyza and Knapaska, 2018). Also in capuchin monkeys (Morimoto and Fujita, 2011) observers display social learning potentially mediated by an affective mechanism. Naïve

observers will reach more and longer for an object when a demonstrator previously displayed positive facial expressions toward the object, and observers will reach less and slower for the object when the demonstrator exhibited negative expressions (see also Dukes and Clément, 2019, for social affective learning in humans). Additionally, others have suggested that a form of visual (emotional) contagion may occur in bystanders of an interaction. While observing grooming in conspecifics, Barbary macaques (*Macaca sylvanus*) show reduced anxiety themselves, are more likely to groom afterwards, and show increased affiliative behaviours toward others (Berthier and Semple, 2018).

These behaviour-focused approaches greatly contribute to information on arousal, but some argue that they are less indicative of the valence of an emotion (see for reviews Paul et al., 2005; Mendl et al., 2009; Briefer, 2018). Changes in arousal indicate increased alertness or attention and prepare the animal for action, yet, such changes are not necessarily accompanied by a valenced, whether positive or negative, response (Edgar and Nicol, 2018). Although we agree that some behaviours, e.g. aggression, are likely to be consistently associated with negative valence, other behaviours are not as straightforward in their interpretation (e.g. stress grooming vs. comfort grooming, play fight vs. real fight). Even the assumption that seemingly straightforward behaviours such as aggression are correlated with either a positively or negatively valenced state may be limited (Paul et al., 2005; Edgar and Nicol, 2018). We greatly depend on the context surrounding the behaviour to determine its positive or negative emotional character, which consequently restricts our interpretation of the observable behaviour and its underlying emotion (Huber et al., 2017; Paul et al., 2005; Mendl et al., 2009).

Accordingly, the methodological struggle to measure animal emotions carries over to the measure of animal emotional contagion. When we define emotional contagion as emotional state-matching this demands the empirical demonstration of (a) an emotional state in the agent, and (b) a matching emotional state in the observer. As mentioned, one of the biggest challenges in assessing an emotional state is its valence dimension (e.g. Mendl et al., 2009, 2010). This is an essential point relevant to emotional contagion research as studies often confound differences in arousal, measured by variations in physiology or attention, with differences in valence. This calls for more caution in the assignment of the presence of emotional contagion (Huber et al., 2017), and consequently its interpretation as an indicator of the presence of empathy (at least, in the view of the Russian doll model, Preston and de Waal, 2002).

2.2.2.1. Variations in physiology. An early study on primate thermography demonstrates that chimpanzees who watch a conspecific being injected with a needle, or watch scenes of only the needle itself, show a decrease in skin temperature (but not when watching conspecifics in general agonism) (Parr, 2001). Importantly, according to the authors this reflects a personal arousal rather than emotional contagion, which is supported by the chimpanzees' aversive reactions during personal experiences with needles during veterinary visits. The development of wireless infrared thermography (Speakman and Ward, 1998) has allowed researchers to non-invasively measure body temperature in experimental settings without the need for restraint (Ioannou et al., 2015), and in natural environments where the use of electronic equipment is usually more limited. For instance, captive chimpanzees show a decrease in nasal temperature upon hearing and seeing conspecifics fighting (Kano et al., 2016), and in a natural context, chimpanzees show a decrease in nasal temperature and an increase in ear temperature upon hearing conspecific's aversive vocalisations (Dezecache et al., 2017). These temperature changes and their assumed link to positive or negative states are supported by thermography studies on emotional states without social context. For instance, studies tend to show an overall relation between negative emotional states and a decrease in nasal temperature (e.g. in humans, Ioannou et al., 2013; in rhesus monkeys, *Macaca mulatta*, Nakayama et al., 2005; in pigs, Boileau et al., 2019), though studies on positive states are less consistent (see Chotard et al., 2018, for an overview). Yet, there are also several discrepancies in the empirical data on facial temperature, which may be due to intricate facial area differences or different experimental stimuli used (Chotard et al., 2018). For example, a recent

study of three monkey species (Common marmosets, *Callithrix jacchus*, white-throated capuchins, *Cebus capucinus*, and rhesus macaques, *Macaca mulatta*) and two ape species (Bornean gibbons, *Hylobates muelleri*, and western lowland gorillas) showed temperature differences between negative and positive conditions, with specific fluctuations for different facial areas (Chotard et al., 2018). These fluctuations include for example a distinction between the nose bridge and the nose tip, due to a poorer or richer blood supply in these regions, respectively. The study shows that (induction of) negative states correlate with increased upper lip temperature, while (induction of) positive states correlate with a decrease in nose tip temperature and an increase in peri-orbital temperature. Still, the positive condition included two distinct behavioural contexts such as playing with a toy (all subjects except for gorillas) and being tickled (gorillas only). Upon removing the gorillas from the dataset, no thermal changes were found for the positive condition. This difference in thermal results highlights the importance of systematic research in the investigation of facial thermal imaging. Under this condition, the use of thermography to assess an emotional state, including establishing a state matching, may provide to be a useful approach.

With regard to other physiological modalities, greylag geese (*Anser anser*) show an increase in heart rate upon seeing conspecifics in agonistic conflict (Wascher et al., 2008), but, for example, pigs show no difference in heart rate when watching their conspecifics being restrained (though, other markers show decreased locomotion, increased freezing, and increased attention) (Goumon and Špinko, 2016). While these reactions (e.g. decreased nasal temperature or increased heart rate) are consistent, in principle, with responding emotionally to a conspecific's emotional state, they may also stem from aversive reactions to the context itself: Seeing or hearing a conflict (e.g. Kano et al., 2016; Dezecache et al., 2017; Wascher et al., 2008), in a similar fashion to seeing a needle (Parr, 2001), may be associated with personal, negative memories. For this reason, rather than emotional contagion, contextual cues may have caused a negative emotional state (i.e. personal distress, see Table 1). For instance, a recent study in chimpanzees showed that upon watching a human experimenter with a (prosthetic) wound and (fake) blood, but without the experimenter behaviourally expressing pain, nasal temperature decreased (Sato et al., 2015). The authors suggest that chimpanzees may become (physiologically, rather than emotionally) aroused by the mere sight of injuries without the need for behavioural cues, which therefore excludes the notion of emotional contagion in this particular study. Consequently, this calls for caution when designing emotional contagion studies. We propose that the source or context of emotion induction in the demonstrating animal should be hidden from the observing animal, so that emotional contagion is based (only) on the expressions of the demonstrator, rather than the context (see also the description of "catching" of Concept 3 in Box 1).

Other studies show physiological state matching measured through hormone levels. Female zebra finches (*Taeniopygia guttata*) respond with increased levels of corticosterone (and vocal responses) upon hearing their mates' distress calls (Perez et al., 2015), and prairie voles (*Microtus ochrogaster*) show a matching of increased corticosterone levels (including anxiety- and fear-related behaviour) upon seeing their distressed mate (Burkett et al., 2016). Naïve zebrafish (*Danio rerio*) show a matching increase in cortisol levels as well, including vicarious antipredator behaviour, upon observing their conspecifics displaying that same behaviour (Oliveira et al., 2017; and see da Silva et al., 2019 for familiarity effect). Notably, physiology-focused approaches contribute to a better understanding of emotional state-matching in animals. Yet, following the two emotional dimensions of valence and arousal, changes in physiology are not necessarily a sign of the presence of, or changes in, valence (see also the description of "physiological matching" of Concept 3 in Box 1). Accordingly, combining multiple components (e.g. Burkett et al., 2016; Oliveira et al., 2017) facilitates the interpretation of observed physiological changes. For example, upon seeing their chicks in distress, mother hens showed a range of physiological and behavioural changes including a decreased eye temperature, increased heart rate, decreased preening, increased attention, and maternal vocalizations (Edgar et al., 2011). The combination of multiple modalities is an

essential aspect of this study and, in addition, the composition of these changes occurred specifically to the distress intervention (contrasted to three other experimental conditions). The latter helps to rule out a response to the context only (i.e. the source of distress was out of sight), or mere behavioural mimicry.

Undeniably, though a multi-componential approach may be preferred, a diverse methodological approach is not always logistically feasible in experimental research, and certainly even less so in an ecologically valid setting (Dezecache et al., 2017). Furthermore, even with the benefits of an experimental design and the opportunity for multiple methods, the authors state themselves that "it is not possible from this study to conclusively differentiate between a non-evaluative behavioural and physiological response (akin, for example, to 'interest' or 'heightened attention') and one that is accompanied by a valenced, emotional component (...)" (Edgar et al., 2011, p. 3133). We agree with this statement as far as that an additional verification of a valenced, emotional component is preferred in order to conclude the presence of an emotional state (see e.g. Chapter 2.2.2.3). Moreover, we commend this particular study in light of research on emotional contagion and other empathy-related phenomena in animals. The observation of a coordinated set of changes in different components underlies the definition of an emotional state (see the beginning of Chapter 2.2.2.). As such, the data collection of this study (Edgar et al., 2011) aids greatly to better understand emotional responses in animals.

2.2.2.2. Variations in attention. Parrots have been shown to be more active and attentive after hearing distress calls from conspecifics (versus a control sound of white noise), including a familiarity effect, although this effect is small and should be treated with caution (in cockatiels, *Nymphicus hollandicus*, Liévin-Bazin et al., 2018). Similar findings have been reported for dogs, who showed increased alert and stress behaviour after hearing distress vocalizations (in contrast to non-conspecific sounds, Quervel-Chaumette et al., 2016). As the authors critically note themselves (Quervel-Chaumette et al., 2016), one could argue that the found increase in activity and attention in dogs, and thus also in the parrot study, rather reflects a general increase in vigilance toward conspecifics' sounds, than an emotional response or a convergence of affective states. To tackle this limitation, another study implemented a broad set of experimental conditions and manipulations, which allowed the authors to exclude the alternative explanation of mere increased attention to conspecifics (Huber et al., 2017). After hearing isolation whines from conspecifics, dogs showed increased freezing and distress behaviours. The observation of behaviours associated with negative valence was interpreted as an emotional convergence between subjects, and the results certainly imply that the observing dogs had a particular reaction to the negative calls. Yet, the findings are not fully conclusive in terms of the valence component. Indeed, an alarm call may provoke intricate escape or freezing behaviour in an observing subject, without necessarily informing us on an accompanying emotional state (see for a discussion Pérez-Manrique and Gomila, 2018). Future work on dogs could however benefit from this paradigm and add physiological parameters, as well as employing live demonstrator dogs, to display and measure the full extent of the potential emotional states and their contagion (such as seen in chickens, in Edgar et al., 2011; or in laboratory mice in Gonzalez-Liencre et al., 2014).

Aside from (non-invasively) investigating changes in behaviour and physiology, additional methods for differentiating between valence and arousal include the use of functionally flexible events, behavioural lateralization, and facial expressions. Briefer (2018) suggests to use stimuli that are 'functionally flexible' to distinguish between different valences upon hearing conspecifics (Briefer, 2018, p. 7). For example, studies have shown that dogs may distinguish between different growl types (see e.g. Faragó et al., 2010a, 2010b; Molnár et al., 2009; Maros et al., 2008). In addition, a number of studies have investigated animal emotional lateralization, which suggests that cerebral lateralization (i.e. structural and functional hemispheric asymmetries, Bisazza et al., 1998) is linked to emotional processing in animals (see Bisazza et al., 1998 and Rogers, 2002 for a review of lateralization in animals). Within this field two main hypotheses are investigated, which postulate that the right hemisphere should be

dominant for processing negative events or withdrawal, while the left hemisphere should be dominant for processing positive events or approach (Leliveld et al., 2013). For instance, when watching scenes of unfamiliar conspecifics in an aggressive conflict, chimpanzees show an increase in temperature of the right tympanic membrane (i.e. inner ear) (Parr and Hopkins, 2000). Additionally, upon inspecting predators animals often show a left-eye preference, such as seen in common wall lizards (*Podarcis muralis*, Martin et al., 2010) and in domestic hens and chicks (Evans et al., 1993; Dharmaretnam and Rogers, 2005); and, upon approaching predators, several fish species show a right-eye and left-hemisphere dominance (Bisazza et al., 1998), which is also observed in Australian magpies (*Gymnorhina tibicen*, Koboroff et al., 2008) (see Leliveld et al., 2013, for a review of the different hypotheses and current evidence). Lastly, there is a long tradition of using facial expressions, either explicitly or implicitly measured, to assess the valence of emotional responses in humans (Fridlund and Cacioppo, 1986), including facial EMG (electromyography) (e.g. Lamm et al., 2008; Hofelich and Preston, 2012). Another (fairly recent) avenue to measure animal emotional state, and in particular its valence, is thus the study of animal facial expressions. Differences in facial expressions have been found to convey aggressive intent as well as emotion-related information in pigs (Camerlink et al., 2018), to relate to a positive treatment (i.e. manual tickling) in rats by showing ear posture and colour differences (Finlayson et al., 2016), and several animal equivalents of the human FACS (Facial Action Coding system, Ekman et al., 2002) have been developed to objectively measure facial movement (see e.g. for chimpanzees, ChimpFACS, Parr et al., 2007; for horses, EquiFACS, Wathan et al., 2015; for cats, CatFACS, Caeiro et al., 2017; for dogs, DogFACS, Waller et al., 2013). In accordance with the multi-component model of emotions, facial expression measurement can be used as an additional component to build a full picture of the internal state of an animal (see e.g. Descovich et al., 2017 for a review of the current empirical data of animal facial expressions). These three additional methods provide interesting approaches for the further exploration of valence discrimination in emotional contagion studies.

2.2.2.3. The cognitive bias approach and valence. An emotional state matching does not necessarily imply a matching of the same modality. For instance, freezing behaviour does not need to necessarily match with only (vicarious) freezing behaviour, but may be matched with other fear related components such as changes in physiology (e.g. heart rate), facial expression (e.g. ear posture), or potential lateralization (e.g. a left-eye inspection of the threatening stimulus). Moreover, observing an alignment of expressions across different components may be empirically preferred in some cases. The display of mobbing behaviour in which an observer matches the mobbing behaviour of a demonstrator does not allow us to disentangle behavioural contagion from emotional contagion (see Chapter 2.2.1.). In contrast, if the behavioural match is accompanied by changes in other components and an additional measurement of valence is applied, researchers will be able to draw stronger conclusions on potential emotional contagion. To this end, it is important to explore the different components of an emotional state in order to widen the scope of potential measurements and, thus, to broaden the sources of information that may facilitate the interpretation of empirical data.

In human psychology research, there is ample evidence of the interaction between emotions and cognitive processing. For example, people with anxiety tend to be more pessimistic and judge ambiguous sentences as more threatening (Eysenck et al., 1991), anticipate future events more negatively (MacLeod and Byrne, 1996), and show an attention bias for negative information (Mathews and MacLeod, 1994). Vice versa, people with less anxiety are more optimistic, and judge ambiguity more positively (Eysenck et al., 1991), and people with positive moods anticipate more positive events (Nygren et al., 1996) (see Paul et al., 2005, for an extensive review of cognitive components in human emotions). Based on this evidence, researchers proposed that also in animals such interaction between emotion and cognition can be observed (see Paul et al., 2005, for a review of a cognitive approach in animals). By analysing an animal's cognitive performance (on for instance memory, attention, or decision-making

tests), researchers may find biases (i.e. deviations) in this performance. The cognitive bias hypothesis predicts that these biases depend on an animal's affective state, such that animals in a negative state should show more pessimistic biases in a given cognitive task, and animals in a positive state should show more optimistic biases (see Mendl et al., 2009, for a review of the literature). Concretely, a cognitive bias test consists of two phases in which animals first undergo a discrimination training of one cue with high reward certainty (i.e. the positive cue) and another cue with low certainty or even full absence of reward (i.e. the negative cue). Once animals learned this discrimination, the next phase introduces a new, ambiguous cue. The responses given to the ambiguous cue may be biased toward the responses given to either the negative or positive cue, which is then said to reflect an animal's pessimistic or optimistic tendencies to how they perceive the ambiguous cue (see e.g. Bethell, 2015, for a review of the paradigm and its relation to measuring animal welfare).

In the first scientific investigation of the bias hypothesis (Harding et al., 2004), rats were trained to press a lever after hearing tone X in order to get a food reward (i.e. positive cue), and to refrain from pressing a lever after tone Y in order to avoid hearing white noise (i.e. negative cue). After this training, rats that had been housed in unpredictable circumstances (e.g. unfamiliar cage or reversal of light/dark cycle to induce a negative state) tended to respond less and with greater latency to presented ambiguous cues, in contrast to rats housed in a predictable environment (control group). Such slower response time reflects that the rats treated this ambiguous cue more similar to the negative cue, and, thus, had more pessimistic tendencies in their reward expectation (see Burman et al., 2008, for a discussion of reward expectancy as an indicator of animal emotion). The cognitive bias test has repeatedly demonstrated consistent findings in both vertebrate (e.g. see Roelofs et al., 2016, for a critical review of the cognitive bias test and current evidence; see Baciadonna and McElligott, 2015, for the use of the bias test to measure welfare in farm animals) and invertebrate species (e.g. pessimism bias in honeybees, *Apis mellifera carnica*, Bateson et al., 2011; optimism bias in bumble bees, *Bombus terrestris*, Perry et al., 2016).

The benefit of the cognitive bias paradigm is that changes in response to ambiguous cues can be predicted a priori, thus allowing a more theoretically motivated framework when studying emotions, and the paradigm may detect emotions not easily observed through overt behaviours. For this reason, a cognitive bias approach offers the opportunity to investigate an additional, valence oriented, component of an animal's emotional state (Paul et al., 2005), therefore suggesting its application to study emotional contagion. This suggestion has been highlighted before (e.g. Edgar et al., 2012), but we find limited empirical examples of this approach (see Saito et al., 2016, in which positive and negative auditory playback in rats generates optimistic and, to a limited degree, pessimistic responses, respectively; see Sümegei et al., 2014, for an alternative approach of cognitive testing to assess stress in dogs and their owners). Recently, however, Adriaense et al. (2019a) implemented a cognitive bias approach to assess emotional contagion in common ravens. The animals underwent either a positive (i.e. removal of a low value food reward while being presented a high value reward) or negative (i.e. removal of the high value food while being shown the low value food) manipulation. As predicted, ravens showed increased attention and interest in the positive condition, and increased redirected behaviour (i.e. beak swipes through ground substrate) and left-eye use upon inspecting the remaining low value food in the negative condition. During this manipulation, these ravens (the demonstrators) were observed by their affiliative partners, the observers, who were naïve to either positive or negative condition of their partner. Before and after the demonstrator's manipulation, observers were tested on a spatial judgment bias test. In this test, positive and negative cues were presented either left or right of the animal, and ambiguous cues in front of the animal. As hypothesized, observer ravens responded more pessimistically to ambiguous cues (i.e. increased latency to approach the cue) after having witnessed the demonstrator raven in the negative condition.

By using the cognitive bias test, the possible occurrence of emotional contagion in ravens could be assessed by gathering information on the (matching) valence of their responses. This study also shows a matching of

different modalities, namely behaviour and cognition, which allows to differentiate emotional contagion from behavioural mimicry (see discussion above). Though in the present study assessment of additional components was not feasible, it remains important that future research continues to aim at working within the preferred multicomponent model, including the use of additional cognitive, physiological, and behavioural components for all tested animals (Adriaense et al., 2019b; Vonk, 2019b). The addition of a cognitive (bias) test, in conjunction with behavioural and physiological assessment, will strongly aid the empathy and emotional contagion field in more confidently establishing potential matches in the multiple components of emotional states. Although we currently cannot measure an animal's conscious feeling(s) (and therefore cannot show that emotional contagion includes a 'felt emotion'), we encourage researchers to embrace this route to investigate the valence of animal emotions.

2.3. Summary of evidence on emotional contagion

Overall, the direct demonstration of emotional contagion presents a tough challenge, and provides us with more intricacies than previously assumed from this 'simple' affective process. Evidence of emotional contagion in many species remains scarce, and there is a clear bias on negative emotions, and their contagion, in research (Boissy et al., 2007; Rozin and Royzman, 2001). Often measurements of behavioural contagion or motor mimicry are interpreted as emotional contagion, and changes in arousal or attention are interpreted as changes in valence. Although both behavioural contagion and arousal changes may form important components of emotional contagion, they are conceptually distinct and should be studied independently. Future work needs to disentangle these presumed components, and design experimental paradigms to overcome the aforementioned interpretive limitations. Furthermore, emotional contagion studies often lack a concrete definition and theoretical framework of an emotion, resulting in post-hoc interpretations. This can be resolved by working with a multi-component model. The multi-component nature of emotions has long been accepted (e.g. Anderson and Adolphs, 2014) and we therefore argue that it should be more systematically incorporated into the design of future studies. For one, this will increase the information input the observing animal is receiving by for example using a combination of auditory and visual cues within positive, negative, and control conditions (Baciadonna and McElligott, 2015). On the other side, a multicomponent approach allows us to combine multiple results to more accurately assess the presence of an emotional state (Paul et al., 2005). Importantly, the source of emotional contagion should specifically be the conspecific's state, and not the context or any environmental cues (Baciadonna and McElligott, 2015). The event that induces a potential emotional state in the demonstrator should be concealed by means of a hidden mechanism or hidden construction, or by controlling for sound and odour (as proposed in e.g. Huber et al., 2017). Finally, we recommend the continued development of methods assessing valence, including further empirical validation of the use of a cognitive approach, such as the cognitive bias paradigm, within social emotion settings.

3. Sympathy, consolation, and targeted helping

3.1. Definitions and terminology

Sympathy is, according to one (out of many) definitions "an emotional response, stemming from the apprehension of another's emotional state of condition, that is not the same as the other's state or condition but consists of feelings of sorrow or concern for the other" (Eisenberg et al., 1991, p. 65). Hence, while empathy is generally described as feeling with (or as) the other, sympathy is usually framed as feeling for the other (see also Table 1 for definitions, and Box 2 for opposing views). Neuroanatomical research supports this distinction and brain networks involved in empathy are mostly separate from those involved in compassion or sympathetic care for others (Ashar et al., 2017; Singer and Klimecki, 2014, and Lamm et al., 2019, for review). Furthermore, sympathy generally implies not only being concerned about the other's

emotional state, but also motivating subsequent prosocial action. Indeed, orientation from self-focused emotion(s) (such as in emotional contagion) to the other's emotion(s) is often an essential element for prosociality. It would not be very efficient to feel as the other, rather than for, in order to help or console someone in distress. For instance, affect matching (i.e. emotional contagion) without other-oriented concern can easily result in egocentric or personal distress (Batson et al., 1997; Eisenberg and Fabes, 1992; Decety and Lamm, 2009), and a cognitive representation of the other's emotional state alone may result in cold disregard, schadenfreude, or strategic self-oriented behaviour (Batson, 1991; Davis, 2015; see also FeldmanHall et al., 2015). Moreover, research in psychopathic offenders shows that emotional contagion and perspective-taking can both occur without increase in prosocial behaviour (e.g. Pfabigan et al., 2015; Keysers and Gazzola, 2014; Decety, 2015). In addition, not all forms of prosociality require affect based sympathy, such as object or food sharing, in which the motivation is more materialistically, rather than emotionally grounded (Paulus, 2014, 2018; Dunfield et al., 2011; note, though, that according to the Russian doll model such sharing is assumed to be emotionally based, de Waal, 2008) (see extensive discussion below and Chapter 3.2.2.).

In the Russian doll model of animal empathy (Preston and de Waal, 2002; de Waal, 2008), sympathetic concern comprises the middle layer building up on the core of affect matching. The authors propose that sympathetic concern does not require fully represented self-other distinction, only a separation between own, internally generated, emotions and externally generated emotions (de Waal, 2008). It is further proposed that sympathetic concern is based on emotional contagion (de Waal and Preston, 2017; de Waal, 2008), and requires self-regulation (de Waal, 2008), which is consistent with the scientific evidence in developmental human research (Eisenberg and Eggum, 2009). Sympathetic concern is considered to be found in expressions of consolation, and when sympathetic concern is associated with cognitive perspective taking, it allows for prosocial behaviour that is more accurate to the other's particular predicament, such as in targeted helping. Thus, the Russian doll model connects sympathetic concern to subsequent prosocial behaviour with more or less accurate understanding. Understanding another's state may indeed drive us to act, whether this takes the shape of consolation or helping, and thus, the proposed linear structure from sympathy to prosociality seems logical. Both the Russian doll model and the combination model assume an emotional basis for consolation, but, while the Russian doll model also entails the basic assumption of an emotional basis in the form of emotional contagion for targeted helping, this phenomenon in the combination model can be described and studied independently of its supposedly required affect matching (Yamamoto, 2017). Based on the research discussed at the beginning of this paragraph, we think that sympathy ought to be conceptualized as an independent, affect-based phenomenon, and sympathy may drive us to perform certain types of emotion-based helping and consolation. Yet, as we will discuss, not all examples of (targeted) helping or prosociality are affect-based, or require a necessary base of emotional contagion, which is in accordance with the combination model (Yamamoto, 2017). We will now discuss in the next chapters how sympathy is measured through consolation and targeted helping.

3.2. Measuring sympathy through consolation and targeted helping

Sympathy in animals is assessed by studying forms of prosocial behaviour that might plausibly indicate other-oriented concern, cognitive perspective taking, or both. In this paper we will not summarize studies on animals' perspective taking skills in general (see e.g. in primates, Burkart and Heschl, 2007; in dogs, Catala et al., 2017; in birds, Lambert et al., 2018; see also Massen et al., 2019); instead, we discuss the oft-used indicators of such skills in relation to sympathy. Targeted helping is one such indicator, and experimental paradigms are often constructed to assess this. Their rationale is that helping requires cognitive perspective taking, in addition to other-oriented concern, because the helper has to understand the other's need from their own perspective, in order to choose the appropriate helping action (de Waal, 2008). A second behavioural indicator of other-oriented concern is comforting/consoling

behaviour. Consolation is defined as unsolicited offering of positive, affective behaviour to another individual that has been a target of aggression (de Waal and van Roosmalen, 1979). Since its early description in chimpanzees, this topic has taken an iconic position in animal empathy research (empathy broadly defined as in the Russian doll model) and it has become the prime example of inferring the presence of sympathy (de Waal, 2008; Palagi et al., 2014b; Romero et al., 2010; Clay et al., 2018). The reason for its iconic status is that it is thought to be a clear case of other-oriented response, which aims to improve the recipient's welfare and, to do so, the subject must be able to suppress its own initial, vicarious emotional state. We will now discuss and comment on several critical aspects in current consolation and targeted helping research. In our view, the main issue is that reports of consolation or helping are often precipitately taken to be evidence of sympathy in animals (or as evidence for empathy, broadly defined). Yet, upon our review of the literature, one should critically scrutinize the involvement of an emotional-based mechanism in the observed behaviours.

3.2.1. Mechanisms and functions of consolation

Based on carefully recorded data from post-conflict interactions in comparison to a baseline of affiliative behaviour, consolation has been documented extensively in great apes and some species of monkeys (reviewed in Clay et al., 2018; Pérez-Manrique and Gomila, 2018). Primate consolation indeed appears sympathy- or emotionally-based, as it is morphologically highly similar to what humans do when consoling a distressed other. Depending on the species' behavioural repertoire, consolation typically involves gentle touching, hugging, kissing, or grooming. It is also perceived by the recipient to be consoling, as indicated by reduced recipient distress - at least in some cases (Romero et al., 2010; Fraser et al., 2008; Palagi and Norscia, 2013), albeit not in all (Koski and Sterck, 2007; McFarland and Majolo, 2012). Furthermore, young individuals that have better self-regulatory skills offer consolation to others more often (Clay and de Waal, 2013b), and consolation is often biased to close partners (i.e. familiarity bias, see e.g. Clay and de Waal, 2013a; Palagi and Norscia, 2013). These aspects speak for processes that are more easily invoked by in-group members and involve control of a subject's own emotional state, other-oriented concern for another's emotional state, and the subsequent prosocial behavioural response. The existence of a familiarity bias has been suggested as evidence for an affect-based mechanism (e.g. Campbell and de Waal, 2011), and has been labelled as an expression of empathy (broadly defined) (e.g. Palagi et al., 2009). Indeed, several studies on consolation, helping (see below), emotional contagion, and mimicry (see above), show that expression of the involved behaviour is increased by the quality of the relationship (Preston and Hofelich, 2012). Yet, findings of such a bias provide indirect evidence of emotion-based, or sympathy-driven, behaviour, rather than direct confirmation, as a familiarity bias is usually not empirically investigated for its emotional basis. Additionally, comparative research shows that the familiarity effect is dependent on the levels of stress one experiences from interacting with strangers (Martin et al., 2015). Unfamiliar partners experience more social stress in their interaction, yet, by blocking the endocrine stress response, emotional contagion can be evoked in stranger pairs, in both mice and humans (and vice versa, stress induction impairs emotional contagion in familiar dyads). Thus, rather than an emotional 'connection' between familiar pairs (Palagi et al., 2009), it seems that the experience of social stress may (partially) modulate the familiarity bias. Based on this evidence, the familiarity account as evidence for an emotion-based mechanism in observations of either mimicry, emotional contagion, helping, or consolation, is questionable, to the least.

Research in rooks (*Corvus frugilegus*, Seed et al., 2007; Logan et al., 2013), ravens (Fraser and Bugnyar, 2010, 2011), jackdaws (*Corvus monedula*, Logan et al., 2013), and budgerigars (*Melopsittacus undulatus*, Ikkatai et al., 2016) demonstrate post-conflict behaviour similar to the consolatory behaviour shown in primates. Dogs, too, have been shown to express affiliative behaviour toward the victim of a conflict, as well as between former opponents (Cools et al., 2008). Further evidence is recorded in for example horses (*Equus caballus*, Cozzi et al.,

2010), prairie voles (Burkett et al., 2016), and bottlenose dolphins (*Tursiops truncatus*, Yamamoto et al., 2015). While such behavioural interactions have been labelled as consolation, we still do not know the exact mechanism(s) of these behaviours, and whether they are indeed equivalent across species. The requirement for the subject to suppress its own emotional state to show (sympathy-based) other-oriented concern is particularly problematic in the light of the available data. Upon perceiving both a crying and a neutral person, dogs show more approach and touch towards the crying person, regardless of the person's position as owner or stranger (Custance and Mayer, 2012). The authors argue that if the approach was self-oriented, dogs would rather approach their owner to find comfort for their own (potentially) distressed state, which was not found. Yet, the data at hand cannot exclude the authors' final conclusion (Custance and Mayer, 2012), which is that the results may imply an adaptation in dogs to approach crying humans in return for a rewarding and affiliative response, instead of expressing concern. In prairie voles the subject, who observes its distressed mate from behind a transparent barrier, has increased cortisone levels which match the recipient's distressed state (interpreted as emotional contagion, see above). Yet, when the pair is in full contact, and the subject directs consolatory contact to its mate, cortisone levels are not increased (Burkett et al., 2016). This may imply that the other's distress serves as a causal factor for consolation, through means of emotional contagion. Nevertheless, this does not include that the voles have (or require) a cognitive representation or understanding of the other's state, nor that consolation occurs due to a switch from self- to other-oriented concern (Vasconcelos et al., 2012). As discussed above, experiencing congruent affective states may result in self-focused distress, and, thus, observed consolation may arise due to the motivation to decrease one's own distress, rather than to ameliorate the other's distress. Thus far, validating this hypothesis has been problematic as there is almost no data available on the relevant physiological parameters. In the only intra-species dog study on consolation it was shown that the subjects, after being exposed to familiar dog whines (vs. stranger whines), expressed more affiliative behaviour to their familiar conspecifics (Quervel-Chaumette et al., 2016). However, playback of familiar whines maintained (the already) high levels of cortisol in contrast to a reduction of cortisol in the stranger whines condition. Because in the familiar condition the cortisol levels did not change, in comparison to baseline, it remains difficult to disentangle the effect of the familiar whines. Therefore, it is entirely possible that the consoler and the target are both distressed, and the actor is merely comforting itself by seeking physical comfort, though, this does not exclude that the act of giving comfort (and subsequently perceiving it to be comforting to the other) may in itself be comforting to the consoler. In this regard, the self-focused benefit of comforting another may not always be so easily dissociated from the other-focused benefit. The problem of the actor potentially merely comforting itself has been long recognized. First, one might argue that it would be safer not to seek contact with the victim of aggression, as the victim might show unpredictable retaliation or redirect aggression to the consoler. This risk may be rather small, though, as research in chimpanzees and mandrills shows that providing comforting behaviour to others actually decreases the risk of receiving redirected aggression as compared to other bystanders (see Koski and Sterck, 2009; Schino and Marini, 2012). Second, it has been noted that the consolers do not appear distressed (de Waal and Aureli, 1996), but thus far there is no quantitative data on the consolers' emotional state prior to consolation. It may well be that an affiliative contact would not be effective in comforting the consoler. Bonobo victims receiving spontaneous consolation from a bystander show reduced distress, yet, when victims receive consolation after initiating it themselves, their distress does not reduce (Palagi and Norscia, 2013). This suggests that the actual affiliative act does not effectively comfort the victim, but that it is rather the spontaneous gesture by the bystander. Indirectly, this also suggests that a bystander aiming to comfort itself by consolation would not experience alleviation of distress by the affiliative act. Yet, without additional data (e.g. physiological measurements) the motivation of other-regard rather than self-regard cannot be unambiguously shown. Interestingly, in the human literature, there has been an extensive debate

on this topic and numerous experimental attempts still result in an insufficient resolution on whether prosocial behaviour is indeed triggered by sympathetic concern, or rather by attempts to reduce personal distress (e.g., [Batson et al., 1988](#); [Decety and Lamm, 2009](#), for review). Furthermore, the occurrence of consolation is difficult to distinguish from similarly looking behaviour that occurs in the same context, but has another function altogether, presumably relying on a different mechanism ([Fraser et al., 2009](#)). For example, a consoler can actually be diverting the threat of spreading aggression away from him- or herself ([Koski and Sterck, 2009](#); [Logan et al., 2013](#)), thereby reducing the general likelihood of further aggression ([Schino and Marini, 2012](#); [Yamamoto et al., 2015](#)), or using affiliation to reconcile the previously occurred conflict on behalf of a relative or friend ([Wittig et al., 2007](#)). These cases may nevertheless appear behaviourally highly similar to a consolatory contact, although their ultimate function is different. It is therefore entirely possible that the prevalence or the spread of sympathy-driven consolation within and across species is overestimated.

3.2.2. The emotional and cognitive basis of helping

Targeted helping does not necessarily require any emotional basis, and therefore may not irrevocably be based on sympathy or any affective-based concept related to empathy. As a result, interpreting helping behaviour in light of sympathy-driven mechanisms is problematic when the context does not require any emotional basis (e.g. food- or object-related helping, see discussion below). Whether or not sympathy is a necessary and sufficient mechanism likely depends on the emotional content of the situation ([Hoffman, 2000](#)), and helping may therefore often involve an emotional basis (though, empirical verification may be missing, see discussion below). In regards of targeted helping without a necessary emotional basis, chimpanzees have been shown to hand an appropriate tool or another out-of-reach object to another ([Yamamoto et al., 2009, 2012](#); [Bullinger et al., 2014](#); [Liebal et al., 2014](#)), or release a latch that delivers or grants access to food to another ([Warneken and Tomasello, 2006](#); [Warneken et al., 2007](#); [Melis and Tomasello, 2013](#)). Similar helping was shown by tufted capuchin monkeys ([Barnes et al., 2008](#)). It is debatable whether targeted helping by handing a tool to another individual has to be grounded in a sympathy-based response to another's emotional state, which in turn would motivate subsequent prosocial behaviour. That is, these contexts of handing a tool require the subject to understand the other's need, and therefore may involve (some) cognitive perspective taking. However, we assume that these types of helping are less likely to involve any particular affective component, and it is therefore not necessary to sympathize with another's affective state to engage in targeted helping ([Yamamoto, 2017](#)). Indeed, a study on the four great ape species' helping in an object-transfer paradigm found that observing the recipient being harmed does not motivate apes' helping behaviour ([Liebal et al., 2014](#)). Such cases of targeted helping are more likely to be based on the subject representing the material goal of the other, rather than their affective state ([Yamamoto, 2017](#)). The action obviously provides help to the recipient and requires, therefore, the motivation to do so, but that motivation does not need to stem from sympathy. Additionally, as [Silk](#) argues in a recent review of the evolution of altruistic behaviour ([Silk and House, 2016](#)), prosocial choices in chimpanzees and other great apes seem to be based on self-interest rather than on benefiting others (see also [Silk et al., 2005](#), in which the authors argue that chimpanzees are not motivated by other-related concern; and [Silk et al., 2013](#) for the many reasons of food sharing). In human research, scholars have argued that prosocial behaviour is motivated by a concern for others (e.g. in children, [Hepach et al., 2013](#)), which is supported by the presence of internal arousal acting as motivator for prosocial behaviour (arousal as measured by pupil dilation, see [Hepach et al., 2015](#)). Though, others have argued for the absence of such other-concern. In developing children, targeted helping, sharing, and comforting distressed others, are unrelated to each other ([Paulus, 2018](#); [Dunfield and Kuhlmeier, 2013](#)). Moreover, in young children, targeted helping may rather reflect an interest in joint action and in completing a goal rather than sympathy per se ([Paulus, 2014](#); [Dahl and Paulus, 2018](#)). This is corroborated by studies showing that distinct neurophysiological patterns characterize these forms of prosociality ([Paulus et](#)

[al., 2013](#); [Malti and Dys, 2018](#)). Additionally, genetic analyses also suggest that helping and comforting are not genetically related, and that their association in adults is rather due to environmental factors ([Knafo-Noam et al., 2018](#)).

In addition to food- or object-related helping, apes are reported to perform helpful actions that occur in highly emotionally charged situations. Indeed, [de Waal \(2008\)](#) describes sympathy-based helping to be particularly apparent in care or rescue behaviour. There are several anecdotal cases of chimpanzees helping others even at great risk to themselves (see [Pérez-Manrique and Gomila, 2018](#), for review; [Koski and Sterck, 2010](#); [de Waal, 2008, 2010](#)). Examples include helping another individual that has fallen into water and who appears in great distress, where the helper is in danger as apes generally cannot swim. Such context evokes highly charged emotions, and the helper must recognize the specific goal of the other and the appropriate actions to help him. This case is, thus, likely to involve all components of sympathy-based, cognitively processed action, such as a cognitive representation of the other's state and situation, and other-oriented concern that motivates the subsequent prosocial action. Examples of care behaviour involve others showing care and compassion toward a wounded individual, or helping an incapacitated individual to move (e.g. [Boesch, 1992](#); reviewed in [Pérez-Manrique and Gomila, 2018](#); [Pruetz, 2011](#); see e.g. also in elephants, [Bates et al., 2008](#); in dolphins, reviewed by [Pérez-Manrique and Gomila, 2018](#)). These cases certainly suggest a cognitively processed understanding of the other's need. Problematically, however, the behaviours mentioned are notoriously difficult to observe systematically (e.g. see [Hammers and Brouwer, 2017](#), for the first evidence of rescue behaviour observed in birds), and ethically impossible to study experimentally. Therefore, such cases are anecdotally recorded, rendering the evidence as tentative at best. Another problematic issue is that experimental studies sometimes fail to overcome a potentially anthropomorphic perspective (see also [Williams et al., this Special Issue](#)). For instance, in one study dogs did not seek the help of another human when their owner was stuck under a bookcase ([Macpherson and Roberts, 2006](#)). Rather than considering this as evidence of an absence of targeted helping in dogs, numerous alternative explanations could be offered. The subjects potentially may not have perceived the owner as being in distress, and even if they did, they may not have understood the need for another human to alleviate the pain, including the lack of human-specific experience with furniture and relevant physical cognition and/or causal reasoning abilities.

Yet, even with a systematic and controlled experimental design we may conclude that helping does not always irrevocably carry an emotional basis. In this regard, studies of rodents' helping behaviour are also somewhat problematic in terms of identifying the underlying mechanisms, and whether they are indeed sympathy-related (e.g. see [Vasconcelos et al., 2012](#) for rescue behaviour without any necessary 'empathy' related interpretation). Several studies have shown helping in highly emotionally charged situations, such as rats releasing a distressed conspecific from a restraining tube ([Bartal et al., 2011](#); and see [Bartal et al., 2014](#), for a familiarity bias), or rats releasing conspecifics being trapped in water ([Sato et al., 2015](#)). In these studies, the helping behaviour was claimed to be empathically motivated (based on the Russian doll model, [Preston and de Waal, 2002](#)), but others have argued against such notion (see [Silberberg et al., 2014](#), and [Ueno et al., 2019](#), who argue for a social-contact account; and see [Schwartz et al., 2017](#), who argue against an empathy-driven release in [Sato et al., 2015](#)). The emotional context and the familiarity bias suggest an emotional or sympathy related response (though see our discussion above on familiarity bias), but we do not currently know whether this involves cognitive perspective taking (as targeted helping is assumed to coincide with perspective taking in both the Russian doll model and the combination model) and, if so, at what level. It would be worth assessing, how far situational familiarity and own experience suffice in eliciting helping behaviour ([Atsak et al., 2011](#)). This does not imply that the observed behaviour cannot be prosocial in its action, still, the claim that this behaviour is underpinned by sympathetic concern or, more generally, an affective mechanism, seems premature (see also [Carrillo et al., 2019](#), for recent work on emotional mirror neurons in rats). Regarding the role of self-regulation of emotions, rats' helping behaviour is impaired by anxiolytic treatment, indicating that helping requires an aroused emotional state ([Bartal et al., 2016](#)).

Thus, this may imply that the distressed state of the conspecific triggers (personal) distress in the helper, which suggests that the observed helping behaviour is perhaps based on the motivation to alleviate one's own distress. Overall, it remains an open question whether the rodent evidence confirms that helping in rats is indeed sympathy-based.

Current research on consolation and helping seems to share a similar problem, which is that often similarly looking behaviours are labelled consolation or helping, respectively, when little is known about their mechanisms and ultimate function (such as also seen in other social behaviours, e.g. in grooming, which functionally serves either maintaining social bonds or gaining resources, Wooddell et al., 2019). The different contexts in which consolation and helping behaviour are perceived highlight the importance of disentangling the different drivers that may underlie these behaviours. Dennett (1989) has argued for the investigation of different levels of intentionality and, as such, studying consolation and helping in animals could benefit from the empirical investigation of the intentionality levels. That is, we ought to verify which intention underlies the observed behaviour, such as the intention to avoid future harassment, to consolidate reproduction success by helping group mates, to improve the wellbeing of the other, or whether it concerns a reflexive reaction to relieve one's own personal distress. This approach to scrutinize the mechanisms of animal behaviour by using and re-evaluating Dennett's levels of intentionality has been applied to primate communication (see Townsend et al., 2017 and references therein). Another interesting paper comparing helping behaviour in rats and ants, labelled rescue behaviour, proposes concrete suggestions in this vein (Hollis and Nowbahari, 2013). The authors recommend a focus on proximate mechanisms by analysing in an algorithmic manner the different behavioural patterns that come about in perceived rescue behaviour. Additionally, another focus should be on the ultimate level of this behaviour with an ecological approach. In that perspective, a framework of rat and mouse behavioural ecology would be relevant in the study of helping behaviour, to understand more how and why certain helping behaviour is expressed (Kondrakiewicz et al., 2019). We argue that the same recommendations could be beneficial in future consolation research.

3.2.3. The relevance of cognitive complexity

Consolation was long thought to be dependent on representational mental skills. Data of its occurrence in chimpanzees, bonobos, and gorillas (Romero et al., 2010; Koski and Sterck, 2007, 2009; Clay and de Waal, 2013a, 2013b; Cordoni et al., 2006) was contrasted with absence of evidence in monkeys (Aureli and de Waal, 2000). However, absence of evidence does not amount to evidence of absence. Moreover, spontaneously offered affiliative contacts by a conflict bystander to the former victim (and aggressor), have now been recorded in stump-tailed macaques (Call et al., 2002), Tonkean macaques (*Macaca tonkeana*, Palagi et al., 2014a, 2014b), Barbary macaques (McFarland and Majolo, 2012), and mandrills (*Mandrillus sphinx*, Schino and Marini, 2012). Furthermore, the requirement of advanced cognitive skills for consolation is not consistent with the early emergence of consolatory contacts in human infants. Human infants usually begin to show other-oriented concern before their first birthday (Hay et al., 1981; Roth-Hanania et al., 2011; Davidov et al., 2013), which expands to active comforting of others at 14–18 months of age by patting, hugging or offering objects of comfort (Knafo et al., 2008; Hoffman, 2000; Zahn-Waxler et al., 1992a, 1992b; Vaish et al., 2009). This is much before their theory of mind skills allow cognitive perspective taking. Thus, consolation does not appear to require particularly highly advanced mentalizing. Other researchers (e.g. Burkett et al., 2016) have noted that despite the general assumption of consolation requiring higher complex cognitive skills, rodents also demonstrate empathy-related phenomena (see consolation in prairie voles, Burkett et al., 2016). In a similar vein, helping may not require high cognitive capacities either, at least if the context is salient and the required action within the species' behavioural repertoire. Without arguing for or against a notion of cognitive complexity in rodents, the combination model (Yamamoto, 2017) might allow us to explore and investigate consolation and helping in animals in a broader and more feasible manner than the doll model (Preston and de Waal,

2002), as the latter does require a necessary advanced cognitive capacity for these phenomena (though note that more recently in de Waal and Preston, 2017, it is mentioned that "There is no a priori reason to exclude perspective-taking in smaller-brained species", p. 2). Though the combination model does not explicitly posit an increasing cognitive complexity alongside 'higher forms of empathy' such as the doll model does, the phenomena sympathy and consolation are nevertheless held against a 'cognitive complex' standard and "Animal species showing phenomena in the category of the combination of plural factors should be inevitably talented (...) "(Yamamoto, 2017, p. 7). Such standard implies the notion that human empirical data serve as a benchmark to which animal data should be compared, which in our view goes against the idea of investigating empathic phenomena for their ecological value (e.g. Hollis and Nowbahari, 2013). Nevertheless, future research is certainly required to hone in on consolation and targeted helping in a diverse set of species, including the investigation of their underlying mechanisms and different components such as by means of physiological methods. This will reveal any potential linkages with either other concepts, or specific cognitive or social skills.

3.3. Summary

We propose that the interpretation of consolation and targeted helping as sympathy- or emotion-based, at the current stage, is not fully warranted. Primates and some other species exhibit behaviour suggesting other-oriented concern, but oftentimes we do not actually know the mechanisms involved, nor is the function of the observed behaviour well understood. The aforementioned forms of consolation and targeted helping could, in certain contexts, be indeed based on sympathetic concern – still, we need to consider that the same outcome can be based on different mechanisms. Helping another could be emotionally neutral or, alternatively, highly emotionally laden in for example a context of high urgency or threat. Most cases of helping are likely to involve at least some cognitive representation of the other's state and situation, but that does not need to be associated with an emotional reaction. Comforting, in contrast, occurs by definition in an emotional context. Care behaviour, in turn, could be based on personal curiosity or concern for the other's welfare, or both. By examining behaviour alone, we can never have full access to the proximate mechanisms. Therefore, it is of crucial importance to find out which ways may access the mechanisms, before drawing direct parallels between similar looking behaviours in different situations and species. We recommend that future research on consolation and targeted helping puts additional emphasis on the assessment of the physiological correlates of behaviour. Undeniably, measuring such parameters is often highly challenging and not always feasible. The majority of physiological applications has been designed for experimental research, though, in recent years applications have been developed to allow for more flexible use. For instance, animals can be trained to wear heart rate tracking equipment (e.g. in chickens, Buijs et al., 2018), so data can be collected without the need for restraint. Contexts of observational research and ecologically valid environments form even bigger challenges, yet, the recent development of for instance infrared thermography holds the potential to bring physiological measurements more efficiently to the field (e.g. Dezechache et al., 2017). In this regard, studies on all three concepts, emotional contagion, consolation, and targeted helping, can benefit from adding the physiological component to their methodological repertoire. Additionally, evidence shows that the capacity for consolation and targeted helping may not necessarily require advanced mentalizing skills, which future work should take into consideration upon reviewing empirical data in light of current theoretical empathy models.

4. Conclusions

As a returning topic in our review on the comparative study of empathy related phenomena in animals, we notice an absence of the assessment of an emotional basis, be it in emotional contagion, or in presumably sympathy-based behaviour, such as consolation or targeted helping. Yet, for both humans and animals, we need to verify the presence of an emotional response in order to

conclude the phenomenon itself, or even empathy. We propose to follow the idea of Pérez-Manrique and Gomila (2018, p. 18), that “simple mechanisms can lead to responses and outcomes very similar to those expected for empathic behaviours but this does not mean that they are the same”. Adopting a multi-component approach that also includes valence related measurements should serve as a potential solution for assessing the emotional basis of empathy-related phenomena. Furthermore, the underlying mechanisms and the ultimate function of the discussed phenomena require more systematic investigation. This knowledge would positively aid us in disentangling distinct phenomena in animals, hence facilitating the accurate labelling of observed behaviours and other parameters. After reviewing the current empirical evidence, we come to conclude that there is still a strong need for more comparative research, across different taxa, and with a focus on more methodical and rigorous study construction that allows to exclude more parsimonious explanations. In the same vein, some of the most exciting study designs (e.g. Reimert et al., 2017), and essential conceptual contributions (Mendl et al., 2010) come from the animal welfare field. The study on emotions and empathy in animals has in the last decade positively stimulated cross-domain collaborations, yet, a consolidation of fundamental and applied scientific practices often remains less explored. Hereby, we also call for fostering such a multi-discipline perspective. Although caution should be exerted when interpreting animal behaviour, anthropomorphism – defined as the attribution of human properties to nonhuman entities – can serve legitimate scientific purposes if it is used to develop hypotheses (Bekoff et al., 2002). Such hypotheses, emerging from data sources including our own perceptions, feelings, and detailed behavioural descriptions, are useful if collected for heuristic purposes, that is, if they can be tested rigorously (see also Williams et al., this Special Issue). For example, while owners readily report empathy-like responding in their pet dogs, systematic empirical confirmation remains elusive (Silva and de Sousa, 2011; Huber et al., 2017).

Although our review shows that current empirical evidence for various empathy-related phenomena is scarcer than perhaps assumed, we should not be discouraged to push through, unravel, and rigorously analyse the different and essential components of each discussed phenomenon. Nor do we conclude that empathy in animals is a naïve or unrealistic concept; on the contrary, our genuine interest in animals and their behaviour strengthens and encourages us to review our current understanding of the proximate mechanisms underlying their social behavioural repertoire. With this review we want to galvanize a critical perspective while at the same time remaining broad-minded of animals’ multi-layered social and emotional complexity.

Funding

JECA is funded by a dissertation completion scholarship by the University of Vienna in Austria. CL and LH acknowledge funding by the Viennese Science and Technology Fund (WWTF, CS11-005 & CS18012), the City of Vienna and ituba Capital AG through project CS18012, and the Austrian Science Fund (FWF, W 1262-B29). LH was additionally funded by the Messerli Foundation (Sörenberg, Switzerland). SEK was funded by the European Union 2020 initiative’s Marie Skłodowska-Curie scheme (grant number 653957). The funders had no role in the design, decision to publish, or preparation of the review manuscript.

Acknowledgements

We thank the organizers (Dr. Eliza Bliss-Moreau, Dr. Mariska E. Kret, Dr. Jorg J.M. Massen) of the Comparative Affective Sciences workshop (Leiden, the Netherlands, 2017) for providing us with the opportunity to take part in this Special Issue. We would also like to thank Jordan S. Martin for insightful discussions on the topic, and the editor and two anonymous reviewers for their constructive feedback on previous versions of the manuscript.

References

- Adolphs, R., 1999. Social cognition and the human brain. *Trends Cogn. Sci.* 3, 469–479.
- Adriaense, J.E., Martin, J.S., Schiestl, M., Lamm, C., Bugnyar, T., 2019a. Negative emotional contagion and cognitive bias in common ravens (*Corvus corax*). *Proc. Natl. Acad. Sci.* 116 (23), 11547–11552.
- Adriaense, J.E., Martin, J.S., Schiestl, M., Lamm, C., Bugnyar, T., 2019b. Reply to Vonk: disentangling emotional contagion from its underlying causes. *Proc. Natl. Acad. Sci.*, 201910556.
- Ahloy-Dallaire, J., Espinosa, J., Mason, G., 2018. Play and optimal welfare: Does play indicate the presence of positive affective states? *Behav. Processes* 156, 3–15.
- Anderson, D.J., Adolphs, R., 2014. A framework for studying emotions across species. *Cell* 157 (1), 187–200.
- Anderson, J.R., Gallup, G.G., 2015. Mirror self-recognition: a review and critique of attempts to promote and engineer self-recognition in primates. *Primates* 56 (4), 317–326.
- Ashar, Y.K., Andrews-Hanna, J.R., Dimidjian, S., Wager, T.D., 2017. Empathic care and distress: predictive brain markers and dissociable brain systems. *Neuron* 94 (6), 1263–1273.
- Atsak, P., Orre, M., Bakker, P., Cerliani, L., Rooszendaal, B., Gazzola, V., ... Keyzers, C., 2011. Experience modulates vicarious freezing in rats: a model for empathy. *Plos one* 6 (7), e21855.
- Aureli, F., de Waal, F.B.M., 2000. *Natural Conflict Resolution*. Univ of California Press.
- Baciadonna, L., McElligott, A.G., 2015. The use of judgement bias to assess welfare in farm livestock. *Anim. Welf.* 24, 81–91.
- Baird, A.D., Scheffer, I.E., Wilson, S.J., 2011. Mirror neuron system involvement in empathy: a critical look at the evidence. *Soc. Neurosci.* 6 (4), 327–335.
- Barnes, J.L., Hill, T., Langer, M., Martinez, M., Santos, L.R., 2008. Helping behaviour and regard for others in capuchin monkeys (*Cebus apella*). *Biol. Lett.* 4 (6), 638–640.
- Barrett, L.F., Mesquita, B., Ochsner, K.N., Gross, J.J., 2007. The experience of emotion. *Annu. Rev. Psychol.* 58, 373–403.
- Bartal, I.B.A., Decety, J., Mason, P., 2011. Empathy and pro-social behaviour in rats. *Science* 334 (6061), 1427–1430.
- Bartal, I.B.A., Rodgers, D.A., Bernardez Sarria, M.S., Decety, J., Mason, P., 2014. Prosocial behaviour in rats is modulated by social experience. *eLife* 3, 114–116.
- Bartal, I.B.A., Shan, H., Molasky, N.M.R., Murray, T.M., Williams, J.Z., Decety, J., Mason, P., 2016. Anxiolytic treatment impairs helping behaviour in rats. *Front. Psychol.* 7 (185) 19–14.
- Bates, L.A., Poole, J.H., Byrne, R.W., 2008. Elephant cognition. *Curr. Biol.* 18 (13), R544–R546.
- Bateson, M., Desire, S., Gartside, S.E., Wright, G.A., 2011. Agitated honeybees exhibit pessimistic cognitive biases. *Curr. Biol.* 21 (12), 1070–1073.
- Batson, C.D., 1991. *The Altruism Question: Toward a Social-psychological Answer*. Erlbaum, Hillsdale, NJ.
- Batson, C.D., 2009. These things called empathy. In: Decety, J., Ickes, W. (Eds.), *The Social Neuroscience of Empathy*. The MIT Press, Cambridge, MA, pp. 3–16.
- Batson, C.D., Dyck, J.L., Brandt, J.R., Batson, J.G., Powell, A.L., McMaster, M.R., Griffitt, C., 1988. Five studies testing two new egoistic alternatives to the empathy-altruism hypothesis. *J. Pers. Soc. Psychol.* 55 (1), 52.
- Batson, C.D., Early, S., Salvarani, G., 1997. Perspective taking: imagining how another feels versus imagining how you would feel. *Pers. Soc. Psychol. Bull.* 23 (7), 751–758.
- Bekkali, S., Youssef, G., Donaldson, P.H., Albein-Urios, N., Hyde, C., Enticott, P., 2019. Is the Putative Mirror Neuron System Associated With Empathy? A Systematic Review and Meta-analysis. Preprint at. <https://psyarxiv.com/6bu4p/>.
- Bekoff, M., Allen, C., Burghardt, G.M. (Eds.), 2002. *The Cognitive Animal: Empirical and Theoretical Perspectives on Animal Cognition*. MIT press.
- Berridge, K.C., 2018. Evolving concepts of emotion and motivation. *Front. Psychol.* 9.
- Berthier, J.M., Semple, S., 2018. Observing grooming promotes affiliation in Barbary macaques. *Proc. R. Soc. B* 285 (1893), 20181964.
- Bethell, E.J., 2015. A “how-to” guide for designing judgment bias studies to assess captive animal welfare. *J. Appl. Anim. Welf. Sci.* 18 (sup1), S18–S42.
- Bisazza, A., Rogers, L.J., Vallortigara, G., 1998. The origins of cerebral asymmetry: a review of evidence of behavioural and brain lateralization in fishes, reptiles and amphibians. *Neurosci. Biobehav. Rev.* 22 (3), 411–426.
- Blair, R.J.R., 2005. Responding to the emotions of others: dissociating forms of empathy through the study of typical and psychiatric populations. *Conscious. Cogn.* 14, 698–718. <https://doi.org/10.1016/j.con-cog.2005.06.004>.
- Boch, M., Lamm, C., 2017. The multiple facets of empathy. *Anim. Sentience: Interdiscip. J. Anim. Feel.* 2 (14), 14.
- Boesch, C., 1992. New elements of a theory of mind in wild chimpanzees. *Behav. Brain Sci.* 15 (1), 149–150.
- Boileau, A., Farish, M., Turner, S.P., Camerlink, I., 2019. Infrared thermography of agonistic behaviour in pigs. *Physiol. Behav.*, 112637.
- Boissy, A., et al., 2007. Assessment of positive emotions in animals to improve their welfare. *Physiol. Behav.* 92 (3), 375–397.
- Briefer, E.F., 2018. Vocal contagion of emotions in non-human animals. *Proc. R. Soc. B: Biol. Sci.* 285 (1873), 20172783.
- Buijs, S., Booth, F., Richards, G., McGaughey, L., Nicol, C.J., Edgar, J., Tarlton, J.F., 2018. Behavioural and physiological responses of laying hens to automated monitoring equipment. *Appl. Anim. Behav. Sci.* 199, 17–23.
- Bullinger, A.F., Melis, A.P., Tomasello, M., 2014. Chimpanzees (*Pan troglodytes*) instrumentally help but do not communicate in a mutualistic cooperative task. *J. Comp. Psychol.* 128 (3), 251–260.

- Burghardt, G.M., 1998. The evolutionary origins of play revisited: lessons from turtles. *Animal Play: Evolutionary, Comparative, and Ecological Perspectives*, pp. 1–26.
- Burkart, J.M., Heschl, A., 2007. Understanding visual access in common marmosets, *Callithrix jacchus*: perspective taking or behaviour reading? *Anim. Behav.* 73 (3), 457–469.
- Burkett, J.P., Andari, E., Johnson, Z.V., Curry, D.C., de Waal, F.B., Young, L.J., 2016. Oxytocin-dependent consolation behaviour in rodents. *Science* 351 (6271), 375–378.
- Burman, O.H., Parker, R.M., Paul, E.S., Mendl, M., 2008. Sensitivity to reward loss as an indicator of animal emotion and welfare. *Biol. Lett.* 4 (4), 330–333.
- Burn, C.C., 2017. Bestial boredom: a biological perspective on animal boredom and suggestions for its scientific investigation. *Anim. Behav.* 130, 141–151.
- Buttner, A.P., Strasser, R., 2014. Contagious yawning, social cognition, and arousal: an investigation of the processes underlying shelter dogs' responses to human yawns. *Anim. Cogn.* 17 (1), 95–104.
- Cairo, C.C., Burrows, A.M., Waller, B.M., 2017. Development and application of CatFACS: Are human cat adopters influenced by cat facial expressions? *Appl. Anim. Behav. Sci.* 189, 66–78.
- Call, J., Aureli, F., de Waal, F.B., 2002. Postconflict third-party affiliation in stump-tailed macaques. *Anim. Behav.* 63 (2), 209–216.
- Camerlink, I., Coulange, E., Farish, M., Baxter, E.M., Turner, S.P., 2018. Facial expression as a potential measure of both intent and emotion. *Sci. Rep.* 8 (1), 17602.
- Campbell, M.W., De Waal, F.B., 2011. Ingroup-outgroup bias in contagious yawning by chimpanzees supports link to empathy. *PLoS One* 6 (4), e18283.
- Carr, L., Iacoboni, M., Dubeau, M.C., Mazziotta, J.C., Lenzi, G.L., 2003. Neural mechanisms of empathy in humans: a relay from neural systems for imitation to limbic areas. *Proc. Natl. Acad. Sci.* 100 (9), 5497–5502.
- Carrillo, M., Han, Y., Migliorati, F., Liu, M., Gazzola, V., Keysers, C., 2019. Emotional mirror neurons in the rat's anterior cingulate cortex. *Curr. Biol.* 29 (8), 1301–1312.
- Catala, A., Mang, B., Wallis, L., Huber, L., 2018. Dogs demonstrate perspective taking based on geometrical gaze following in a Guesser-Knower task. *Anim. Cogn.* 20 (4), 581–589.
- Chartrand, T.L., Bargh, J.A., 1999. The chameleon effect: the perception-behaviour link and social interaction. *J. Pers. Soc. Psychol.* 76 (6), 893.
- Chotard, H., Ioannou, S., Davila-Ross, M., 2018. Infrared thermal imaging: positive and negative emotions modify the skin temperatures of monkey and ape faces. *Am. J. Primatol.* 80 (5), e22863.
- Church, R.M., 1959. Emotional reactions of rats to the pain of others. *J. Comp. Physiol. Psychol.* 52 (2), 132.
- Clay, Z., de Waal, F.B., 2013a. Bonobos respond to distress in others: consolation across the age spectrum. *PLoS One* 8 (1), e55206.
- Clay, Z., de Waal, F.B.M., 2013b. Development of socio-emotional competence in bonobos. *Proc. Natl. Acad. Sci.* 5, 18121–18126.
- Clay, Z., Palagi, E., de Waal, F.B., 2018. Ethological approaches to empathy in primates. *Neuronal Correlates of Empathy*, pp. 53–66.
- Cools, A.K., Van Hout, A.J.M., Nelissen, M.H., 2008. Canine reconciliation and third-party-initiated postconflict affiliation: do peacemaking social mechanisms in dogs rival those of higher primates? *Ethology* 114 (1), 53–63.
- Coplan, A., 2011. Will the real empathy please stand up? A case for a narrow conceptualization. *South. J. Philos.* 49, 40–65.
- Cordoni, G., Palagi, E., Tarli, S.B., 2006. Reconciliation and consolation in captive western gorillas. *Int. J. Primatol.* 27 (5), 1365–1382.
- Cozzi, A., Sighieri, C., Gazzano, A., Nicol, C.J., Baragli, P., 2010. Post-conflict friendly reunion in a permanent group of horses (*Equus caballus*). *Behav. Processes* 85 (2), 185–190.
- Cuff, B.M., Brown, S.J., Taylor, L., Howat, D.J., 2016. Empathy: a review of the concept. *Emot. Rev.* 8 (2), 144–153.
- Custance, D., Mayer, J., 2012. Empathic-like responding by domestic dogs (*Canis familiaris*) to distress in humans: an exploratory study. *Anim. Cogn.* 15 (5), 851–859.
- da Silva, P.F., de Leaniz, C.G., Luchiani, A.C., 2019. Fear contagion in zebrafish: a behaviour affected by familiarity. *bioRxiv*, 521187.
- Dahl, A., Paulus, M., 2018. From interest to obligation: the gradual development of human altruism. *Child Dev. Perspect.* 13 (1), 10–14.
- Darwall, S., 1998. Empathy, sympathy, care. *Philos. Stud.* 89, 261–282.
- Davidov, M., Zahn-Waxler, C., Roth-Hanania, R., Knafo, A., 2013. Concern for others in the first year of life: theory, evidence, and avenues for research. *Child Dev. Perspect.* 7 (2), 126–131.
- Davila-Ross, M., Menzler, S., Zimmermann, E., 2007. Rapid facial mimicry in orangutan play. *Biol. Lett.* 4 (1), 27–30.
- Davis, M.H., 1996. *Empathy. A Social Psychological Approach*. Westview Press, Boulder, CO.
- Davis, M.H., 2015. Empathy and prosocial behaviour. *The Oxford Handbook of Prosocial Behaviour*, pp. 282–306.
- De Vignemont, F., Singer, T., 2006. The empathic brain: how, when and why? *Trends in Cognitive Sciences* 10, 435–441.
- de Waal, F.B.M., 2008. Putting the altruism back into altruism: the evolution of empathy. *Annu. Rev. Psychol.* 59, 279–300.
- de Waal, F.B.M., 2010. *The Age of Empathy: Nature's Lessons for a Kinder Society*. Broadway Books.
- de Waal, F.B., 2019. Fish, mirrors, and a gradualist perspective on self-awareness. *PLoS Biol.* 17 (2), e3000112.
- de Waal, F.B.M., Aureli, F., 1996. Consolation, reconciliation, and a possible cognitive difference between macaques and chimpanzees. *Reaching Into Thought: The Minds of the Great Apes*, pp. 80–110.
- de Waal, F.B.M., Preston, S.D., 2017. Mammalian empathy: behavioural manifestations and neural basis. *Nat. Rev. Neurosci.* 18 (8), 498–509.
- de Waal, F.B.M., van Roosmalen, A., 1979. Reconciliation and consolation among chimpanzees. *Behav. Ecol. Sociobiol.* 5 (1), 55–66.
- Decety, J., 2010. To what extent is the experience of empathy mediated by shared neural circuits? *Emot. Rev.* 2 (3), 204–207.
- Decety, J., 2015. The neural pathways, development and functions of empathy. *Curr. Opin. Behav. Sci.* 3, 1–6.
- Decety, J., Lamm, C., 2009. Empathy versus personal distress – recent evidence from social neuroscience. In: Decety, J., Ickes, W. (Eds.), *The Social Neuroscience of Empathy*. MIT Press, Cambridge, pp. 199–214.
- Decety, J., Michalska, K.J., 2010. Neurodevelopmental changes in the circuits underlying empathy and sympathy from childhood to adulthood. *Dev. Sci.* 13 (6), 886–899. <https://doi.org/10.1111/j.1467-7687.2009.00940.x>.
- Decety, J., Sommerville, J.A., 2003. Shared representations between self and other: a social cognitive neuroscience view. *Trends Cogn. Sci.* 7 (12), 527–533. <https://doi.org/10.1016/j.tics.2003.10.004>.
- Decety, J., Svetlova, M., 2012. Putting together phylogenetic and ontogenetic perspectives on empathy. *Dev. Cogn. Neurosci.* 2 (1), 1–24.
- Demuru, E., Palagi, E., 2012. In bonobos yawn contagion is higher among kin and friends. *PLoS One* 7 (11), e49613.
- Deng, H., Hu, P., 2018. Matching your face or appraising the situation: two paths to emotional contagion. *Front. Psychol.* 8, 2278.
- Dennett, D.C., 1989. *The Intentional Stance*. MIT press.
- Descovich, K., Wathan, J.W., Leach, M.C., Buchanan-Smith, H.M., Flecknell, P., Farningham, D., Vick, S.J., 2017. Facial expression: an under-utilized tool for the assessment of welfare in mammals. *ALTEX: Altern. Anim. Exp.* 34 (3), 409–429.
- Dezechache, G., Zuberbühler, K., Davila-Ross, M., Dahl, C.D., 2017. Skin temperature changes in wild chimpanzees upon hearing vocalizations of conspecifics. *R. Soc. Open Sci.* 4 (1), 160816.
- Dharmaretnam, M., Rogers, L.J., 2005. Hemispheric specialization and dual processing in strongly versus weakly lateralized chicks. *Behav. Brain Res.* 162 (1), 62–70.
- Dukes, D., Clément, F. (Eds.), 2019. *Foundations of Affective Social Learning: Conceptualizing the Social Transmission of Value*. Cambridge University Press.
- Dunfield, K.A., Kuhlmeier, V.A., 2013. Classifying prosocial behaviour: children's responses to instrumental need, emotional distress, and material desire. *Child Dev.* 84 (5), 1766–1776.
- Dunfield, K., Kuhlmeier, V.A., O'Connell, L., Kelley, E., 2011. Examining the diversity of prosocial behaviour: helping, sharing, and comforting in infancy. *Infancy* 16 (3), 227–247.
- Edgar, J.L., Nicol, C.J., 2018. Socially-mediated arousal and contagion within domestic chick broods. *Sci. Rep.* 8 (1), 10509.
- Edgar, J.L., Lowe, J.C., Paul, E.S., Nicol, C.J., 2011. Avian maternal response to chick distress. *Proc. R. Soc. Lond., B, Biol. Sci.*, rspb20102701.
- Edgar, J.L., Nicol, C.J., Clark, C.C.A., Paul, E.S., 2012. Measuring empathic responses in animals. *Appl. Anim. Behav. Sci.* 138 (3–4), 182–193.
- Eisenberg, N., Eggum, N.D., 2009. Empathic responding: sympathy and personal distress. *Soc. Neurosci. Empathy* 6, 71–83.
- Eisenberg, N., Fabes, R.A., 1992. Emotion, regulation, and the development of social competence. In: Clark, M.S. (Ed.), *Review of Personality and Social Psychology*, Vol. 14. Emotion and Social Behaviour, pp. 119–150.
- Eisenberg, N., Shea, C.L., Carlo, G., Knight, G., 1991. Empathy-related responding and cognition: a “chicken and the egg” dilemma. In: Kurtines, W., Gewirtz, J. (Eds.), *Handbook of Moral Behavior and Development*. Vol. 2: Research. Erlbaum, Hillsdale, NJ, pp. 63–88.
- Eisenberg, N., Fabes, R.A., Murphy, B., Karbon, M., Maszk, P., Smith, M., ... Suh, K., 1994. The relations of emotionality and regulation to dispositional and situational empathy-related responding. *J. Psychol. Pers. Soc. Psychol.* 66, 776–797. <https://doi.org/10.1037/0022-3514.66.4.776>.
- Ekman, P., Friesen, W.V., Hager, J.C., 2002. *Facial Action Coding System*. Research Nexus, Salt Lake City.
- Evans, C.S., Evans, L., Marler, P., 1993. On the meaning of alarm calls: functional reference in an avian vocal system. *Anim. Behav.* 46 (1), 23–38.
- Eysenck, M.W., Mogg, K., May, J., Richards, A., Mathews, A., 1991. Bias in interpretation of ambiguous sentences related to threat in anxiety. *J. Abnorm. Psychol.* 100, 144–150.
- Faragó, T., Pongrácz, P., Miklósi, Á., Huber, L., Virányi, Z., Range, F., 2010a. Dogs' expectation about signalers' body size by virtue of their growls. *PLoS One* 5 (12), e15175.
- Faragó, T., Pongrácz, P., Range, F., Virányi, Z., Miklósi, Á., 2010b. 'The bone is mine': affective and referential aspects of dog growls. *Anim. Behav.* 79 (4), 917–925.
- FeldmanHall, O., Dalgleish, T., Evans, D., Mobbs, D., 2015. Empathic concern drives costly altruism. *NeuroImage* 105 (C), 347–356.
- Finlayson, K., Lampe, J.F., Hintze, S., Würbel, H., Melotti, L., 2016. Facial indicators of positive emotions in rats. *PLoS One* 11 (11), e0166446.
- Fitch, W.T., 2017. Empirical approaches to the study of language evolution. *Psychon. Bull. Rev.* 24 (1), 3–33.
- Franzen, A., Mader, S., Winter, F., 2018. Contagious yawning, empathy, and their relation to prosocial behavior. *J. Exp. Psychol. Gen.*
- Fraser, O.N., Bugnyar, T., 2010. Do ravens show consolation? Responses to distressed others. *PLoS One* 5 (5), e10605.
- Fraser, O.N., Bugnyar, T., 2011. Ravens reconcile after aggressive conflicts with valuable partners. *PLoS One* 6 (3), e18118.

- Fraser, O.N., Stahl, D., Aureli, F., 2008. Stress reduction through consolation in chimpanzees. *Proc. Natl. Acad. Sci.* 105 (25), 8557–8562.
- Fraser, O.N., Koski, S.E., Wittig, R.M., Aureli, F., 2009. Why are bystanders friendly to recipients of aggression? *Commun. Integr. Biol.* 2 (3), 285–291.
- Fridlund, A.J., Cacioppo, J.T., 1986. Guidelines for human electromyographic research. *Psychophysiology* 23 (5), 567–589.
- Gallese, V., Fadiga, L., Fogassi, L., Rizzolatti, G., 1996. Action recognition in the premotor cortex. *Brain* 119 (2), 593–609.
- Gallup, G.G., 1970. Chimpanzees: self-recognition. *Science* 167 (3914), 86–87.
- Gallup Jr., G.G., Anderson, J.R., 2018. The “olfactory mirror” and other recent attempts to demonstrate self-recognition in non-primate species. *Behav. Processes* 148, 16–19.
- Gallup, A.C., Militello, J., Swartwood, L., Sackett, S., 2017. Experimental evidence of contagious stretching and ingroup bias in budgerigars (*Melopsittacus undulatus*). *J. Comp. Psychol.* 131 (1), 69.
- Gonzalez-Liencreas, C., Juckel, G., Tas, C., Friebe, A., Brüne, M., 2014. Emotional contagion in mice: the role of familiarity. *Behav. Brain Res.* 263, 16–21.
- Goumon, S., Špinková, M., 2016. Emotional contagion of distress in young pigs is potentiated by previous exposure to the same stressor. *Anim. Cogn.* 19 (3), 501–511.
- Gu, X., Han, S., 2007. Attention and reality constraints on the neural processes of empathy for pain. *Neuroimage* 36 (1), 256–267.
- Guggisberg, A.G., Mathis, J., Schneider, A., Hess, C.W., 2010. Why do we yawn? *Neurosci. Biobehav. Rev.* 34 (8), 1267–1276.
- Hammers, M., Brouwer, L., 2017. Rescue behaviour in a social bird: removal of sticky ‘bird-catcher tree’ seeds by group members. *Behaviour* 154 (4), 403–411.
- Harding, E.J., Paul, E.S., Mendl, M., 2004. Animal behaviour: cognitive bias and affective state. *Nature* 427 (6972), 312.
- Harr, A.L., Gilbert, V.R., Phillips, K.A., 2009. Do dogs (*Canis familiaris*) show contagious yawning? *Anim. Cogn.* 12, 833e837.
- Hatfield, E., Cacioppo, J.T., Rapson, R.L., 1994. *Emotional Contagion*. Cambridge University Press, Cambridge.
- Hay, D.F., Nash, A., Pedersen, J., 1981. Responses of six-month-olds to the distress of their peers. *Child Dev.* 1071–1075.
- Hein, G., Singer, T., 2008. I feel how you feel but not always: the empathic brain and its modulation. *Curr. Opin. Neurobiol.* 18, 153–158. <https://doi.org/10.1016/j.conb.2008.07.012>.
- Held, S.D., Špinková, M., 2011. Animal play and animal welfare. *Anim. Behav.* 81 (5), 891–899.
- Hepach, R., Vaish, A., Tomasello, M., 2013. A new look at children’s prosocial motivation. *Infancy* 18 (1), 67–90.
- Hepach, R., Vaish, A., Tomasello, M., 2015. Novel paradigms to measure variability of behavior in early childhood: posture, gaze, and pupil dilation. *Front. Psychol.* 6, 858.
- Hess, U., Blairy, S., 2001. Facial mimicry and emotional contagion to dynamic emotional facial expressions and their influence on decoding accuracy. *Int. J. Psychophysiol.* 40 (2), 129–141.
- Hess, U., Fischer, A., 2014. Emotional mimicry: why and when we mimic emotions. *Soc. Personal. Psychol. Compass* 8 (2), 45–57.
- Hickok, G., 2009. Eight problems for the mirror neuron theory of action understanding in monkeys and humans. *J. Cogn. Neurosci.* 21 (7), 1229–1243.
- Hodges, S.D., Biswas-Diener, R., 2007. Balancing the empathy expense account: strategies for regulating empathic response. In: Farrow, T.F.D., Woodruff, P.W.R. (Eds.), *Empathy in Mental Illness*. Cambridge University Press, Cambridge, UK, pp. 389–407.
- Hodges, S.D., Wegner, D.M., 1997. Automatic and Controlled Empathy.
- Hofelich, A.J., Preston, S.D., 2012. The meaning in empathy: distinguishing conceptual encoding from facial mimicry, trait empathy, and attention to emotion. *Cogn. Emot.* 26 (1), 119–128.
- Hoffman, M.L., 2000. *Empathy and Moral Development: Implications for Caring and Justice*. Cambridge University Press.
- Hollis, K.L., Nowbahari, E., 2013. Toward a behavioral ecology of rescue behavior. *Evol. Psychol.* 11 (3), 147470491301100311.
- Hoogland, J.L., Sherman, P.W., 1976. Advantages and disadvantages of bank swallow (*Riparia riparia*) coloniality. *Ecol. Monogr.* 46, 33–58.
- Huber, A., Barber, A.L., Faragó, T., Müller, C.A., Huber, L., 2017. Investigating emotional contagion in dogs (*Canis familiaris*) to emotional sounds of humans and conspecifics. *Anim. Cogn.* 20 (4), 703–715.
- Ikkatai, Y., Watanabe, S., Izawa, E.I., 2016. Reconciliation and third-party affiliation in pair-bond budgerigars (*Melopsittacus undulatus*). *Behaviour* 153 (9–11), 1173–1193.
- Ioannou, S., Ebisch, S., Aureli, T., Bafunno, D., Ioannides, H.A., Cardone, D., ... Merla, A., 2013. The autonomic signature of guilt in children: a thermal infrared imaging study. *PLoS one* 8 (11), e79440.
- Ioannou, S., Chotard, H., Davila-Ross, M., 2015. No strings attached: physiological monitoring of rhesus monkeys (*Macaca mulatta*) with thermal imaging. *Front. Behav. Neurosci.* 9, 160.
- Isern-Mas, C., Gomila, A., 2019. Making sense of emotional contagion. *HUMANANA. MENTE J. Philos. Stud.* 12 (35), 71–100.
- Joly-Mascheroni, R.M., Senju, A., Shepherd, A.J., 2008. Dogs catch human yawns. *Biol. Lett.* 4, 446e448.
- Kano, F., Hirata, S., Deschner, T., Behringer, V., Call, J., 2016. Nasal temperature drop in response to a playback of conspecific fights in chimpanzees: a thermo-imaging study. *Physiol. Behav.* 155, 83–94.
- Keum, S., Shin, H.S., 2016. Rodent models for studying empathy. *Neurobiol. Learn. Mem.* 135, 22–26.
- Keyser, C., Gazzola, V., 2014. Dissociating the ability and propensity for empathy. *Trends Cogn. Sci.* 18 (4), 163–166.
- Kiss, A., Tóth, K., Kanizsár, O., Topál, J. (in press). The effect of oxytocin on yawning by dogs (*Canis familiaris*) exposed to human yawns. *Appl. Anim. Behav. Sci.*
- Knafo, A., Zahn-Waxler, C., Van Hulle, C., Robinson, J.L., Rhee, S.H., 2008. The developmental origins of a disposition toward empathy: genetic and environmental contributions. *Emotion* 8 (6), 737.
- Knafo-Noam, A., Vertsberger, D., Israel, S., 2018. Genetic and environmental contributions to children’s prosocial behaviour: brief review and new evidence from a reanalysis of experimental twin data. *Curr. Opin. Psychol.* 20, 60–65.
- Knapska, E., Mikosz, M., Werka, T., Maren, S., 2010. Social modulation of learning in rats. *Learn. Mem.* 17 (1), 35–42.
- Koboroff, A., Kaplan, G., Rogers, L.J., 2008. Hemispheric specialization in Australian magpies (*Gymnorhina tibicen*) shown as eye preferences during response to a predator. *Brain Res. Bull.* 76 (3), 304–306.
- Kohda, M., Hotta, T., Takeyama, T., Awata, S., Tanaka, H., Asai, J.Y., Jordan, A.L., 2019. If a fish can pass the mark test, what are the implications for consciousness and self-awareness testing in animals? *PLoS Biol.* 17 (2), e3000021.
- Kondrakiewicz, K., Kostecki, M., Szadzińska, W., Knapska, E., 2019. Ecological validity of social interaction tests in rats and mice. *Genes Brain Behav.* 18 (1), e12525.
- Koski, S.E., Sterck, E.H., 2007. Triadic postconflict affiliation in captive chimpanzees: does consolation console? *Anim. Behav.* 73 (1), 133–142.
- Koski, S.E., Sterck, E.H., 2009. Post-conflict third-party affiliation in chimpanzees: What’s in it for the third party? *Am. J. Primatol.* 71 (5), 409–418.
- Koski, S.E., Sterck, E.H., 2010. Empathic chimpanzees: a proposal of the levels of emotional and cognitive processing in chimpanzee empathy. *Eur. J. Dev. Psychol.* 7 (1), 38–66.
- Krebs, D.L., 1975. Empathy and altruism. *J. Pers. Soc. Psychol.* 32, 1134–1146.
- Kujala, M.V., 2017. Canine emotions as seen through human social cognition. *Anim. Sentience: Interdiscip. J. Anim. Feeling* 2 (14), 1.
- Kujala, M.V., 2018. Canine emotions: guidelines for research. *Anim. Sentience* 2 (14), 18.
- Lahvis, G.P., 2016. Social reward and empathy as proximal contributions to altruism: the camaraderie effect. *Social Behavior from Rodents to Humans*. Springer, Cham, pp. 127–157.
- Lakin, J.L., Chartrand, T.L., 2003a. Using nonconscious behavioural mimicry to create affiliation and rapport. *Psychol. Sci.* 14 (4), 334–339.
- Lakin, J.L., Jefferis, V.E., Cheng, C.M., Chartrand, T.L., 2003b. The chameleon effect as social glue: evidence for the evolutionary significance of nonconscious mimicry. *J. Nonverbal Behav.* 27 (3), 145–162.
- Lambert, M.L., Jacobs, I., Osvath, M., von Bayern, A.M., 2018. Birds of a feather? Parrot and corvid cognition compared. *Behaviour* 1, 1–90.
- Lamm, C., Majdandžić, J., 2015. The role of shared neural activations, mirror neurons, and morality in empathy – a critical comment. *Neurosci. Res.* 90, 15–24.
- Lamm, C., Batson, C.D., Decety, J., 2007. The neural substrate of human empathy: effects of perspective-taking and cognitive appraisal. *J. Cogn. Neurosci.* 19 (1), 42–58.
- Lamm, C., Porges, E.C., Cacioppo, J.T., Decety, J., 2008. Perspective taking is associated with specific facial responses during empathy for pain. *Brain Res.* 1227, 153–161.
- Lamm, C., Bukowski, H., Silani, G., 2016. From shared to distinct self–other representations in empathy: evidence from neurotypical function and socio-cognitive disorders. *Philos. Trans. Biol. Sci.* 371 (1686), 20150083.
- Lamm, C., Rütgen, M., Wagner, I.C., 2019. Imaging empathy and prosocial emotions. *Neurosci. Lett.* 693, 49–53.
- Langford, D.J., Crager, S.E., Shehzad, Z., Smith, S.B., Sotocinal, S.G., Levenstadt, J.S., ... Mogil, J.S., 2006. Social modulation of pain as evidence for empathy in mice. *Science* 312 (5782), 1967–1970.
- LeDoux, J., 1996. *The Emotional Brain: The Mysterious Underpinnings of Emotional Life*. Simon and Schuster.
- Lehmann, H.E., 1979. Yawning: a homeostatic reflex and its psychological significance. *Bull. Menninger Clin.* 43 (2), 123.
- Leliveld, L.M., Langbein, J., Puppe, B., 2013. The emergence of emotional lateralization: evidence in non-human vertebrates and implications for farm animals. *Appl. Anim. Behav. Sci.* 145 (1–2), 1–14.
- Liebal, K., Vaish, A., Haun, D., Tomasello, M., 2014. Does Sympathy Motivate Prosocial Behaviour in Great Apes? *PLoS One* 9, e84299.
- Liévin-Bazin, A., Pineaux, M., Clerc, O., Gahr, M., von Bayern, A.M., Bovet, D., 2018. Emotional responses to conspecific distress calls are modulated by affiliation in cockatiels (*Nymphicus hollandicus*). *PLoS One* 13 (10), e0205314.
- Lipps, T., 1903. Einfühlung, inner Nachahmung, und Organ-empfindungen. *Archiv für die gesamte Psychologie* 1, 185–204.
- Logan, C.J., Ostojić, L., Clayton, N.S., 2013. Rook, but not jackdaw, post-conflict third-party affiliation reduces aggression for aggressors. *Ethology* 119 (5), 427–435.
- Lorenz, K., 1966. *On Aggression*. (Das sogenannte Böse. Zur Naturgeschichte der Aggression, 1963), original edition. Verlag Dr. G Borothea-Schoeler.
- MacLeod, A.K., Byrne, A., 1996. Anxiety, depression, and the anticipation of future positive and negative experiences. *J. Abnorm. Psychol.* 105, 286–289.
- Macpherson, K., Roberts, W.A., 2006. Do dogs (*Canis familiaris*) seek help in an emergency? *J. Comp. Psychol.* 120 (2), 113.
- Malti, T., Dys, S.P., 2018. From being nice to being kind: development of prosocial behaviours. *Curr. Opin. Psychol.* 20, 45–49.

- Maros, K., Pongrácz, P., Bárdos, G., Molnár, C., Faragó, T., Miklósi, Á., 2008. Dogs can discriminate barks from different situations. *Appl. Anim. Behav. Sci.* 114 (1–2), 159–167.
- Martin, J., López, P., Bonati, B., Csermely, D., 2010. Lateralization when monitoring predators in the wild: a left eye control in the common wall lizard (*Podarcis muralis*). *Ethology* 116, 1226–1233.
- Martin, L.J., Hathaway, G., Isbester, K., Mirali, S., Acland, E.L., Niederstrasser, N., ... Sternberg, W.F., 2015. Reducing social stress elicits emotional contagion of pain in mouse and human strangers. *Current Biology*. *Biol.* 25 (3), 326–332.
- Massen, J.M., Behrens, F., Martin, J.S., Stocker, M., Brosnan, S.F., 2019. A comparative approach to affect and cooperation. *Neurosci. Biobehav. Rev.* 370–387.
- Massen, J.J., Gallup, A.C., 2017. Why contagious yawning does not (yet) equate to empathy. *Neurosci. Biobehav. Rev.* 80, 573–585.
- Massen, J.J., Šlipogor, V., Gallup, A.C., 2016. An observational investigation of behavioural contagion in common marmosets (*Callithrix jacchus*): indications for contagious scent-marking. *Front. Psychol.* 7, 1190.
- Masserman, J.H., Wechkin, S., Terris, W., 1964. "Altruistic" behaviour in rhesus monkeys. *Am. J. Psychiatry*.
- Mathews, A., MacLeod, C., 1994. Cognitive approaches to emotion and emotional disorders. *Annu. Rev. Psychol.* 45 (1), 25–50.
- McFarland, R., Majolo, B., 2012. The occurrence and benefits of postconflict bystander affiliation in wild Barbary macaques, *Macaca sylvanus*. *Anim. Behav.* 84 (3), 583–591.
- McIntosh, D.N., 2006. Spontaneous facial mimicry, liking and emotional contagion. *Polish Psychol. Bull.* 37 (1), 31.
- Melis, A.P., Tomasello, M., 2013. Chimpanzees' (Pan troglodytes) strategic helping in a collaborative task. *Biol. Lett.* 9 (2), 20130009.
- Mendl, M., Burman, O.H., Parker, R.M., Paul, E.S., 2009. Cognitive bias as an indicator of animal emotion and welfare: emerging evidence and underlying mechanisms. *Appl. Anim. Behav. Sci.* 118 (3–4), 161–181.
- Mendl, M., Burman, O.H., Paul, E.S., 2010. An integrative and functional framework for the study of animal emotion and mood. *Proc. R. Soc. B: Biol. Sci.* 277 (1696), 2895–2904.
- Meyza, K., Knapska, E., 2018. What can rodents teach us about empathy? *Curr. Opin. Psychol.* 24, 15–20.
- Meyza, K.Z., Bartal, I.B.A., Monfils, M.H., Panksepp, J.B., Knapska, E., 2017. The roots of empathy: through the lens of rodent models. *Neurosci. Biobehav. Rev.* 76, 216–234.
- Millen, A., Anderson, J.R., 2010. Neither infants nor toddlers catch yawns from their mothers. *Biol. Lett.* 7 (3), 440–442.
- Miller, M.L., Gallup, A.C., Vogel, A.R., Vicario, S.M., Clark, A.B., 2012. Evidence for contagious behaviors in budgerigars (*Melopsittacus undulatus*): an observational study of yawning and stretching. *Behav. Processes* 89 (3), 264–270.
- Molenberghs, P., Cunningham, R., Mattingley, J.B., 2009. Is the mirror neuron system involved in imitation? A short review and meta-analysis. *Neurosci. Biobehav. Rev.* 33 (7), 975–980.
- Molnár, C., Pongrácz, P., Faragó, T., Dóka, A., Miklósi, Á., 2009. Dogs discriminate between barks: the effect of context and identity of the caller. *Behav. Processes* 82 (2), 198–201.
- Morimoto, Y., Fujita, K., 2011. Capuchin monkeys (*Cebus apella*) modify their own behaviors according to a conspecific's emotional expressions. *Primates* 52 (3), 279–286.
- Nakahashi, W., Ohtsuki, H., 2015. When is emotional contagion adaptive? *J. Theor. Biol.* 380, 480–488.
- Nakayama, K., Goto, S., Kuraoka, K., Nakamura, K., 2005. Decrease in nasal temperature of rhesus monkeys (*Macaca mulatta*) in negative emotional state. *Physiol. Behav.* 84 (5), 783–790.
- Norscia, I., Palagi, E., 2011. Yawn contagion and empathy in *Homo sapiens*. *PLoS One* 6 (12), e28472.
- Nygren, T.E., Isen, A.M., Taylor, P.J., Dulin, J., 1996. The influence of positive affect on the decision rule in risky situations. *Org. Behav. Hum. Decis. Proc.* 66, 59–72.
- O'Hara, S.J., Reeve, A.V., 2011. A test of the yawning contagion and emotional connectedness hypothesis in dogs, *Canis familiaris*. *Anim. Behav.* 81 (1), 335–340.
- Ohsaki, N., 1995. Preferential predation of female butterflies and the evolution of Batesian mimicry. *Nature* 378 (6553), 173.
- Oliveira, T.A., Idalencio, R., Kalichak, F., dos Santos Rosa, J.G., Koakoski, G., de Abreu, M.S., ... Barcellos, L.J.G., 2017. Stress responses to conspecific visual cues of predation risk in zebrafish. *PeerJ* 5, e3739.
- Oliveira-Silva, P., Gonçalves, O.F., 2011. Responding empathically: a question of heart, not a question of skin. *Appl. Psychophysiol. Biofeedback* 36, 201–207. <https://doi.org/10.1007/s10484-011-9161-2>.
- Olzhanowski, M., Wróbel, M., Hess, U., 2019. Mimicking and sharing emotions: a reexamination of the link between facial mimicry and emotional contagion. *Cogn. Emot.* 1–10.
- Osvath, M., Sima, M., 2014. Sub-adult ravens synchronize their play: a case of emotional contagion. *Anim. Behav. Cognit.* 1, 197–205.
- Palagi, E., Norscia, I., 2013. Bonobos protect and console friends and kin. *PLoS One* 8 (11), e79290.
- Palagi, E., Leone, A., Mancini, G., Ferrari, P.F., 2009. Contagious yawning in gelada baboons as a possible expression of empathy. *Proc. Natl. Acad. Sci.* 106 (46), 19262–19267.
- Palagi, E., Norscia, I., Demuru, E., 2014a. Yawn contagion in humans and bonobos: emotional affinity matters more than species. *PeerJ* 2, e519.
- Palagi, E., dall'Olio, S., Demuru, E., Stanyon, R., 2014b. Exploring the evolutionary foundations of empathy: consolation in monkeys. *Evol. Hum. Behav.* 1–37.
- Palagi, E., Nicotra, V., Cordoni, G., 2015. Rapid mimicry and emotional contagion in domestic dogs. *R. Soc. Open Sci.* 2 (12), 150505.
- Palagi, E., Marchi, E., Cavicchio, P., Bandoli, F., 2019a. Sharing playful mood: rapid facial mimicry in *Suricata suricatta*. *Anim. Cogn.* 1–14.
- Palagi, E., Norscia, I., Cordoni, G., 2019b. Lowland gorillas (*Gorilla gorilla gorilla*) failed to respond to others' yawn: experimental and naturalistic evidence. *J. Comp. Psychol.* 133 (3), 406.
- Panksepp, J., 1991. Affective neuroscience: a conceptual framework for the neurobiological study of emotions. *Int. Rev. Stud. Emot.* 1 (59–99), 57.
- Panksepp, J., 2004. *Affective Neuroscience: The Foundations of Human and Animal Emotions*. Oxford university press.
- Parr, L.A., 2001. Cognitive and physiological markers of emotional awareness in chimpanzees (*Pan troglodytes*). *Anim. Cogn.* 4 (3–4), 223–229.
- Parr, L.A., Hopkins, W.D., 2000. Brain temperature asymmetries and emotional perception in chimpanzees, *Pan troglodytes*. *Physiol. Behav.* 71 (3–4), 363–371.
- Parr, L.A., Waller, B.M., Vick, S.J., Bard, K.A., 2007. Classifying chimpanzee facial expressions using muscle action. *Emotion* 7 (1), 172.
- Paukner, A., Anderson, J.R., 2005. Video-induced yawning in stump-tail macaques (*Macaca arctoides*). *Biol. Lett.* 2 (1), 36–38.
- Paul, E.S., Harding, E.J., Mendl, M., 2005. Measuring emotional processes in animals: the utility of a cognitive approach. *Neurosci. Biobehav. Rev.* 29 (3), 469–491.
- Paul, E.S., Sher, S., Tamietto, M., Winkielman, P., Mendl, M.T., 2020. Towards a comparative science of emotion: Affect and consciousness in humans and animals. *Neuroscience & Biobehavioral Reviews* 108, 749–770.
- Paulus, M., 2014. The early origins of human charity: developmental changes in preschoolers' sharing with poor and wealthy individuals. *Front. Psychol.* 5, 344.
- Paulus, M., 2018. The multidimensional nature of early prosocial behaviour: a motivational perspective. *Curr. Opin. Psychol.* 20, 111–116.
- Paulus, M., Kühn-Popp, N., Licata, M., Sodian, B., Meinhardt, J., 2013. Neural correlates of prosocial behaviour in infancy: different neurophysiological mechanisms support the emergence of helping and comforting. *Neuroimage* 66, 522–530.
- Perez, E.C., Elie, J.E., Boucaud, I.C., Crouchet, T., Soulage, C.O., Soula, H.A., ... Vignal, C., 2015. Physiological resonance between mates through calls as possible evidence of empathic processes in songbirds. *Hormones and Behaviour* 75, 130–141.
- Pérez-Manrique, A., Gomila, A., 2018. The comparative study of empathy: sympathetic concern and empathic perspective-taking in non-human animals. *Biol. Rev.* 93 (1), 248–269.
- Perry, C.J., Baciadonna, L., Chittka, L., 2016. Unexpected rewards induce dopamine-dependent positive emotion-like state changes in bumblebees. *Science* 353 (6307), 1529–1531.
- Pfäbigen, D.M., Seidel, E.M., Wucherer, A.M., Keckeis, K., Derrl, B., Lamm, C., 2015. Affective empathy differs in male violent offenders with high- and low-trait psychopathy. *J. Pers. Disord.* 29 (1), 42–61.
- Piaget, J., 1953. *The Origins of Intelligence in the Child*. International Universities Press, New York.
- Povinelli, D.J., 1993. Reconstructing the evolution of mind. *Am. Psychol.* 48, 493–509.
- Preston, S.D., 2007. A perception-action model for empathy. In: Farrow, T.F.D., Woodruff, P.W.R. (Eds.), *Empathy in Mental Illness*. Cambridge University Press, Cambridge, UK, pp. 428–447.
- Preston, S.D., de Waal, F.B.M., 2002. Empathy: its ultimate and proximate bases. *Behav. Brain Sci.* 25, 1–72.
- Preston, S.D., Hofelich, A.J., 2012. The many faces of empathy: parsing empathic phenomena through a proximate, dynamic-systems view of representing the other in the self. *Emot. Rev.* 4 (1), 24–33.
- Prochazkova, E., Kret, M.E., 2017. Connecting minds and sharing emotions through mimicry: a neurocognitive model of emotional contagion. *Neurosci. Biobehav. Rev.* 80, 99–114.
- Provine, R.R., 1992. Contagious laughter: laughter is a sufficient stimulus for laughs and smiles. *Bull. Psychon. Soc.* 30 (1), 1–4.
- Pruetz, J.D., 2011. Targeted helping by a wild adolescent male chimpanzee (*Pan troglodytes verus*): evidence for empathy? *J. Ethol.* 29 (2), 365–368.
- Quervel-Chaumette, M., Faerber, V., Faragó, T., Marshall-Pescini, S., Range, F., 2016. Investigating empathy-like responding to conspecifics' distress in pet dogs. *PLoS One* 11 (4), e0152920.
- Reimert, I., Fong, S., Rodenburg, T.B., Bolhuis, J.E., 2017. Emotional states and emotional contagion in pigs after exposure to a positive and negative treatment. *Appl. Anim. Behav. Sci.* 193, 37–42.
- Rice, G.E., Gainer, P., 1962. "Altruism" in the albino rat. *J. Comp. Physiol. Psychol.* 55 (1), 123.
- Rizzolatti, G., Caruana, F., 2017. Some considerations on de Waal and Preston review. *Nat. Rev. Neurosci.* 18 (12), 769.
- Rizzolatti, G., Fadiga, L., Gallese, V., Fogassi, L., 1996. Premotor cortex and the recognition of motor actions. *Cogn. Brain Res.* 3 (2), 131–141.
- Roelofs, S., Boleij, H., Nordquist, R.E., van der Staay, F.J., 2016. Making decisions under ambiguity: judgment bias tasks for assessing emotional state in animals. *Front. Behav. Neurosci.* 10, 119.
- Rogers, L.J., 2002. Lateralization in vertebrates: its early evolution, general pattern, and development. *Advances in the Study of Behavior* Vol. 31. Academic Press, pp. 107–161.
- Rolls, E.T., 2013. *Emotion and Decision Making Explained*. Oxford University Press.
- Romero, T., Castellanos, M.A., de Waal, F.B., 2010. Consolation as possible expression of sympathetic concern among chimpanzees. *Proc. Natl. Acad. Sci.* 107 (27), 12110–12115.
- Romero, T., Konno, A., Hasegawa, T., 2013. Familiarity bias and physiological responses in contagious yawning by dogs support link to empathy. *PLoS One* 8 (8), e71365.

- Roth-Hanania, R., Davidov, M., Zahn-Waxler, C., 2011. Empathy development from 8 to 16 months: early signs of concern for others. *Infant Behav. Dev.* 34 (3), 447–458.
- Rozin, P., Royzman, E.B., 2001. Negativity Bias, negativity dominance, and contagion. *Personal. Soc. Psychol. Rev.* 5 (4), 296–320.
- Ruby, P., Decety, J., 2004. How would you feel versus how do you think she would feel? A of neuroimaging study of perspective taking with social emotions. *J. Cogn. Neurosci.* 16, 988–999.
- Russell, J.A., 2003. Core affect and the psychological construction of emotion. *Psychol. Rev.* 110 (1), 145.
- Russell, Y.I., Phelps, S., 2013. How do you measure pleasure? A discussion about intrinsic costs and benefits in primate allogrooming. *Biol. Philos.* 28 (6), 1005–1020.
- Rütgen, M., Seidel, E.M., Silani, G., Riečanský, I., Hummer, A., Windischberger, C., ... Lamm, C., 2015. Placebo analgesia and its opioidergic regulation suggest that empathy for pain is grounded in self pain. *Proceedings of the National Academy of Sciences. Natl. Acad. Sci.* 112 (41), E5638–E5646.
- Saito, Y., Yuki, S., Seki, Y., Kagawa, H., Okanoya, K., 2016. Cognitive bias in rats evoked by ultrasonic vocalizations suggests emotional contagion. *Behav. Processes* 132, 5–11.
- Sato, N., Tan, L., Tate, K., Okada, M., 2015. Rats demonstrate helping behaviour toward a soaked conspecific. *Anim. Cogn.* 18 (5), 1039–1047.
- Sauer, E.F., Sauer, E.M., 1967. Yawning and other maintenance activities in the South African Ostrich. *Auk* 571–587.
- Schino, G., Marini, C., 2012. Self-protective function of post-conflict bystander affiliation in mandrills. *PLoS One* 7 (6), e38936.
- Schwartz, L.P., Silberberg, A., Casey, A.H., Kearns, D.N., Slotnick, B., 2017. Does a rat release a soaked conspecific due to empathy? *Anim. Cogn.* 20 (2), 299–308.
- Schwing, R., Nelson, X.J., Wein, A., Parsons, S., 2017. Positive emotional contagion in a New Zealand parrot. *Curr. Biol.* 27 (6), R213–R214.
- Seed, A.M., Clayton, N.S., Emery, N.J., 2007. Postconflict third-party affiliation in rooks, *Corvus frugilegus*. *Curr. Biol.* 17 (2), 152–158.
- Sharpe, L.L., 2005. Play does not enhance social cohesion in a cooperative mammal. *Anim. Behav.* 70 (3), 551–558.
- Sharpe, L.L., Cherry, M.I., 2003. Social play does not reduce aggression in wild meerkats. *Animal Behaviour* 66, 989–997.
- Shimada, M., Sueur, C., 2018. Social play among juvenile wild Japanese macaques (*Macaca fuscata*) strengthens their social bonds. *Am. J. Primatol.* 80 (1), e22728.
- Silberberg, A., Allouch, C., Sandfort, S., Kearns, D., Karpel, H., Slotnick, B., 2014. Desire for social contact, not empathy, may explain “rescue” behaviour in rats. *Anim. Cogn.* 17 (3), 609–618.
- Silk, J.B., House, B.R., 2016. The evolution of altruistic social preferences in human groups. *Philos. Trans. Biol. Sci.* 371 (1687), 20150097.
- Silk, J.B., Brosnan, S.F., Vonk, J., Henrich, J., Povinelli, D.J., Richardson, A.S., ... Schapiro, S.J., 2005. Chimpanzees are indifferent to the welfare of unrelated group members. *Nature* 437 (7063), 1357.
- Silk, J.B., Brosnan, S.F., Henrich, J., Lambeth, S.P., Shapiro, S., 2013. Chimpanzees share food for many reasons: the role of kinship, reciprocity, social bonds and harassment on food transfers. *Anim. Behav.* 85 (5), 941–947.
- Silva, K., de Sousa, L., 2011. ‘Canis empathicus’? A proposal on dogs’ capacity to empathize with humans. *Biol. Lett.* 7 (4), 489–492.
- Silva, K., Bessa, J., de Sousa, L., 2012. Auditory contagious yawning in domestic dogs (*Canis familiaris*): first evidence for social modulation. *Anim. Cogn.* 15 (4), 721–724.
- Singer, T., Klimecki, O.M., 2014. Empathy and compassion. *Curr. Biol.* 24 (18), R875–R878.
- Singer, T., Lamm, C., 2009. The social neuroscience of empathy. *Ann. N. Y. Acad. Sci.* 1156 (1), 81–96.
- Singer, T., Seymour, B., O’Doherty, J., Kaube, H., Dolan, R.J., Frith, C.D., 2004. Empathy for pain involves the affective but not sensory components of pain. *Science* 303 (5661), 1157–1162.
- Sivaseelachandran, S., Acland, E.L., Abdallah, S., Martin, L.J., 2018. Behavioural and mechanistic insight into rodent empathy. *Neurosci. Biobehav. Rev.* 91, 130–137.
- Sommerville, R., O’Connor, E.A., Asher, L., 2017. Why do dogs play? Function and welfare implications of play in the domestic dog. *Appl. Anim. Behav. Sci.* 197, 1–8.
- Speakman, J.R., Ward, S., 1998. Infrared thermography: principles and applications. *Zoology-Jena* 101, 224–232.
- Szűmegi, Z., Oláh, K., Topál, J., 2014. Emotional contagion in dogs as measured by change in cognitive task performance. *Appl. Anim. Behav. Sci.* 160, 106–115.
- Thorpe, W.H., 1963. *Learning and Instinct in Animals*, 2nd ed. Harvard, Cambridge, MA.
- Tinbergen, N., 1960. *The Herring Gull’s World*. Doubleday, Garden City, NY.
- Titchener, E.B., 1909. *Lectures on the Experimental Psychology of the Thought Processes*. Macmillan, New York.
- Toohey, P., 2011. *Boredom: A Lively History*. Yale University Press.
- Townsend, S.W., Koski, S.E., Byrne, R.W., Slocombe, K.E., Bickel, B., Boeckle, M., ... Glock, H.J., 2017. Exorcising G rrice’s ghost: an empirical approach to studying intentional communication in animals. *Biological Reviews. Rev.* 92 (3), 1427–1433.
- Ueno, H., Suemitsu, S., Murakami, S., Kitamura, N., Wani, K., Takahashi, Y., ... Ishihara, T., 2019. Rescue-like Behaviour in Mice is Mediated by their Interest in the Restraint tool. *Scientific reports. Rep.* 9 (1), 1–10.
- Vaish, A., Carpenter, M., Tomasello, M., 2009. Sympathy through affective perspective taking and its relation to prosocial behaviour in toddlers. *Dev. Psychol.* 45 (2), 534.
- van Buuren, M., Auersperg, A., Gajdon, G., Tebbich, S., von Bayern, A., 2018. No evidence of mirror self-recognition in keas and Goffin’s cockatoos. *Behaviour* 1 (aop), 1–24.
- Van Der Schalk, J., Fischer, A., Doosje, B., Wigboldus, D., Hawk, S., Rotteveel, M., Hess, U., 2011. Convergent and divergent responses to emotional displays of ingroup and outgroup. *Emotion* 11 (2), 286.
- Vasconcelos, M., Hollis, K., Nowbahari, E., Kacelnik, A., 2012. Pro-sociality without empathy. *Biol. Lett.*, rsbl20120554.
- Vonk, J., 2019a. A fish eye view of the mirror test. *Learn. Behav.* 1–2.
- Vonk, J., 2019b. Emotional contagion or sensitivity to behavior in ravens? *Proc. Natl. Acad. Sci.* 116 (37), 18168.
- Waller, B.M., Peirce, K., Caeiro, C.C., Scheider, L., Burrows, A.M., McCune, S., Kaminski, J., 2013. Paedomorphic facial expressions give dogs a selective advantage. *PLoS One* 8 (12), e82686.
- Warneken, F., Tomasello, M., 2006. Altruistic helping in human infants and young chimpanzees. *Science* 311 (5765), 1301–1303.
- Warneken, F., Hare, B., Melis, A.P., Hanus, D., Tomasello, M., 2007. Spontaneous altruism by chimpanzees and young children. *PLoS Biol.* 5 (7), e184.
- Wascher, C.A., Scheiber, I.B., Kotrschal, K., 2008. Heart rate modulation in bystanding geese watching social and non-social events. *Proc. R. Soc. Lond., B, Biol. Sci.* 275 (1643), 1653–1659.
- Wathan, J., Burrows, A.M., Waller, B.M., McComb, K., 2015. EquiFACS: the equine facial action coding system. *PLoS One* 10 (8), e0131738.
- Winkielman, P., Berridge, K.C., 2004. Unconscious emotion. *Curr. Dir. Psychol. Sci.* 13 (3), 120–123.
- Wispé, L., 1968. Sympathy and empathy. In: In: Sills, D.L. (Ed.), *International Encyclopedia of the Social Sciences* Vol. 15. Free Press, New York, pp. 441–447.
- Wispé, L., 1986. The distinction between sympathy and empathy: to call forth a concept a word is needed. *J. Pers. Soc. Psychol.* 50, 314–321.
- Wittig, R.M., Crockford, C., Wikberg, E., Seyfarth, R.M., Cheney, D.L., 2007. Kin-mediated reconciliation substitutes for direct reconciliation in female baboons. *Proc. R. Soc. B: Biol. Sci.* 274 (1613), 1109–1115.
- Wooddell, L.J., Vandelee, J.J., Nathman, A.C., Beisner, B.A., McCowan, B., 2019. Not all grooming is equal: differential effects of political vs affiliative grooming on cytokines and glucocorticoids in rhesus macaques. *PeerJ Prepr.* 7, e27961v1.
- Yamamoto, S., 2017. Primate empathy: three factors and their combinations for empathy-related phenomena. *Wiley Interdiscip. Rev. Cogn. Sci.* 8 (3), 1–11.
- Yamamoto, S., Humle, T., Tanaka, M., 2009. Chimpanzees help each other upon request. *PLoS One* 4 (10), e7416.
- Yamamoto, S., Humle, T., Tanaka, M., 2012. Chimpanzees’ flexible targeted helping based on an understanding of conspecifics’ goals. *Proc. Natl. Acad. Sci.* 109 (9), 3588–3592.
- Yamamoto, C., Morisaka, T., Furuta, K., Ishibashi, T., Yoshida, A., Taki, M., ... Amano, M., 2015. Post-conflict affiliation as conflict management in captive bottlenose dolphins (*Tursiops truncatus*). *Sci* 5, 14275.
- Yamanashi, Y., Nogami, E., Teramoto, M., Morimura, N., Hirata, S., 2018. Adult-adult social play in captive chimpanzees: Is it indicative of positive animal welfare? *Appl. Anim. Behav. Sci.* 199, 75–83.
- Yoon, J.M., Tennie, C., 2010. Contagious yawning: a reflection of empathy, mimicry, or contagion? *Anim. Behav.* 79 (5), e1–e3.
- Zahn-Waxler, C., Radke-Yarrow, M., Wagner, E., Chapman, M., 1992a. Development of concern for others. *Dev. Psychol.* 28 (1), 126.
- Zahn-Waxler, C., Robinson, J.L., Emde, R.N., 1992b. The development of empathy in twins. *Dev. Psychol.* 28 (6), 1038.
- Zentall, T.R., 2001. Imitation in animals: evidence, function, and mechanisms. *Cybern. Syst.* 32 (1–2), 53–96.