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“The origins of empathy: A comparative investigation of empathy and its emotional basis in an avian and primate species.”

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Chapter 1.

We are brothers and sisters under the skin, with all the other animals. (...)

And once we understand them, we will finally understand ourselves.

— Prof. Dr. Jaak Panksepp

(The science of emotions, 2013, TedX)

Introduction

Human empathy: Feeling as the other

In their daily life, humans are confronted continuously with a multitude of social encounters. These may range from well-known, regular conversations at the coffee shop to important meetings at work, or less common situations such as dealing with the sudden loss of a colleague's friend. We may not always find the right words, or respond how we're socially supposed to respond. Yet, in a remarkable way, humans often navigate these interactions successfully. And they do so thanks to, amongst others, emotional and cognitive skills that are combined together in what we call empathy (Decety & Jackson, 2004). As a result, the empathic life of humans is an intriguing exercise of trying to emotionally and cognitively relate to the other's predicament, and also their joys, while balancing our own feelings and thoughts in parallel (Singer & Lamm, 2009). Through their empathic mindset, medical doctors attempt at healing us physically, while therapists aim at helping us mentally (Lamm et al., 2019). And even our everyday, seemingly irrelevant encounters are often filled with effort in order to understand the other better, to manage our social connections, and eventually, to improve our own lives along with those of the people we are connected to.

Specifically, an essential aspect of this affective resonance, or feeling as the other, is emotional contagion (Hatfield et al., 1994; de Waal, 2008). Emotional contagion is defined as taking on the other's emotional state as if it were one's own state, often described as an instantaneous *catching* of emotions. In that respect, it differs from empathy which in addition entails a cognitive representation of the other's state, and thus, the ability to differentiate between the emotional state of the self and the other, and an understanding of what the other is emotionally experiencing. Emotional contagion may happen when we see a theatre play and experience the emotions of the actors on scene, or when we're in a busy street where one loud frightened scream may cause a contagious wave of panic through the crowd.

Subsequently, what we then do with these feelings depends on further, conscious or unconscious, emotional and cognitive processing (Lamm et al., 2007). Emotional contagion might remain at the self-centered level where no further action is taken, and we continue to feel unsettled, which may include an increasing personal distress about the situation (Decety & Lamm, 2009). Yet, consequential actions can take the form of prosocial behavior, where the loud scream will not only make us feel upset, but will also raise concern about the other and perhaps prompt us to move toward the source of distress, to offer help or consolation. This shift from a self-centered emotional experience, and feeling *as* the other, to a other-focused experience, and feeling *for* the other, is also labelled sympathy (Eisenberg & Eggum, 2009). As an impressive result, when emotional contagion allows us to emotionally relate to one another, it additionally provides us with the possibility to better regulate our social interactions, and it may motivate us to engage as well as to cooperate with others. Accordingly, aside from serving as mechanism for empathy and its related phenomena such as sympathy, emotional contagion may also facilitate other social processes, rendering it a compelling phenomenon of human behavior.

Comparative empathy: Understanding the evolutionary origins

Due to this fascinating and apparent fundamental role of emotional contagion in various human social behaviors, many researchers have set out to study it in our own and other species. The first related studies in animals date back to the 1960's (e.g. Church, 1959), followed by a surge in interest in the early 2000's until today, in which various animal experts from different disciplines focused on investigating emotional contagion and other empathy-related phenomena (see Pérez-Manrique & Gomila, 2018, for review). This scientific interest has contributed tremendously to our general knowledge about the social lives of different species, including their emotional behaviors towards one another (Clay & de Waal, 2013). So far, parental care has been suggested as one of the fundamental evolutionary drivers for empathy, and in particular for emotional contagion, as an emotional connection between parent and offspring is crucial for facilitating offspring care, leading to increased offspring survival, and in turn, increases parent fitness (Preston & de Waal, 2002). Further, it is proposed that a more generalized ability has evolved from this parent-offspring connection, so we're also able to emotionally relate to other conspecifics (Decety et al., 2015). Sharing the same emotional state may help us to communicate and coordinate better with others, and as a result, emotional contagion is suggested to facilitate group life and social bonding (de Waal, 2008). Still, precisely understanding the biological costs and benefits of emotional contagion, as well as how emotional contagion affects group formation, remains greatly understudied. In recent work, emotional contagion was suggested to serve fast information transmission between group members about the environment (Nakahashi & Ohtsuki, 2018). This transmission, or signaling function, leads to beneficial outcomes for other members when they show relevant behavior to the emotion (e.g. escape from threat). However, fast signaling may be costly when

inappropriate behavior is shown, leading to adverse consequences (e.g. mass panic). This is supported through formal modelling, showing that a greater group size is more adaptive for animals with emotional contagion as this results in a greater chance of receiving information, yet, to balance out costly errors to trivial events these animals evolved to respond with decreased sensitivity to environmental cues. Additional empirical research is needed to further confirm this hypothesis, and a discussion of the adaptive value of emotion contagion is outside the scope of this thesis.

On account of emotional contagion's assumed widespread importance, scholars have proposed it to be one of the oldest evolutionary conserved mechanisms of empathy (de Waal, 2008; Isern-Mas & Gomila, 2019). That said, it remains controversial whether emotional contagion is (phylogenetically) preserved in one specific lineage such as in mammals, or whether it is also present in other taxonomic groups (de Waal & Preston, 2017). Therefore, to better understand the evolutionary origins of human emotional contagion, and whether emotional contagion emerged as the result of a shared common ancestor or due to similar environmental pressures, it is essential to examine emotional contagion comparatively in different species (Osvath & Sima, 2014). Still, the field strongly reflects a mammalian bias, in which mostly primate and rodent species are studied. The rodent literature contributes significantly to our understanding of the brain in relation to emotional contagion (Panksepp & Lahvis, 2011; Meyza et al., 2017), yet, the mammalian bias is still surprising as various other taxa demonstrate behavior potentially facilitated by emotional contagion. For instance, many avian species demonstrate extensive and biparental care, social life in groups, and long-term pair bonds, and thus, birds would make ideal study candidates (Emery et al., 2007). Hence, for our evolutionary understanding and to establish a more comprehensive comparative framework, we need to broaden the scope to additional, less-studied species. I specifically incorporate this notion into my own work by investigating emotional contagion in both an avian and a primate species (i.e., common ravens and common marmosets).

Limitations of comparative empathy and emotional contagion research

Despite its popular appeal, emotional contagion remains an elusive topic that is highly complex and challenging to investigate empirically. The research field shows a negativity bias, meaning that the majority of the scientific studies includes intense, negative emotions, such as in the context of pain, fear, or undefined general distress (though see, e.g. Rygula et al., 2012). These states are more salient than positive emotions, and thus easier to induce, as well as to observe (Boissy et al., 2007). Some argue that responding to negative states is more adaptive, which is supported by a widespread, cross-species attention bias for negative information (Rozin & Royzman, 2001). Yet, positive emotions are incredibly important for both humans and animals, and research shows the extensive beneficial impact of social support and affiliative relations, and thus (assumed) positive emotions, on mental and physical health

(e.g. in humans, Uchino et al., 2006; in farm animals, Rault, 2012; primates, Silk et al., 2010; birds, Wascher et al., 2019; see Wooddell et al. 2019, for discussion). Following this premise, I included both negative and positive experimental conditions in my empirical investigation of emotional contagion.

Importantly, the biggest limitation and difficulty in emotion (contagion) research arises from the lack of (human) language in animals (Paul et al., 2005). Indeed, studies on the emotional experience in humans typically rely heavily on self-report to determine emotions. Participants in a study may either write down or say what they think they feel, and this assessment may then be combined with other measures, such as heart rate, pupil size, electrodermal variation, brain region activity, or hormonal levels. Generally, though we may quantify the emotional experience in humans by combining self-report and physiological correlate measures, this approach is also limited as it excludes pre-verbal children or those who are speech-impaired, and it is known that self-report does not always accurately reflect the present emotional state (Winkielman & Berridge, 2004). Still, self-report is currently the most common measure of emotions in humans, and so, in (non-human) animals we face the challenge of measuring emotions without verbal report, and additionally, we are often also more limited with respect to physiological measures. This difficulty not only confronts us with the question *“What are animal emotions?”*, but also extends to other questions such as *“How do we measure emotions without self-report?”*, and *“How do we measure social emotions?”*, as in the case of emotional contagion. Because after all, “Empathy relies on emotions: the capacity makes no sense without them” (de Waal, 2011, p. 198; Clay et al., 2018). Therefore, the systematic quantification of affective components in a social setting is needed to substantially enhance and push forward the current emotional contagion and broader empathy research field.

Animal emotions: What are they and how do we measure them?

As concluded in the previous paragraph, at the core of emotional contagion are emotions. Hence, in order to measure emotional contagion, we ought to measure emotions in different subjects and a potential convergence between their states. This brings us to the first foundational question: what are (animal) emotions? The various fields and subdisciplines of emotion research are infamous for using differing terminology and definitions, resulting in great confusion (Fox, 2018). It is thus of particular importance to define and declare the theoretical framework I adopted here and in the empirical work later on. I apply a functionalist definition (Panksepp, 1998; Adolphs & Andler, 2018; but see Barrett, 2017), which states that emotions are adaptive responses to deal with environmental opportunities and challenges, and to obtain resources and avoid harm (e.g. de Vere & Kuczaj, 2016). Emotions are multi-componential, and consist of coordinated changes in subjective feelings, behavior, physiology, and cognition (Anderson & Adolphs, 2014). For instance, the emotion fear is an adaptive reaction to a

threatening environment, and is associated with specific changes in feelings (e.g. feeling afraid), behavior (e.g. running away from the threat), physiology (e.g. increased heart rate and pupil size), and cognition (e.g. increased attention for negative information). With this multi-componential definition in mind, we can tackle the next important question: how do we measure emotions without self-report? The contemporary scientific consensus is that measuring the subjective feeling component is currently still impossible in animals (e.g. Paul et al., 2005), and in this regard, the functionalist approach focusses on the other components, rather than lingering on the feeling experience (Adolphs & Andler, 2018; but see Panksepp, 2005; LeDoux, 2012). With this approach, we are able to objectively assess each of the other three components, serving as evidence for an emotion, and this multi-component model allows for comparative research between species (Panksepp & Watt, 2011; Anderson & Adolphs, 2014; Adolphs, 2018). Importantly, it has been suggested that emotions are represented in a two-dimensional model (i.e. “dimensional approach”) (see Mendl et al., 2010 for discussion). This model embodies two universal characteristics, namely arousal (i.e. levels of intensity) and valence (i.e. positivity or negativity) (both form what is known as “core-affect”, see Russell, 1980). For instance, fear is a high arousal, negative state, and excitement is a high arousal, positive state. Therefore, empirical research that aims to study animal emotions should consider both dimensions as equally contributing to an emotional state, and thus, as equally important to investigate (Paul et al., 2005; Edgar et al., 2012). Still, studying these dimensions in animals, and in particular valence, is challenging, which is mostly due to the lack of self-report, as discussed previously.

Behavior serves as an immense source of information, and impressive contributions have been made to investigate emotions (e.g. in rats, Knapska et al., 2010; in pigs, Reimert et al., 2017; in primates, Berthier & Semple, 2018). Nonetheless, and certainly in light of emotion research, it remains pivotal to acknowledge this component’s limitations. When studying animal behavior, we draw conclusions from what is overtly observable with the human eye. Without additional information on the context, the use of objective methods, or the assessment of other components, our interpretation of the behavior and, moreover, its valence, remains limited (Paul et al., 2005). The need for additional information is appropriately illustrated by the example of grooming, which is often assumed to be related to a positive (relaxed) state (Shutt et al., 2007). Yet, grooming may also concur in contexts of distress (see e.g. Semple et al., 2013, for discussion) and may have different functions (e.g. bonding, stress-relieving, strategic), as well as opposite physiological effects on health (Wooddell et al., 2019). Therefore, ample information on the context in which a behavior is observed is important, as a behavior such as grooming does not necessarily indicate the same valence in each instance. Still, even with sufficient information, which may increase our certainty to infer positive or negative valence, observational methods often lack an objective approach. For instance, by means of a detailed morphological analysis, researchers found four subtle variations in the expression of silent bared-teeth display in crested macaques, each linked to

different functional outcomes (Clark et al., 2020). This research emphasizes the extensive variation in what is assumed to be a single expression, and highlights the need for analytical, objective methods. As a final comment, the benefit of including other components is elegantly demonstrated by research on rat tickling and its assumed positive state. Tickling in rats has been extensively studied in cross-disciplinary and multi-modal research (e.g. in behavior, Panksepp & Burgdorf, 2003; cognition, Rygula et al., 2012), providing evidence that tickling increases positive vocalizations and approach behavior, and decreases measures of anxiety and levels of stress-related hormones (see LaFollette et al., 2017, for review). As a result, the multi-component approach allows to draw conclusions on positive valence with more certainty. My argument on measures of behavior and its limitations is also supported by recent research in humans, providing accumulating evidence that a one-on-one match between behavior and emotions is questionable (Barrett et al., 2019). Some even question the existence of so-called emotional fingerprints, as supported by cross-cultural research showing that the meaning of human facial expressions may not be as universal as thought for a long time (Crivelli et al., 2016; Gendron et al., 2020).

In regards of measuring emotional contagion through behavior, some scholars have emphasized the importance of synchronized behavior (e.g. behavioral contagion and mimicry) as a primary indicator of emotional contagion (Palagi et al., 2015). The rationale of using observations of mimicry as evidence for emotional contagion (partially) stems from the feedback-hypothesis: mimicking the other's expressions may result in an emotional feedback from those expressions, leading to a congruent emotional state with the other (Hatfield et al., 1994). Yet, the current human evidence does not unanimously support this hypothesis, nor the idea that behavioral matching automatically implies emotional matching (Briefer, 2018; Edgar & Nicol, 2018), or that an emotional match necessarily involves mimicry (Isern-Mas & Gomila, 2019) (further discussion of mechanisms is outside the scope of this thesis, but see Isern-Mas & Gomila, 2019; Wróbel & Imbir, 2019). Therefore, using synchronized behavior in animals as sole indicator for emotional contagion may obstruct accurate inference of the present emotional state. Furthermore, and as just discussed, interpreting this (synchronized) behavior remains highly difficult without relevant information on the context, without objective methods, or without investigating other parameters.

In the same vein, physiological approaches have greatly advanced our understanding of animal emotions and its transfer between individuals (e.g. in birds, Edgar et al., 2011; in rodents, Burkett et al., 2016; in fish, Oliveira et al., 2017). Similarly to the behavioral method, the main focus is often on finding patterns of synchrony, for instance, in matching cortisol levels or heart rate (e.g. Wascher et al., 2008). Yet, and correspondingly to the argument above, physiological changes are not necessarily indicative of emotional changes. In fact, recent research on physiological methods that presumably assess valence in animals, and this in particular in reference to changes in cortisol/corticosteroid levels, provides insight that these methods more likely assess arousal rather than negative distress (i.e. valence) (Ralph &

Tilbrook, 2016; MacDougall-Shackleton et al., 2019). A discussion of physiological methods to study animal emotions would not be complete without an honorable mention of the work by Panksepp and colleagues in the field of affective neuroscience (Panksepp, 1998; Panksepp & Panksepp, 2013). However, in my research I focus on easily transferable methods, often with a non-invasive approach, and so this discussion does not include further summary of the neuroscientific work. In conclusion, to demonstrate emotional contagion, one needs to demonstrate a similar emotional state in both subjects, including both emotional dimensions of arousal and valence (Edgar and Nicol, 2018). Therefore, acknowledging both the benefits and limitations of behavioral and physiological methods is an important step forward in animal emotion research, and underlines the need for objective and valence-focused methods.

Measuring animal emotions: The cognitive approach

Emotions are multi-componential and, consequently, emotions allow a global response to an event (Boissy et al., 2007), which has led emotions to be labelled “special intelligent interfaces” (Scherer, 1994, as cited in de Waal, 2011, p. 196). This contemporary notion is in contrast to the outdated belief that emotions are inferior and uncontrollable passions, regularly standing in the way of our more superior reasoning, a notion going back to Plato (Solomon, 1993). There is now an extensive amount of research providing evidence that, metaphorically speaking, emotion takes up a prominent position next to cognition, instead of a subpar one below (Pessoa, 2013). For instance, emotions can be inhibited, hidden, or used for strategic reasons (de Waal, 2011), and without emotion our cognitive reasoning may not be sufficient to efficiently evaluate a situation. This is supported by neuroscientific evidence demonstrating the strong interlinkage between emotions and cognition, in which both often use common processes and overlapping neural systems (Clore, 2018), to the extent that impaired emotional understanding may impede cognitive performance (e.g. decision-making and risk aversion, Damasio, 1994). Additional psychiatric research supports this bidirectional emotion-cognition connection, by providing evidence that cognition positively or negatively alters the processing of affective information (e.g. cognitive appraisal changes self-reported anxiety, Mathews & Macleod, 2002), and in return, that emotional states impact cognitive processing, either in an improving or impeding manner. 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 & Byrne, 1996), show an attention bias for negative information (Mathews & MacLeod, 1994), and report more negative memories (Burke & Mathews, 1992). 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). Moreover, cognitive biases are also observed outside the psychiatric domain, with the general notion that emotions change how we perceive the world around us. In the example of

decision-making, people in a positive mood will judge the proverbial glass as half-full and people in a more negative mood will judge it half-empty.

Until recently, the cognitive component of an emotion was less explored in animals. Based on the human psychology research just discussed and its cognitive bias hypothesis, scholars have suggested that cognition may serve as a proxy to assess animal emotions (Paul et al., 2005; Mendl et al., 2009). Concretely, analyzing the cognitive performance on a given test (e.g. on attention or decision-making) may reveal *biases* or deviations in this performance. Then, the specific positive or negative cognitive biases would allow to derive the positive or negative valence of an emotional state. Accordingly, the cognitive approach offers the opportunity to investigate other components aside from the usually studied behavior and physiology, and, moreover, it provides an objective way of assessing the more challenging dimension of an emotion, namely valence. The cognitive bias hypothesis was scientifically tested in animals for the first time by Harding and colleagues (2004), by what we call a *cognitive bias test*. This study showed that rats living in unpredictable circumstances performed slower and less in a decision-making test, providing evidence for the cognitive bias hypothesis that a negative state induces negative biases. Following its publication (2004) the cognitive bias test as a potential means to assess an animal's affective state has been applied in a great amount of research, involving a variety of species (i.e. mammals, birds, and insects), numerous experimental conditions (e.g. enrichment or stress interventions, husbandry procedures, stereotypies) and different disciplines (from animal welfare science, behavioral biology, to neuroscience and psychopharmacology) (see for reviews, Mendl et al., 2009; Roelofs et al., 2016; Baciadonna & McElligott, 2015; and for meta-analyses, Neville et al., 2020; Lagisz et al., 2020). The test has repeatedly demonstrated consistent findings, providing support for its hypothesis that either positive or negative valence induces positive or negative cognitive biases, respectively.

The most popular application of the cognitive bias test is the judgment bias paradigm, which measures biases in decision-making under ambiguity. The standard procedure of this paradigm is two-folded. First, animals undergo a discrimination training in which they learn to specifically respond to one cue (labelled 'positive cue') in order to obtain a reward, while also learning a different response to another cue (labelled 'negative cue') to avoid a negative outcome. Second, after animals reach training criterion, they are presented with both the trained positive and negative cue, with in addition a new, 'ambiguous' cue. The response to this ambiguous cue is measured and compared to the responses given to the positive and negative cue: if the response to the ambiguous cue is similar to the positive response, it suggests that the animal perceives the ambiguous cue as positive and anticipates a positive reward, and if the response is similar to the negative response, it suggests that the animal expects a negative outcome. For that reason, the response given to the ambiguous cue is the key element to determine which bias is present in the animal's cognitive performance, and, therefore, which positive or negative

valence is potentially present. For operational purposes, a positive response to the ambiguous cue is labelled as an 'optimism bias', and a negative response is labelled as a 'pessimism bias' (note that this does not imply an optimistic or pessimistic feeling similar to the human experience, see e.g. Lagisz et al., 2020). The judgment bias paradigm allows for a theoretically motivated framework when studying animal affect and emotions, with *a priori*-defined predictions, and the option to detect affect or emotions not easily observed through overt behavior. In conclusion, this paradigm lends itself perfectly to study the emotional basis of empathy, and in particular, emotional contagion. Accordingly, in my investigation of animal emotional contagion, I applied a judgment bias paradigm in combination with a variety of behavioral assessments.

Measuring animal emotional contagion: Outline of the thesis

The experimental investigation of emotional contagion is considered a popular research topic due to its important link with empathy. Surprisingly, the field lacks a systematic and objective approach in its empirical study. Its foremost, for now, studied mechanism is mimicry, yet the evidence for the hypothesis that mimicry is a necessary prerequisite for emotional contagion is tentative. Similarly, in terms of its function, emotional contagion has been broadly suggested to serve group life, but additional empirical analyses are lacking. The absence of systematic research of emotional contagion is in part due to the considerable challenges inherent to animal emotion research and, thus, any progress in our understanding of emotional contagion goes together with scientific developments in the broader animal emotion domain. For that reason, to examine emotional contagion we ought to integrate scientific contributions from behavioral and theoretical biology, animal welfare research, and comparative psychology.

Based on this conclusion, my PhD was an extensive collaboration between different fields, for which I worked in both the Faculties of Psychology and of Life Sciences. As a result, I incorporated these discipline perspectives in my research of emotional contagion. Chapter 2 of this thesis consists of a review of the current comparative work on empathy, with particular emphasis on emotional contagion. In this paper I aimed at critically analyzing empirical data of empathy and its related phenomena, as well as discussing contemporary theoretical models of empathy. This review sets the foundation for my further empirical work, which are two scientific studies on animal emotional contagion, in ravens and marmosets. To overcome limitations of previous studies such as the (sole) observation of behavioral contagion and emotional arousal taken as evidence for emotional contagion, I specifically focused on investigating emotional valence. To this end, my studies use a multi-component approach including an assessment of the cognitive component by means of a judgment bias paradigm, and an assessment of behavior.

Chapter 3 of this thesis is a study on emotional contagion in sub-adult common ravens (*Corvus corax*), as measured by a judgment bias test. Like humans, ravens are known for their complex social relations. Adult ravens are characterized by long-term pair bonding, serving reproductive success and territorial defense (Bugnyar, 2013). Interestingly, bonding in ravens occurs also outside breeding pairs (e.g. sub-adult age), emphasizing the social relevance of stable and dynamic relationships. For instance, ravens form intense bonds with specific others in their social group (Fraser & Bugnyar 2012), in which they provide support for each other in conflicts (Fraser & Bugnyar, 2010a; 2010b; 2012), including reconciliation between valuable partners (Fraser & Bugnyar, 2011). These bonds are also important for gaining status and providing access to resources (Bugnyar & Kotrschal, 2001; Braun & Bugnyar, 2012). Ravens rely on these social bonds, and their social groups are structured by these relationships. Notably, the groups do not have a stable composition but show moderate to high fission-fusion dynamics (i.e. social groups continuously come together and split up again, Bugnyar, 2013). It is suggested that these dynamics of switching groups and thus, social partners, creates specific challenges, and that as a result, underlying mechanisms have emerged to deal with this complex and diverse social life (Aureli et al., 2008). Importantly, both cognitive and emotional mechanisms (Schino & Aureli, 2009) are proposed to be relevant in facilitating this social system. In that regard, research shows that common ravens exhibit remarkable socio-cognitive abilities aiding their social relations (Fraser & Bugnyar, 2010; Massen et al., 2014; Bugnyar et al., 2016). For this reason, I suggested that in particular emotional contagion plays an important role as well in facilitating common ravens' social relations and group life.

Chapter 4 is a follow-up of my research in ravens, by semi-replicating its experimental procedure to investigate emotional contagion in common marmosets (*Callithrix jacchus*). Similar to humans (Hrady, 1999), common marmosets are cooperative breeders, in which both the breeding pair and non-breeders take care of the offspring (Snowdon & Ziegler, 2007). This cooperative care requires attention and sensitivity between group members, as it may facilitate the needed coordination and group cohesion (Burkart & van Schaik, 2010). Indeed, previous research demonstrates impressive social skills of marmosets, facilitating their cooperative lifestyle (Massen et al., 2016; Burkart & van Schaik, 2020). It is hypothesized that in particular affective mechanisms underly cooperation, rather than mainly, or solely, cognitive ones (Massen et al., 2020). Emotional contagion may serve as such affective mechanism, and through its information transmission function it may contribute to increased coordination and group cohesion required for cooperation. Therefore, I suggested that emotional contagion may serve as affective mechanism to facilitate the marmosets' cooperative social system.

After these two empirical chapters, I give a general discussion and conclusion of my PhD in Chapter 5, followed by the Appendix which includes a general abstract, and one additional research paper related to my PhD.

Terminology list

Term	Description
Affect or affective state	Any experience that is pleasant or unpleasant. Emotions and mood are affective states.
Arousal	Bodily activation or excitation. Forms together with valence the two dimensions of affect or an emotion.
Cognitive bias	A bias or change in cognitive processing due to an emotional state.
Emotion or emotional state	A mental and/or bodily state which consists of a synchronized suite of behavioral, physiological, cognitive, and subjective responses.
Emotional contagion	The transfer of one subject's emotional state to the other; an emotional state-matching between subjects.
Empathy	The ability to experientially share, understand, and respond to the feelings of others.
Feeling	The subjective experience of an emotion.
Mood	Persistent emotional or affective states due to an accumulation of positive or negative experiences.
Valence	Positivity or negativity of an experience. Forms together with arousal the two dimensions of affect or an emotion.

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Chapter 2.

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

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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.

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). 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 Winkielman 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.

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.

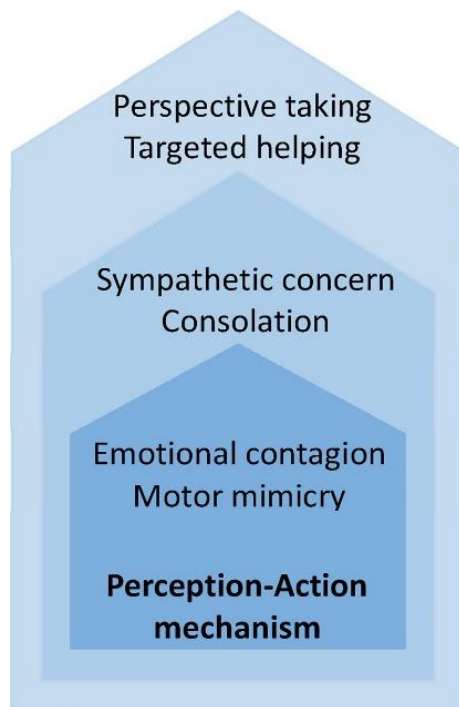


Fig. 1. Russian doll model of empathy

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).

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). 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. Sümegi 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,

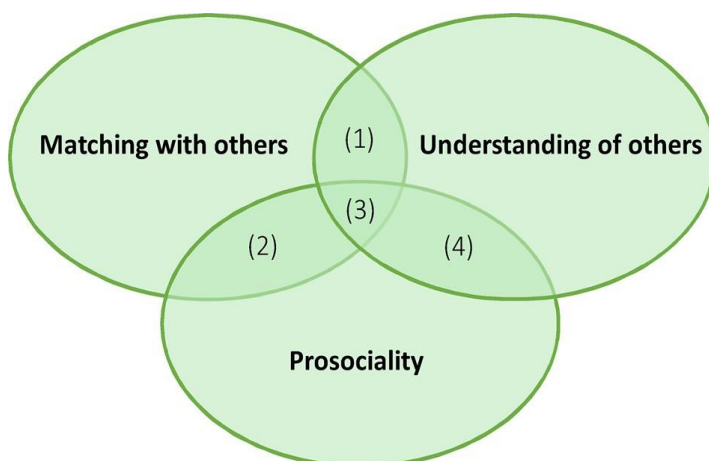


Fig. 2. Combination model of empathy

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).

research might resolve ambiguous conceptual and empirical boundaries. 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; Isern-Mas 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 Blair, 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 Špinka, 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).

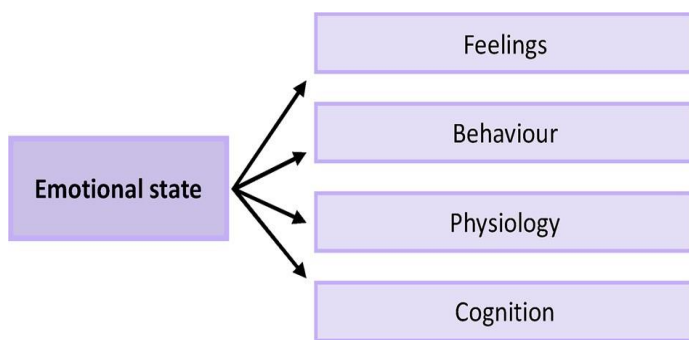


Fig. 3. Multi-component model of an emotion

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 (Knapska et al., 2010; Meyza and Knapska, 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 macaques, *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

rhinus macaques) 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 Špinka, 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; Dezechache 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 Sümegi 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; Keyzers 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 undulates*, 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 benefitting 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; RothHanania 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; ZahnWaxler 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.

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Table 1: Empathy and related phenomena.

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.

Box 1: Batson's eight empathy-related phenomena, or "These things called empathy" (Batson, 2009, p3.)

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.”

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Chapter 3.

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Negative emotional contagion and cognitive bias in common ravens (*Corvus corax*)

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ABSTRACT

Emotional contagion is described as an emotional state matching between subjects, and has been suggested to facilitate communication and coordination in complex social groups. Empirical studies typically focus on the measurement of behavioral contagion and emotional arousal, yet, while highly important, such an approach often disregards an additional evaluation of the underlying emotional valence. Here, we studied emotional contagion in ravens by applying a judgment bias paradigm to assess emotional valence. We experimentally manipulated positive and negative affective states in demonstrator ravens, to which they responded with increased attention and interest in the positive condition, as well as increased redirected behavior and a left-eye lateralization in the negative condition. During this emotion manipulation, another raven observed the demonstrator's behavior, and we used a bias paradigm to assess the emotional valence of the observer to determine whether emotional contagion had occurred. Observers showed a pessimism bias toward the presented ambiguous stimuli after perceiving demonstrators in a negative state, indicating emotional state matching based on the demonstrators' behavioral cues and confirming our prediction of negative emotional contagion. We did not find any judgment bias in the positive condition. This result critically expands upon observational studies of contagious play in ravens, providing experimental evidence that emotional contagion is present not only in mammalian but also in avian species. Importantly, this finding also acts as a stepping stone toward understanding the evolution of empathy, as this essential social skill may have emerged across these taxa in response to similar socioecological challenges.

Emotions are functionally adaptive states consisting of coordinated sets of physiological, cognitive, and behavioral changes. These changes occur in response to fitness-relevant stimuli to facilitate decision making and resource allocation (Nesse, 1990; Nettle & Bateson, 2012; de Waal, 2011). Although research in humans often focuses on subjective states, emotions are multicomponential phenomena that manifest through various observable aspects of the phenotype. This facilitates comparative research on the biology of emotions in nonhuman animals (Mendl et al., 2010; Panksepp, 2012). Emotional contagion in particular, which refers to emotional state matching between individuals (de Waal, 2008), is a powerful mechanism for information sharing (Preston & de Waal, 2002) and, as a consequence, an increased defense against predation (Plutchik, 1987) and the facilitation of group living (Decety et al., 2015). It has been proposed as one of the core elements of empathy (de Waal, 2008; Yamamoto, 2017), and has been demonstrated in a variety of species (Reimert et al., 2013; Edgar et al., 2011; Knapska et al., 2009; Parr, 2001).

Noticeably, the majority of emotional contagion (and empathy) research focuses on distress and negative emotions (Boissy et al., 2007), which is most likely due to a taxonomically widespread attention bias for negative information (Rozin & Royzman, 2001). Another limitation is that reports on emotional contagion are frequently linked to and inferred from behavioral mimicry (i.e., behavioral contagion) (Palagi et al., 2009). Empirically, however, there is no conclusive support for this relationship or its directionality (Deng & Hu, 2018), as mimicry of a specific behavior does not necessarily imply contagion of a corresponding emotion (Massen & Gallup, 2017). Likewise, while behavioral and physiological measures form meaningful indicators of an animal's emotional state, and thus potential contagion, these components largely assess emotional arousal (Edgar & Nicol, 2018). However, an emotion is defined by both

its arousal level and positive or negative valence (Rolls, 2014). So, in contrast to measurements of arousal, the quantification of emotional valence often remains unexplored (Mendl et al., 2010; Russell, 1980; Barrett, 2006). For this reason, arousal changes, such as fluctuations in heart rate (Wascher et al., 2008), may not necessarily be accompanied by a consistent change in valence, and thus may not be fully informative about the specific quality or even mere presence of an emotional response.

Changes in emotional states correlate with changes in behavioral, physiological, and cognitive components (Nettle & Bateson, 2012, Anderson & Adolphs, 2014). Human emotions often entail an additional subjective "feeling" component, which is currently considered challenging or even impossible to directly measure in nonhuman animals (Paul et al., 2005). Accordingly, the majority of animal research has focused on objectively measurable components to establish the presence and type of an emotional state (Perry & Baciadonna, 2017). Locomotor activity, for instance, is one of the most direct, noninvasive behavioral measures for emotional expressions (Anderson & Adolphs, 2014), that is, whether animals approach or avoid a stimulus may inform us on the rewarding or nonrewarding qualities of that stimulus, therefore assuming its positive or negative characteristics. However, animals tend to show consistent variation in how they respond to environmental manipulations (i.e., personality), such that individuals may differ in their vigilance toward threatening stimuli (Jones & Godin, 2010), motivation to explore novel contexts, or activity levels more generally (Réale et al., 2007). Hence, by measuring merely one (behavioral) component instead of a larger set, we narrow and potentially confound our interpretations of the particular emotional state (Paul et al., 2005). For this reason, it is valuable to expand efforts to investigate a collection of multiple components (Reefmann et al., 2009; Perry et al., 2016), ranging from behaviors such as redirected behavior (Kuhne et al., 2011),

visual orientation (Huber et al., 2017), activity level (Zimmerman et al., 2011), or body posture (Reefmann et al., 2009), to vocalizations (Briefer, 2018) and, if possible, measurements of physiological parameters (Perez et al., 2015). Recent studies have also focused on the cognitive component of emotions through means of the cognitive bias paradigm (Mendl et al., 2009). Human psychology research has shown that, for example, more anxious people make more pessimistic judgments when appraising ambiguous stimuli (Paul et al., 2005; Bateson, 2016), while humans in a positive mood make more optimistic judgments (Eysenck et al., 1991; MacLeod & Byrne, 1996). Correspondingly, the rationale of the cognitive bias paradigm is that biases found in an animal's cognitive performance serve as an objective proxy to measure the positive or negative valence of its affective states (Mendl et al., 2009).

The most popular application of this paradigm is the judgment bias task (Bethell, 2015; Roelofs et al., 2016). Here, animals are first trained on a discrimination task with distinct positive and negative stimuli, followed by the introduction of a novel, ambiguous stimulus. The bias hypothesis predicts that animals in a negative affective state should judge the new ambiguous stimulus more similar to a negative stimulus (i.e., display a pessimism bias suggestive of expecting punishment or no reward), while animals in a positive state should judge the ambiguous stimulus as more similar to a positive one (i.e., display optimism bias suggesting the expectation of a reward) (Mendl et al., 2009). This paradigm has been repeatedly confirmed as a promising and noninvasive solution to assess emotional valence in animals (Paul et al., 2005; Mendl et al., 2009). For example, rats living in unpredictable housing showed a pessimism bias (Harding et al., 2004), while pigs housed in enriched environments demonstrated an optimism bias (Douglas et al., 2012), and the manipulation of both anxiety- and depression-like states in chicks resulted in an enhanced pessimism bias and reduced optimism bias,

respectively (Salmato et al., 2011). Moreover, the bias paradigm has been successfully employed in a variety of species (Bethell, 2015), including invertebrates (Perry et al., 2016; Bateson et al., 2011; Schlüns et al., 2017). Finally, this paradigm has the potential for identifying less overtly expressed states, and thus phenomena that are not easily detectable by means of behavioral measures. The latter might be of particular importance for animals using bystander information, for example in the form of emotional contagion. To our knowledge, the bias paradigm has so far been used for assessing the emotional state of animals that experience a particular treatment, but not for assessing the emotional state of bystanders that merely observe the others' response to that treatment.

Here we apply a judgment bias paradigm together with behavioral measures to identify emotional contagion in common ravens. These birds are renowned for using social information (Schwab et al., 2008; Kulahci et al., 2016; Massen et al., 2014; Massen et al., 2014) and displaying emotional sensitivity through behaviors such as consolation (Fraser & Bugnyar, 2010); furthermore, some of the best evidence for emotional contagion comes from birds (Edgar et al., 2011; Edgar & Nicol, 2018), including observations of physiological resonance in zebra finches (Perez et al., 2015) and play contagion in common ravens (Osvath & Sima, 2014) and kea parrots (Schwing et al., 2017). Experimentally disentangling the effects of behavioral contagion and arousal changes from the concept of emotional contagion is an important next step in our understanding of this phenomenon in birds, which will decisively extend our knowledge of the evolution of this core building block of empathy.

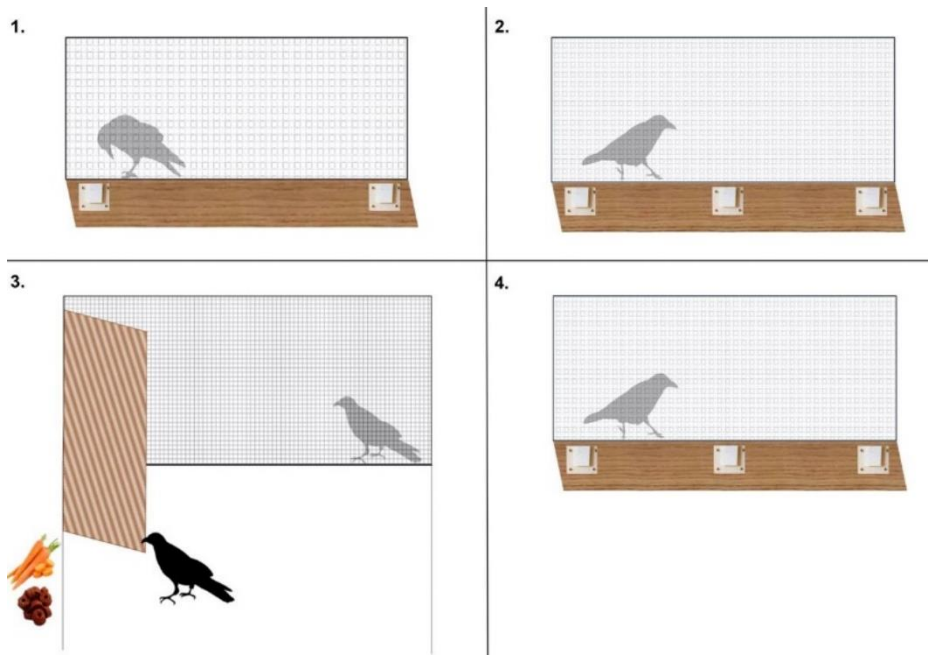


Fig. 1. Experimental procedure. The procedure consists chronologically of a discrimination training before the experiment (1), a pre-manipulation cognitive bias test (2), a positive or negative emotion manipulation of the demonstrator (3), and a post-manipulation bias test (4).

Results and Discussion

1. Emotional Expressions in Demonstrators

Ravens participated in dyads, with one subject being a demonstrator and one an observer. We experimentally manipulated the affective state of demonstrator birds by presenting two food items of different quality (phase 1), then taking one item away (phase 2), followed by handling the remaining item (phase 3) (Methods and Fig. 1).

In the positive condition, the unappealing food item was removed and the appealing item remained visible to the demonstrator, suggesting the induction of reward anticipation. In the negative condition, the appealing food item was taken away and the unappealing item remained visible, suggesting potential “frustration” in the demonstrator instead of reward anticipation. In the positive condition, we expected animals to look more toward the food item and locate themselves more in front of the food presentation, whereas in the negative condition, we expected the animals to lose interest in the stimulus presentation and show

more redirected behavior toward the environment, such as digging in the sand. For exploratory purposes, we also coded for either left- or right-eye use when inspecting the food items (SI Appendix, Table S1).

As predicted, the demonstrator’s behavioral expressions differed significantly between the two conditions (Fig. 2). Moreover, we were able to capture a change in the demonstrator’s behavior across two phases, namely between the first 30 s of presenting the two items (i.e., phase 1) and the final 30 s of handling the remaining preferred or unpreferred food item (i.e., phase 3) (Methods). Across phase 1 and phase 3 of the positive condition, ravens showed less locomotion (difference within condition: $\beta = -1.31$, $z = -4.37$, $P = 0.01$; difference in phase 3 between condition: $\beta = -0.79$, $z = -2.48$, $P = 0.01$), spent more time looking at and being in front of the preferable food item (within condition: $\beta = 3.17$, $z = 5.16$, $P = 0.01$; between condition: $\beta = 2.27$, $z = 3.69$, $P = 0.01$), while also displaying more arousal (i.e., increase in body and head movements in front of the food item) (within condition: $\beta = 0.24$, $z = 2.26$, $P = 0.03$; between condition: $\beta = 0.66$, $z = 5.27$, $P = 0.01$). This implies heightened attention, and suggests that

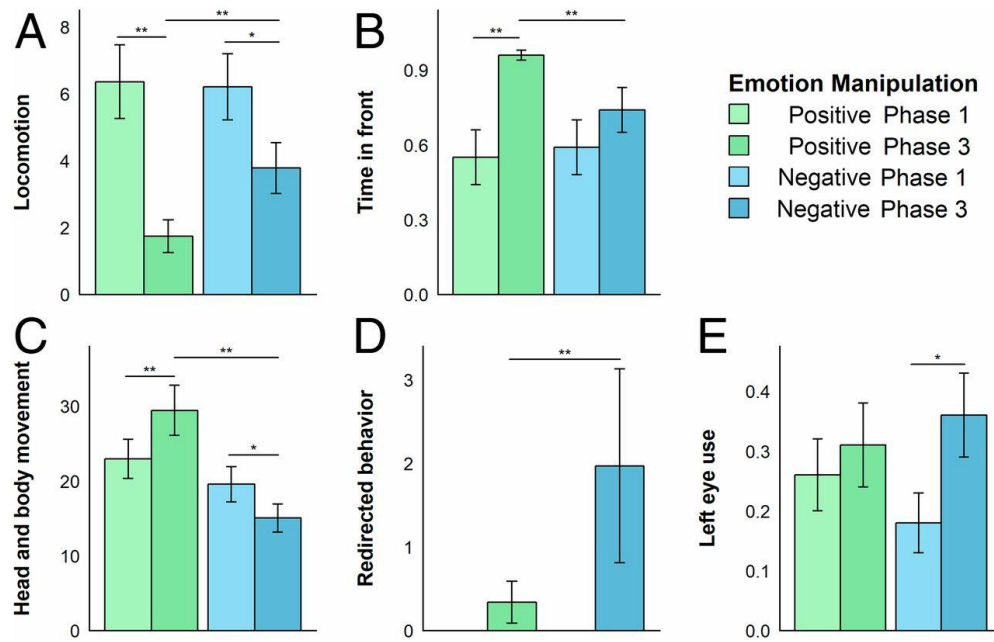


Fig. 2. Demonstrator behavior. Predicted behavioral responses (mean \pm SE) for an average demonstrator before and after the positive and negative conditions, including locomotion (A), time spent in front of the food items (B), head and body movements (C), redirected behavior (D), and left-eye use upon inspecting the food items (E). Note that A, C, and D, are count frequencies, while B and E are duration proportions (s). Planned comparisons were conducted within conditions from phase 1 to phase 3 and between positive and negative conditions for phase 3 (see SI Appendix, Table S2 for further details). * $P < 0.05$; ** $P \leq 0.01$.

the ravens indeed anticipated receiving this food item (34, 55). In the negative condition, ravens showed less locomotion around the experimental room (within condition: $\beta = -0.50$, $z = -2.19$, $P = 0.03$) but remained more active than in the positive condition, while displaying an increase in redirected behavior toward the environment ($\beta = 1.76$, $z = 3.63$, $P = 0.01$). Redirected behavior may occur in situations when an expected reward is omitted or is spatially restricted and reflects frustration about unrewarded outcomes (Kuhne et al., 2011; Falk, 1971). However, when periodically returning to inspect the remaining unappealing food item, ravens showed less body and head movements when standing in front of the food item ($\beta = -0.26$, $z = -2.04$, $P = 0.03$), as well as a significant increase in left-eye use ($\beta = 1.00$, $z = 2.50$, $P = 0.03$), implying a negative emotional lateralization and providing support for the

emotional valence hypothesis [which suggests that the right hemisphere is dominant for processing negative stimuli (Leliveld et al., 2013)]. We did not find a significant difference between left-eye use across the positive and negative conditions during phase 3, which is potentially a consequence of a higher baseline proportion of left-eye use in phase 1 of the positive condition (Fig. 2).

Nevertheless, the significant increase in left-eye use from phase 1 to phase 3 within the negative condition suggests an important behavioral change according to that condition. The combination of different behavioral variables in the positive condition indicated attention and interest for the manipulation. In addition, less attention and an increase in redirected behavior in only the negative condition suggested a meaningful difference in emotional expressions

in demonstrators. For this distinction between conditions, the difference in saliency between the loss of preferred food and the dislike of unpreferred food was irrelevant and, moreover, none of the demonstrators' behaviors were specifically indicative of food presence or loss, respectively (Szipl et al., 2015; Bugnyar et al., 2001). Instead, the combination of certain behaviors and the frequency of their expression seemed to reflect the predicted differences in the demonstrators' affective state. To further support this interpretation, we aimed to independently assess the valence of our manipulation by means of a judgment bias test in the demonstrator birds. However, due to unanticipated procedural constraints, the obtained data were unsuitable for interpretation (SI Appendix, Results).

2. Emotional Contagion

The demonstrator's behavioral expressions to the different manipulations were witnessed by an observer raven present in an adjacent room (Fig. 1). On average, observers were visually oriented toward the demonstrator for 74 to 77% (~23 to 27 s/30 s) of the time during the positive and negative manipulations, respectively, suggesting that observers were attentive to the demonstrators' behavioral expressions. Importantly, the observer was naïve about the food items presented to the demonstrator and the handling of these items by an experimenter. By means of a judgment bias paradigm, we investigated whether the observer's affective state would change according to the demonstrator's state.

We first assessed the efficacy of the discrimination training (Methods), for which we found that, across box locations, observers showed significantly shorter peck latencies at the positive location ($\beta = -0.67$, $z = -3.67$, $P = 0.01$) and significantly longer latencies at the negative location ($\beta = 1.23$, $z = 6.95$, $P = 0.01$). This indicates that the ravens effectively learned to discriminate between positive and negative

locations and their respective reward value, and that our training was successful. Additionally, during testing, nonsignificant differences were observed before and after emotion manipulation at the trained locations, suggesting that the effect of our training and the motivation to participate were sustained throughout the duration of the experiment (positive condition: positive location: $\beta = 0.27$, $z = 1.17$, $P = 0.26$; negative location: $\beta = 0.03$, $z = 0.14$, $P = 0.90$; negative condition: positive location: $\beta = 0.18$, $z = 0.72$, $P = 0.50$; negative location: $\beta = 0.11$, $z = 0.44$, $P = 0.67$).

Essential to our central hypothesis, we predicted that, compared with a bias test taken before the experimental manipulation, the observers' responses after manipulation would become more pessimistic or optimistic depending on whether they had experienced the demonstrator in the negative or positive condition, respectively. Such pessimistic or optimistic tendencies were quantified by measuring latency to approach a box placed on an ambiguous location, in comparison with the latencies of approaching trained positive and negative locations. Our analysis shows that observers significantly increased their latency to peck the ambiguous location after witnessing the demonstrator in the negative condition (within-condition pre- and post-manipulation response: $\beta = 0.84$, $z = 3.22$, $P = 0.02$; between-condition post-manipulation response: $\beta = 0.76$, $z = 2.91$, $P = 0.01$), confirming the predicted pessimism bias (Fig. 3). In contrast, we did not observe the expected decrease in observer response latency after the positive manipulation (within condition: $\beta = 0.40$, $z = 1.53$, $P = 0.16$). Notably, in our study procedure, we opted to compare pre- and post-manipulation bias results, instead of using an additional control session or merely relying on post-manipulation results. The pre-manipulation results are considered as a baseline to which we compared the post-manipulation results within each condition, allowing us to exclude any general mood effect that perhaps already existed in our subjects

beforehand. Both our within- and between-condition comparisons confirm our negative manipulation predictions, and demonstrated that the post-manipulation test was able to pick up the negative manipulation effect. Importantly, the finding of a nonsignificant, small difference in pecking latency across ambiguous trials ($\beta = 0.01$, $SE = 0.01$, $z = 1.11$, $P = 0.30$) suggested that the response to this location was not detectably extinguished due to lack of reinforcement (SI Appendix, Results). The observers' distinct responses in the cognitive bias test after the negative manipulation, compared with the positive, indicate that the observer ravens were influenced by the demonstrators' behaviors and affective states. Observers did not perform similar behaviors themselves but showed a pessimistic judgment of an ambiguous stimulus. Hence, we find support for negative emotional contagion, whereas our results remain inconclusive about positive emotional contagion.

Our study experimentally disentangles effects of behavioral contagion and arousal changes from the concept of emotional contagion, by taking the valence element of an emotional state into account. Behavioral contagion and arousal are frequently used as evidence for emotional contagion. However, though they may mechanistically underpin emotional contagion, they are distinct phenomena (Edgar & Nicol, 2018). For instance, examples of behavioral contagion such as yawn or play contagion do not necessarily disclose information on the underlying affective state (Massen & Gallup, 2017; Ahloy-Dallaire et al., 2018). Similarly, different emotions may show similar physiological profiles (Paul et al., 2005), and thus variations in arousal levels such as a decrease in body temperature may be observed in both positively and negatively valenced contexts (Travain et al., 2016).

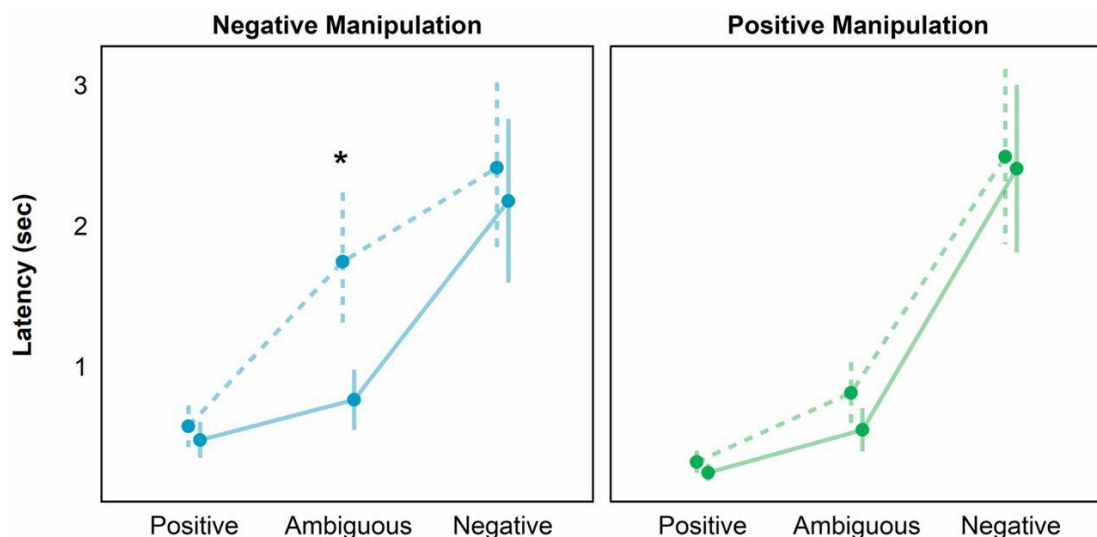


Fig. 3. Observer cognitive bias test. Predicted latencies to peck (mean \pm SE) for an average observer raven in an average dyad at each location across the positive and negative conditions. We conducted planned comparisons of observer response latencies at each location before (full line) and after (dotted line) the emotion manipulations (see SI Appendix, Table S3 for further details). * $P \leq 0.05$.

Therefore, to exclude these alternative explanations and overcome the limitations of previous studies, researchers need to employ methodologies focusing on the measurement of different modalities instead of a single measure of emotion (Anderson & Adolphs, 2014; Perry et al., 2016). The cognitive bias test is a favorable approach to tap into the multicomponential nature of emotions, as it not only allows us to investigate an additional cognitive element but also provides the opportunity to differentiate between changes in valence. Here we used two different components to assess potential state matching and found an alignment between the expressions of these two components; in the negative condition, the avoidance behavior shown by the demonstrator was matched with a pessimistic judgment in the observer. These results are consistent with the interpretation that an underlying negative affective state was transferred to the observer, subsequently biasing their response in the judgment test. We consider this convergence to suggest emotional contagion between the demonstrator and the observer.

The observers' pessimistic response to seeing others in a negative state indicates that the cognitive bias paradigm is a useful method to detect changes in the affective states of ravens. Our study design meets two imperative bias paradigm requirements, which are relevant in supporting our conclusions about the pessimism bias and excluding alternative explanations (Roelofs et al., 2016). First, we found the expected training effect, suggesting that the ravens successfully learned the positive and negative discrimination, and their performance before and after manipulations remained consistent. This finding is important to exclude potential effects of "boredom": Observer ravens could have become disinterested in the demonstrator's situation, which could carry over to the bias task, resulting in a drop in performance and, potentially, a "pessimism" bias because of boredom rather than emotional contagion. However, we see a consistent pattern

of motivation for both conditions and both the negative and positive trials, which allows us to rule out this explanation. Second, our data show the absence of a clear learning effect across unreinforced ambiguous trials, indicating that the ravens' responses did not decrease due to the lack of reward in these trials. This suggests that ravens treated these trials as truly ambiguous throughout the whole study, and that their responses were thus based on an evaluation of the anticipated reward value. When trials remain unreinforced, animals may become less motivated to perform, which could result in the observation of an apparent pessimism bias. The absence of a learning effect is thus relevant to our interpretation, as it provides evidence that such learning is not the underlying reason for the observed pessimism bias. The observers' response to ambiguous stimuli in the negative condition, and the significant differences for both within- and between-condition comparisons, emphasizes that the negative manipulation effect on the demonstrator was in turn picked up by the bias test for the observer. This verifies that the cognitive bias paradigm is sensitive not only to long-term manipulations of affective states (i.e., moods), for example due to housing conditions (Douglas et al., 2012), but also to short-term manipulations (e.g., 30 s in Rygula et al., 2012). Furthermore, our study demonstrates that subjects do not have to be involved in a social interaction themselves but that merely witnessing a conspecific's response to a mild negative manipulation is sufficient to elicit an effect. Notably, the demonstrators showed numerous behavioral expressions, but they did not give any food-specific signals such as food-associated calls or cues toward food caching. Although parts of the redirected behavior observed in the demonstrators consisted of digging in gravel substrate, these sweep-like beak motions clearly differ from caching (whereby an item is inserted in the substrate by means of vertical head movements). Hence, it seems unlikely that observers detected the cause of the demonstrators' negative state, namely change in food availability, and more

likely that they responded to the “negativity” of the situation experienced by the demonstrator. Our interpretation of negative emotional contagion is therefore supported by the found pessimism bias in the observer, which is confirmed by both between- and within-condition comparisons, the presence of a consistent discrimination training effect, and the absence of a learning effect for the unrewarded stimuli. While our results confirm contagion of a relatively mild negative affective state, our unclear findings for potential positive contagion might be explained by the following factors. Negative emotions may be easier to experimentally induce than positive emotions, and they may be more salient in their expression than positive emotions (Reimert et al., 2013; Boissy et al., 2007; Rygula et al., 2012). Moreover, animals (as well as humans) attend more to negative than positive information in their environment (Rozin & Royzman, 2001; Huber et al., 2017). Accordingly, the demonstrators’ reduction in locomotion and shift in visual attention in the positive condition could have been less informative for observers than the demonstrators’ redirected behavior and increased locomotion displayed in the negative condition. Alternatively, the affective states of both birds may not have matched in the positive condition. Upon seeing demonstrators in a positive state, observers might have experienced negativity due to being unable to access the source of excitement themselves. Although we cannot exclude this possibility, we aimed to reduce such an effect by testing birds in highly affiliated dyads only, so that observers might have anticipated getting (bits of) the reward shared by their affiliate after the experiment. In the same vein, demonstrators may have initially experienced an anticipation of reward, but the positive effect was short and partially masked by our aforementioned procedural constraints. Note that demonstrators never received the presented food item for consumption before the post-manipulation bias test was performed (SI Appendix, Results). This procedure might have elicited additional frustration in the

demonstrators for not receiving their preferred item and consequently eliminated any potentially present positive state. If observers picked up on this change in the demonstrators’ state, this would explain the observers’ “neutral” responses in the cognitive bias test following the positive condition. In the negative condition, the affective state of the demonstrators likely remained negative throughout the procedure, facilitating the detected effect in the observers.

Overall, by combining an emotional contagion setup with a cognitive bias paradigm, our study contributes to the investigation of different emotion components. So far, animal emotional contagion studies have depended solely on behavioral parameters (Huber et al., 2017; Osvath & Sima, 2014; Schwing et al., 2017) or a combination of behavioral and physiological measures (Reimert et al., 2013; Edgar et al., 2011). Future research should therefore consider using a cognitive bias test as an additional tool to behavioral and physiological methods for measuring the valence underlying emotional contagion. This will allow us to construct a full picture of an animal’s emotional state in an empathy setting; moreover, it enables us to measure emotional contagion in situations that are characterized by low or no direct behavioral matching, such as when using bystander vocalizations (i.e., observing others or eavesdropping on others’ communicative interactions) (Huber et al., 2017; Saito et al., 2016). Unfortunately, we were unable to interpret the cognitive bias results of demonstrators due to our design decisions. Future work should address these limitations to further explore the application of the bias paradigm in assessing emotional state matching and strengthening interpretations of behavioral findings. Current research on (avian) emotions is still in its early developmental stages, and thus, although we may classify the demonstrator’s situation as negative or frustrating, we do not have direct indicators of a specific emotional state.

Some major contemporary discussions in comparative affective science concern what we label in animals as emotions, whether animals truly feel and experience such emotions, and what the best objective measures are to assess these questions (Bateson et al., 2011; Mason, 2011). This may be seen as a limitation when concluding emotional contagion of a specific emotion, in any species for that matter. However, the apparent disadvantage of having no verbal report, or direct measures of subjective feelings, prompts us to systematically and rigorously evaluate our observations in animals with the prevailing methods available. For this reason, given the current state of the art and theoretical consensus in animal emotion research, the componential approach proposed here offers the opportunity to accumulate information derived from various modalities. This accumulation may provide evidence of the convergence of congruent emotional components, such as the congruency found in our data between the demonstrators' behavior and the observers' pessimism bias, which supports our interpretation of converging emotional states. Future studies need to address whether the birds would react similarly to different negative situations (within and outside of a food context), and thus to valence in general compared with specific details of the context. Correspondingly, future studies should incorporate nonfood contexts for testing positive emotions. Note that early studies on social learning, for example observational conditioning in blackbirds, hint at an emotional transfer between individuals (Curio et al., 1978); yet such an explanation was nonexistent at the time, and it is unclear whether the observed learning implied an emotional response. Nonetheless, matching the other's emotional state is indeed a plausible mechanism for facilitating adaptive responses to various social situations requiring rapid information sharing, such as predator mobbing (Curio et al., 1978), foraging under risk (Greggor et al., 2016), or conflict management (Fraser & Bugnyar, 2012). We are convinced that these topics would

be highly relevant for future emotional contagion research.

Taken together, our study shows differences in the behavioral expression of demonstrator ravens that have been informed about the quality of hidden food items and, critically, a pessimistic response of naïve ravens in a cognitive bias test after they witnessed the informed conspecific in the negative condition. This finding provides experimental support for emotional contagion in ravens, which is in line with previous observations on corvid and parrot play (Osvath & Sima, 2014; Schwing et al., 2017) and the claim that this fundamental component of empathy is present not only in mammalian but also in avian taxa (de Waal, 2008). Previous research demonstrates that similarities in cognitive complexity between distantly related taxonomic groups, such as primates and corvids, are typically the result of convergent evolution (Emery, 2006; Seed et al., 2009). Similar socioecological challenges may have therefore led to independent selection for emotional contagion in ravens and various mammalian species. Alternatively, given that primary emotions are localized in phylogenetically ancient brain structures (Panksepp & Panksepp, 2013), the underlying neural mechanisms of emotional contagion might be homologous in both mammals and birds. While answering this question is beyond the scope of our study, the present findings may act as a crucial stepping stone toward a better comparative understanding of complex social skills, such as empathy, and their evolution.

Methods

Study Animals and Housing. Eight common ravens (5 M, 3 F) participated in the study. All birds were individually marked and socially housed in a nonbreeder group at the Haidlhof Research Station (see SI Appendix, Methods for further details).

Ethical Note. The study followed Austrian law and local government guidelines, and the design was approved by the ethical board of the Behavioral Research Group at the Faculty of Life Sciences, University of Vienna (2018-004). After the study, the ravens remained at the Haidlhof Research Station for further research projects.

Pilot and Habituation. Before the experiment, two pilot studies were conducted and a habituation period of 3 mo took place.

Cognitive Bias Paradigm: Discrimination Training. A wooden box was presented consecutively either on the left or right side of the animal. Only one side contained a reward (positive location), while the other side remained unrewarded (negative location). The criterion to pass was a minimum of 95% correct pecking on the positive location and 70% correct no pecking on the negative location, calculated over 3 consecutive days with 12 trials per session per d (SI Appendix, Table S4).

Cognitive Bias Paradigm: Testing. After successful training, the ravens were assessed on a bias test immediately before and after the emotion manipulation of the demonstrator. During this test, the box was consecutively presented on the trained positive and negative location, as well as on one new, ambiguous location. The maximum latency to peck was 3.5 s, and trial order presentation was semirandom.

Experimental Procedure. The study had a within-subject design. On each testing day, a dyad was called into the experimental compartment and given a cognitive bias test. Afterward, the demonstrator went into another compartment for either the positive or negative manipulation. The manipulation included a baseline of 30 s followed by a presentation of two different food items. The food items were out of view of the observer. After this presentation (phase 1, duration 30 s), one food item was taken away and the other remained visible (phase 2, duration 30 s). This was followed by an

experimenter handling the remaining item (phase 3, duration 30 s). The experimenter held and moved the food item in the palm of the hand, between two fingers, broke the food into pieces, and lifted the pieces in the direction of the demonstrator. After the food handling, the demonstrator went back into the initial compartment and both birds underwent a post-manipulation cognitive bias test. At the end of the test, both birds were free to join their social group and the demonstrator was given the food item according to the emotion condition.

Video Coding. The experiment was recorded by four video cameras. All coding was done by the main author and a second, trained observer blind to the experimental hypotheses independently video-coded for 15% of the behavior and cognitive bias sessions. Interobserver reliability was found to be high across all parameters, intra-class correlation coefficient (3,1) range: 0.95–1.00.

Quantification and Statistical Analysis. We utilized generalized linear mixed models (GLMMs) for all analyses to account for repeated measurements within subjects and dyads, enhance statistical power, and avoid artificially reducing the variability in our dataset through aggregation (Gygax, 2014). GLMMs were fit with the lme4 package (Bates et al., 2015) for the R 3.4.4 statistical environment (2019). To ensure the robustness of the P values returned from these models, we implemented a parametric bootstrapping procedure.

Demonstrator Behavior Analysis. To assess the validity of our demonstrator emotion manipulations, we estimated behavioral variation in demonstrators both between and within the positive and negative conditions. We analyzed a subset of behaviors hypothesized to reflect components of arousal and valence, which are further described in our ethogram (SI Appendix, Table S1). In particular, we analyzed differences across phases 1 and 3 of the manipulation, as the latter phase was expected

to elicit the strongest emotional response in the demonstrators.

Cognitive Bias Test Analysis. Considering that pecking occurred frequently across all conditions and latencies to peck exhibited more consistent differences, we utilized latencies to peck rather than peck/no peck responses for our primary analyses. To assess potential differences in subjects' reaction times across experimental conditions, GLMMs were specified with Gamma error distributions and log link functions appropriate for modeling proportional change in response latencies (Lo & Andrews, 2015). We first assessed whether latency to peck at the ambiguous location increased across sessions due to the absence of reinforcement (Doyle et al., 2010), and we determined the efficacy of our discrimination training. We then compared before and after manipulation latencies across all locations in each condition to test our main hypothesis. A likelihood ratio testing comparing this full model to a reduced model without the interactions among location and condition fixed effects for observers supported further consideration of the specific pairwise comparisons of interest, $\chi^2(6) = 22.84$, $P < 0.001$.

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Supplemental Information

1. Supplemental Results

Demonstrator cognitive bias test

As noted, demonstrator results are not reported in the main text because of confounds in our experimental design which prevent us from meaningfully interpreting differences in response latency before and after emotional manipulation. Demonstrators never received the presented food item for consumption after the demonstration session; we aimed to avoid that the observer would see the food items presented or the consumption of them by the demonstrator. Instead, the demonstrators were called out of the experimental compartment and positioned in an adjacent room for performing the post-manipulation bias test in parallel with an observer raven. Importantly, to standardize the cognitive bias test procedure for both animals of a pair, it was required to use this adjacent room for the demonstrator. The delay in food consumption combined with the change of compartments might have induced a negative affective state in the demonstrators and likely masked effects of our experimental manipulation. Future studies should aim to avoid these limitations.

Demonstrator results: In comparison to the ambiguous location, demonstrators exhibited significantly shorter peck latencies pre-manipulation at the positive location ($\beta = -1.03$, $z = -5.85$, $17 p = 0.01$) and significantly longer latencies at the negative location ($\beta = 0.86$, $z = 4.91$, $p = 0.01$). 18 Their responses did not significantly change pre- and post-manipulation at the positive (positive, $\beta = -0.33$, $z = -1.44$, $p = 0.22$; negative, $\beta = -0.07$, $z = -0.29$, $p = 0.83$) and negative (positive, $\beta = -0.27$, $z = -1.18$, $p = 0.31$; negative, $\beta = -0.02$, $z = -0.08$, $p = 0.95$) locations. Demonstrators did not exhibit statistically significant differences in peck latency at the ambiguous location after the emotion manipulations (positive, $\beta = 0.13$, $z = 0.49$, $p = 0.68$; negative, $\beta = -0.22$, $z = -0.85$, $p = 0.49$). Prior experience as a demonstrator also did not have a significant effect on observers' response latencies at the ambiguous location (positive, $\beta = -0.02$, $z = -0.07$, $p = 0.96$; negative, $\beta = 0.16$, $z = 0.38$, $p = 0.76$). In contrast to the observer effects, removal of the interaction effects among location and condition for demonstrators also did not significantly reduce model fit, $\chi^2(6) = 2.53$, $p = 0.86$.

Observer cognitive bias test

In the positive condition, post-manipulation responses at the ambiguous location significantly differed from the positive ($\beta = -0.94$, $z = -3.85$, $p = 0.01$) and negative locations ($\beta = 1.11$, $z = 4.56$, $p = 0.01$). In contrast, post-manipulation latency in the negative condition did not significantly differ between the ambiguous and negative locations ($\beta = 0.32$, $z = 1.29$, $p = 0.25$), while there was a large significant difference between ambiguous and positive locations ($\beta = -1.12$, $z = -4.46$, $p = 0.01$).

2. Supplemental Methods

Housing

All birds are housed at the Haidlhof Research Station in Austria. Here the birds live in an aviary (15 x 15 x 3.75m), including roofed and non-roofed compartments with various perches, trees, rocks, and bathing tubs. All birds were hand-raised and trained to come by name, and were familiar with daily observations, cognitive tests, and behavioral studies. None of the birds had previous experience with

the cognitive bias paradigm. In general, the ravens were fed twice a day with a mix of fruits, milk products, and meat, and water was provided *ad libitum*. All ravens came from zoos in Austria (Zoo Wels, Wildpark Haag), Germany (Nationalpark Bayerischer Wald), and Sweden (Spanga Gymnasium).

Pilot studies

Two pilot studies were conducted prior to the study. The first pilot was to determine food preference. A variety of food items was presented to each bird (chosen from items used often at the research station) and the order of consumption was used to rank preferences for these items. All birds showed the same ranking preference in which the most preferred item was eaten first, the second immediately after, and the least preferred item was not consumed at all. We used the most preferred food (cheese) for the positive location in the bias test, the second preferred food (dried dog food) as appealing remaining item in the positive condition, and the least preferred food (raw carrot) as unappealing remaining item in the negative condition. This ranking preference was again confirmed during the study as upon receiving the raw carrot at the end of the negative experiment none of the demonstrator ravens consumed this item. During our pilot study we explored non-food alternatives for the emotion manipulation of the demonstrator. Any stimuli related to pain, intense distress, invasive housing/enrichment changes, etc. were excluded as the animal group remains at the research station and these events could influence other studies ongoing in parallel or the future. None of the other explored stimuli had a sufficiently strong effect on the demonstrator, so ultimately we opted for food to elicit the strongest reaction.

To ensure a strong anticipatory or disappointing effect of the food items, we put the following guidelines in place to control the amount of rewards each raven received daily. We did not food deprive the ravens, and we split the daily breakfast consumption into 10% before the experiment and 90% after the experiment. Normally ravens receive breakfast daily around 8.30 AM (testing ended at 9 AM), so to avoid that the subjects would be too hungry before participating, and potentially confounding the cognitive bias test, we gave a small portion before testing started. The food items used for discrimination training, experimental manipulation, and overall motivation were only given in the context of the experiment and we restricted the use of these food items during the remaining hours of the day throughout the 5 days of the study (4 testing days + 1 break day in between). Each raven received per day: a total of 6 small pieces of cheese from the cognitive bias test ($\pm 0.5 \times 0.5$ cm) and 2 pieces of food reward for general motivation when the researchers entered the aviary (small dried cat food). The additional piece of dried dog food or raw carrot only happened once during its specific condition and the amount was therefore also limited. As comparison, ravens often get double the amount during general daily training sessions.

The second pilot aimed to estimate attention span and motivation during the cognitive bias test as our study is the first to conduct such paradigm with ravens and they are known to rapidly lose interest in a task (e.g. seen also in Range et al., 2008). Initially ravens were given 10 minutes time to walk over to a box and peck the lid. However, the birds often would fly away from the test location and when they left for more than two minutes they started engaging in other activities without returning (within 10 minutes). Therefore we kept track of the minimum number of trials a raven would complete during discrimination training before leaving for more than two minutes (with a maximum of 20 trials per session). Between ravens this number ranged from 12 to 19 trials per training session and we used a minimum number of 11 trials for all birds to standardize the cognitive bias test later during testing.

Habituation

All ravens underwent a habituation and training period for three months. The ravens were trained to be separated from their social group, come into isolated compartments on command, and to fly up on

wooden shelves on command. These training sessions involved approximately 15 minutes of isolation per session and were completed when the animal was visibly comfortable with the surroundings (e.g. self-preening, caching, etc.). Five ravens habituated to this isolation within approximately two to three weeks, a sixth bird within four to five weeks, and a seventh and eighth bird within six to eight weeks. We also habituated the animals to the experimental material and cameras by placing these items inside the compartments during habituation sessions.

Cognitive bias paradigm, discrimination training

The wooden box measured 10 x 10 x 3 cm and was presented either on the left or right side of the animal (distance between left and right: approx. 120 cm). The box was placed on a shelf, which was separated by wire mesh from a raven sitting on a shelf on the other side. The ravens were trained to peck the lid of the box through the wire mesh, which consequently led to the removal of the lid so that they could take out the reward or look inside the box. Only one side was rewarded while the other side remained unrewarded (counterbalanced). The discrimination training sessions always started and ended with the positive location. During the first two sessions, the negative location was rewarded to motivate birds to pay attention to both locations; from the 3rd session, only the positive location remained rewarded. In addition, animals were verbally encouraged to open the box when presented on either of both locations during the first 3 sessions, with no encouragement in subsequent sessions. Inherent to our approach is the potential risk of a learning effect for the unreinforced ambiguous trials. As these trials remain unrewarded during testing, an increased response latency might simply result from a demotivation to approach this location (Roelofs et al., 2016). We therefore applied a variable reinforcement ratio (VRR) for the positive location during training and testing to increase the actual ambiguity of the ambiguous trials. When ravens reached criterion during two consecutive days, we applied the VRR during the third day of consecutive testing and one positive location trial remained unrewarded. Initially we set maximum latency to peck at 10 seconds, but due to experimental error some trials had a cut-off of 3,5 seconds. Therefore, all trials were standardized to a maximum latency of 3.5 seconds.

Cognitive bias paradigm, testing

The boxes during the ambiguous trials were presented 60 cm from the left, and the right location respectively. To avoid increased response latency due to moving between the different locations, we first presented the box at 10 cm distance from the wire mesh, followed by a baseline of 5 seconds after which the box was immediately moved forward against the mesh. This provided time to the subjects to orientate themselves toward the desired location. Trial order presentation was consecutive and semi-random, with the first trial always positive, an equal balance of ambiguous trials following negative and positive trials, and at least one positive or negative trial between ambiguous trials. Only the positive boxes were rewarded and with a VRR similar to the training procedure. For each test session, all ravens went through 11 before- and 11 after-manipulation trials with a total of 8 positive, 8 negative, and 6 ambiguous trials. After four testing days, each raven had been presented 88 cognitive bias trials with a total of 32 positive, 32 negative, and 24 ambiguous trials.

Experimental procedure

Our experiment followed a within-subject design with four conditions, namely demonstrator positive, observer positive, demonstrator negative, and observer negative. The conditions were tested in a counterbalanced order. A dyad participated once per day, which resulted in total in five days with four testing days and one break day in between. The food items were presented to the demonstrator on a wooden board (30 cm x 20 cm), which the demonstrator could perceive through a peephole or wire

mesh above the peephole. The amount and size of the food items was kept equal across manipulations. During phase 3 the food items were handled by the experimenter in a specific manner. The ravens are accustomed to staff handing over food through a wire mesh and so we imitated these movements to simulate that demonstrators would actually receive the food. All ravens participated on a voluntary basis and testing only began when the ravens remained in the compartment without displaying overt signs of stress.

Video coding

The digital videos were converted to .mp4 files using HandBrake (<https://handbrake.fr/>), and coded using Solomon coder (<http://solomoncoder.com>). Inter-observer reliability was estimated by two-way mixed, absolute agreement, single measure intra-class correlation coefficients, ICC(3,1). The reliability was found to be high across behavioral parameters ICC(3,1) range: 0.95-1.00, and the independent video coding for the cognitive bias tests also strongly supported the reliability of our latency measurement, ICC(3,1) = 0.99.

3. Quantification and statistical analyses

We implemented a parametric bootstrapping procedure for the parameters of interest using the 'pbkrtest' package (Green & Macleod, 2016).

Demonstrator behavior

GLMMs for count measurements were specified with Poisson error distributions and log link functions. Duration proportion measures were rescaled to the (0,1) interval (Smithson & Verkuilen, 2006) and subsequently logit transformed to approximate Gaussian responses (Warton & Hui, 2011). We predicted population means and SEs for these measures using the parametric bootstrap sampling distributions of original scale model expectations. All models except for redirected behavior, in which there were no phase 1 responses, included handling phase nested within emotion condition as fixed effects. Note that 'nested' here refers to the structure of the interaction terms in our model, which produce regression coefficients at the appropriate level of comparison for our study. In this case, model parameters were estimated for the difference between Phase 3 and Phase 1 within each emotion manipulation condition, as well for the difference between Phase 3 responses across conditions. We therefore did not estimate nor interpret all possible comparisons, but only those pertinent to our main hypotheses. Demonstrator identity and dyad were specified as random effects for all models. In R formula syntax, these models took the form of:

$$\text{demonstrator behavior} \sim \text{condition/phase} + (1|\text{subject}) + (1|\text{dyad})$$

where "/" specifies a nested interaction term. Please note that this model produces equivalent results to a model specified with a nested random effect for subjects within dyads, i.e. (1|dyad/subject), as our data were appropriately coded such that the 'lme4' R package treated each subject as only being in one dyad and partitioned these distinct sources of variance accordingly. Due to technical failure with the data of one demonstrator in the positive and one demonstrator in the negative condition, we were only able to analyze the 'locomotion' data of these subjects.

Cognitive bias test

In our study, pecking at the experimental box occurred frequently across all conditions (43% of the negative location trials, 100% of the positive location trials and 85% of the ambiguous location trials).

In contrast, latencies to peck exhibited more consistent differences across box locations, suggesting that this measure more effectively distinguishes the efficacy of our training and emotion manipulations. The high frequency of pecking even at the negative location likely reflects a lack of response suppression as a go/no-go test requires behavioral inhibition in which the animal needs to refrain from taking action (Roelofs et al., 2016). Given that we observed an appreciably small and non-significant effect for trial number on peck latency across ambiguous trials ($\beta = 0.02$, $z = 1.18$, $p = 0.21$), the relative difference in latency across sessions likely provides a more generalizable measure for comparing our results with prior studies. Upon seeing the box positioned on the positive location, birds would position themselves on this location during the baseline and hold their beak ready in place at exactly the spot where the lid of the box would come after the 5 seconds baseline. This behavior confirms the discrimination training, and also explains the very short latencies to peck. For this reason, a small constant close to the minimum observed value (constant = 0.009, minimum value = 0.01) was added to all values to ensure that 0 sec responses fell within the Gamma $(0, \infty)$ interval. We assessed the sensitivity of our results to this data transformation by fitting an additional Bayesian hurdle Gamma GLMM with diffuse priors, $\beta \sim \text{Normal}(0, 106)$, $\sigma^2 \sim \text{Half-Cauchy}(0, 106)$, which appropriately accounts for observed zeroes in addition to the Gamma process. The latter model was estimated using Hamiltonian Monte Carlo (HMC) with the Stan statistical programming language via the 'brms' R package (Bürkner, 2017). Both models produced highly comparable estimates to our reported model, suggesting that our results are appropriately insensitive to the magnitude of this constant.

We first assessed whether latency to peck at the ambiguous location increased across sessions due to the absence of reinforcement, which would necessitate the modeling of potential learning effects in subsequent analyses. This was done by estimating a GLMM with response time measures across all ambiguous location trials as the response variable, order of presentation for each subject as a fixed effect, and subject identity and dyad as random effects. We then fit a GLMM comparing pre-manipulation response times across locations to determine the efficacy of our discrimination training. In particular, we fit a model with box location nested within role as fixed effects and subject and dyad identity as random effects. This allowed us to assess the effect of location (positive, negative, ambiguous) on pecking latency for a given role (demonstrator or observer) prior to emotion manipulation. In R formula syntax, our model structure was therefore:

$$\text{response time} \sim \text{role/location} + (1|\text{subject}) + (1|\text{dyad})$$

It is likely that our demonstrator cognitive bias results were confounded, resulting in no significant differences at the ambiguous location for demonstrators. Nonetheless, this model structure including both observer and demonstrator responses facilitates the distinct evaluation of subjects' responses in each role for each condition, while also providing more information for estimating individual differences among subjects and dyads in their expected response tendencies across all conditions. This approach therefore effectively partitions heterogeneity across subjects and dyads from the main effects of our manipulations, thus contributing more statistical power to our fixed effect analyses. We then fit a full model with fixed effects nesting time of presentation within role within box location within experimental condition. Comparisons were therefore made for observers and demonstrators before and after the emotion manipulation across the positive, negative, and ambiguous box locations in each experimental condition. Subject and dyad identity were again specified as random effects. In R formula syntax, this model was therefore specified as:

$$\text{response time} \sim \text{condition/location/role/time} + (1|\text{subject}) + (1|\text{dyad})$$

Further comparisons of post-manipulation responses across conditions and locations were conducted by modifying the structure of nested terms in this model. Please note that by simultaneously estimating all conditions within our model, as well as subject and dyad random intercepts, we directly account for the possible effects of consistent individual and dyad differences as well as responses to the positive and negative locations on responses at the ambiguous location. In addition, by modeling all trials across conditions rather than average responses, we effectively account for the variability present in our data rather than artificially reducing it through aggregation. More generally, this full interaction structure best represents the nested, multi-factorial design of our experiment, allowing direct and parsimonious examination of our primary hypotheses within a single statistical model.

Although the reported uncensored Gamma GLMM produced standard errors and predictions within the observed latency range, we fit an additional censored Gamma Bayesian GLMM using the 'brms' package to ensure that our main conclusions were robust. The censored model estimates supported our primary conclusions from the non-censored model and suggested an even larger effect size for the difference in observer response latency at the ambiguous location after the negative manipulation (mean posterior $\beta = -1.17$, $SD = 0.39$, 95% credibility interval $[-1.93, -0.42]$, posterior probability of $\beta > 0 = 0.002$). Moreover, these results were insensitive to the use of diffuse priors comparable to frequentist model estimation, $\beta \sim \text{Normal}(0, 106)$, $\sigma^2 \sim \text{Half-Cauchy}(0, 103)$, or weakly regularizing priors, $\beta \sim \text{Normal}(0, 10)$, $\sigma^2 \sim \text{Half-Cauchy}(0, 3)$, which produce more conservative estimates with a lower probability of Type 1 error (McElreath, 2016).

Supplemental Tables

Table S1. Behavioural coding

Behavior	Description
Pecking latency ^a	We measured the latency to peck the lid of the presented box during the cognitive bias test. This was measured from the moment the box touched the wire mesh to the moment the raven pecked the lid of the box.
Locomotion ^b	9 location grids were visually drawn on the ground of the experimental compartment. Here we measured frequency of moving between the different grids.
Front location ^c	This parameter refers to the demonstrator raven standing within 30 cm of the food items presented. <i>Front</i> is considered as one of the location grids in the coded behavior <i>Locomotion</i> .
Head and body movement ^b	We counted the total number of head movements and body movements made when the demonstrator was in <i>Front</i> of the stimulus. Head movements include a count of all the parameters coded for under <i>Looking Direction</i> , and body movements include a count of all the parameters coded for under <i>Looking Types</i> .
Looking types ^c	This parameter refers to three different vertical movements of the body. We measured this when the demonstrator ravens were standing in <i>Front</i> and looking at the food items presented. These movements include: (i) Looking through the peephole, (ii) Looking through the peephole by stretching the upper body, and (iii) Looking over the peephole through the wire mesh above peephole.
Looking direction ^c	This parameter refers to three different horizontal movements of the head. We measured this when demonstrators stood in <i>Front</i> . These movements include: (i) Looking with the left eye to the food items (considered when the beak tip was pointing to the right and the body remained in its initial, forward position), (ii) Looking straight to the food items (considered when the beak tip was pointing directly at the items), and (iii) Looking away from the stimulus (head turns 180° away).
Redirected behavior ^b	A sweep-like motion with the beak through the ground substrate. This is different from caching where the ravens take an object and hide it in the ground with a pecking movement.

Footnote. a = continuous duration measure; b = continuous count measures, c = duration proportion measures.

Table S2. Predicted variation in demonstrator behavior across experimental manipulation phases within each condition.

Behavior	Phase 1			Phase 3			β	z	p
	M	SE	95% CI	M	SE	95% CI			
Positive condition									
Locomotion ^a	6.37	1.10	[4.39, 8.38]	1.74	0.49	[0.87, 2.75]	1.31	4.37	0.01
Front location ^b	0.55	0.11	[0.34, 0.75]	0.96	0.02	[0.92, 0.99]	-3.17	-5.16	0.01
Head and body movement ^a	22.95	2.63	[18.40, 28.08]	29.43	3.35	[23.55, 36.01]	-0.24	-2.26	0.03
Looking into peephole ^b	0.38	0.06	[0.26, 0.49]	0.59	0.06	[0.46, 0.70]	-0.89	-2.89	0.02
Looking away ^b	0.13	0.04	[0.07, 0.21]	0.05	0.02	[0.03, 0.08]	1.07	2.47	0.04
Left eye use ^b	0.26	0.06	[0.16, 0.38]	0.31	0.07	[0.20, 0.44]	-0.27	-0.69	0.60
Negative condition									
Locomotion ^a	6.21	0.99	[4.41, 8.25]	3.78	0.76	[2.41, 5.38]	0.50	2.19	0.03
Front location ^b	0.59	0.11	[0.36, 0.79]	0.74	0.09	[0.53, 0.88]	-0.73	-1.18	0.31
Head and body movement ^a	19.56	2.35	[15.05, 24.04]	15.05	1.88	[11.43, 18.83]	0.26	2.04	0.03
Looking into peephole ^b	0.49	0.06	[0.37, 0.61]	0.64	0.06	[0.52, 0.76]	-0.64	-2.06	0.11
Looking away ^b	0.08	0.02	[0.04, 0.13]	0.06	0.02	[0.03, 0.10]	0.26	0.60	0.58
Left eye use ^b	0.18	0.05	[0.10, 0.28]	0.36	0.07	[0.23, 0.50]	-1.00	-2.50	0.03

Footnote. The expected original scale responses for an average demonstrator in each condition were predicted using a parametric bootstrapping procedure accounting for uncertainty in the fixed effect estimates of our models. Means (M) and standard errors (SE) therefore reflect the expected value and standard deviation of the bootstrap sampling distribution, respectively. Note that 95% CIs are asymmetric due to back transformation to the response scale.

^a = continuous count measures; ^b = duration proportion measures are the standardized regression coefficients on the ^alog-link and ^blogit-transformed scales for the expected change from Phase 3 (the reference category) to Phase 1.

Table S3. Predicted observer response latency before and after emotion manipulation.

Behavior	Before Manipulation			After Manipulation		
	M	SE	95% CI	M	SE	95% CI
Positive condition						
Positive location	0.24	0.06	[0.15, 0.37]	0.32	0.08	[0.19, 0.50]
Negative location	2.40	0.60	[1.44, 3.75]	2.49	0.62	[1.47, 3.91]
Ambiguous location	0.55	0.15	[0.30, 0.90]	0.81	0.22	[0.45, 1.29]
Negative condition						
Positive location	0.48	0.13	[0.26, 0.76]	0.57	0.15	[0.34, 0.90]
Negative location	2.17	0.58	[1.22, 3.42]	2.41	0.61	[1.35, 3.75]
Ambiguous location	0.76	0.21	[0.42, 1.26]	1.74	0.49	[0.98, 2.90]

Footnote. The expected original scale responses (sec) for an average observer in each condition were predicted using a parametric bootstrapping procedure accounting for uncertainty in the fixed effect estimates of our models. Means (M) and standard errors (SE) therefore reflect the expected value and standard deviation of the bootstrap sampling distribution, respectively. 95% CIs are asymmetric due to back transformation to the response scale.

Table S4. Subject information and discrimination training results

Pair	Subject	Sex	Age	Hand-reared	Kin (per pair)	Total number of trained trials	Total number of training sessions
1	Louise	F	3	Yes	Yes	116	8
1	Horst	M	3	Yes		122	9
2	Nobel	F	3	Yes	Yes	138	11
2	George	M	3	Yes		150	11
3	Tom	M	3	Yes	Yes	185	12
3	Laggie	M	3	Yes		164	11
4	Joey	F	5	Yes	No	123	9
4	Rocky	M	3	Yes*		122	9

*Most likely hand-reared (gifted from a sanctuary)

Footnote. All 8 ravens passed the training criterion after an average of 10 training sessions (range: 8 - 12 sessions) and an average of 140 trials (range: 116 - 185 trials). In comparison to other cognitive bias studies and their discrimination training the ravens passed the criterion with a remarkably low number of trials, which is in line with previous reports on their performance in discrimination tasks (Range et al., 2008).

References – Chapter 3

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Chapter 4.

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Watching others in a positive state does not induce optimism bias in common marmosets (*Callithrix jacchus*), but leads to behaviour indicative of competition.

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ABSTRACT

Emotional contagion is suggested to facilitate group life by enhancing synchronized responses to the environment. Cooperative breeders are an example of a social system that requires such intricate coordination between individuals. Therefore, we studied emotional contagion in common marmosets. Demonstrators were exposed to an emotion manipulation (i.e. positive, negative, control), and observers perceived only the demonstrator's behaviour, without exposure to the manipulation. We predicted that the positive or negative states of the demonstrator would induce matching states in the observer, indicating emotional contagion. All subjects' emotional states were assessed through behaviour and cognition, the latter by means of a judgement bias test. Behavioural results showed a successful emotion manipulation of demonstrators, with manipulation-congruent expressions (i.e. positive calls in the positive condition, and negative calls and piloerection of the tail in the negative condition). Observers showed no manipulation-congruent expressions, and they showed more scratching and arousal-related behaviour after the positive manipulation. Concerning the judgement bias test, we predicted that subjects in a positive state should judge ambiguous cues as more rewarding (i.e. optimism bias), and subjects in a negative state should judge these cues as less rewarding (i.e. pessimism bias). This prediction was not supported as neither demonstrators nor observers showed such bias in either manipulation. Additional analyses of the judgement bias test showed an effect of researcher identity, as well as a manipulation effect on the reference cues. We discuss all results combined, as well as the judgement bias results in light of recently raised validation concerns of its paradigm.

Introduction

Affective (emotional) mechanisms are assumed to underly many primate social behaviours (Schaffner and Aureli, 2002; de Waal, 2011), such as allogrooming (Russell and Phelps, 2013; Schino et al., 2016), offspring care (Preston and de Waal, 2002), and affiliative bonding (Aureli and Schino, 2004), as well as self-directed behaviours elicited by social interactions (e.g. self-scratching, Troisi et al., 1991). Social processes such as emotionally mediated reciprocity (Aureli and Schaffner, 2002), fairness (Yamamoto, 2012), and cooperation (Massen et al., 2019), have also been suggested to be underpinned by affect-based mechanisms. Emotional contagion is suggested as one of the more fundamental affective mechanisms of empathy (de Waal, 2008), and of other empathy-related and social behaviour such as social learning and affect-based helping (see Adriaense et al., 2020, for review). It is defined as an emotional state-matching between individuals (Hatfield, 1994; Preston and de Waal, 2002), and as such, it does not imply a cognitive representation of, or concern for, the other's emotional state (e.g. Adriaense et al., 2019b). Functionally, it is proposed to facilitate group life through fast, emotion-based responses which enhance information transmission (Nakahashi and Ohtsuki, 2018), improve social interactions and affiliative bonding, and increase defence against predation (Preston and de Waal, 2002; Decety et al., 2016; Isern-Mas and Gomila, 2019). For this reason, the study of emotional contagion is of particular interest in group-living (e.g. in pigs, Reimert et al., 2017) and pair-bonding species (e.g. in prairie voles, Burkett et al., 2016; in common ravens, Adriaense et al., 2019b).

Here, we argue that emotional contagion is also one of the potential affective mechanisms in cooperative breeding species (Massen et al., 2019). In particular, this reproductive system, where non-parents help in taking care of offspring (e.g. in humans, Kramer, 2010; Martin et al., 2020), requires efficient communication,

intricate spatial and temporal coordination between group members, as well as an increased attention to others (Burkart et al., 2009). Common marmosets are cooperative breeders of the callitrichid family, and in their social alloparenting system the dominant breeding pair lives together with their offspring and non-breeding adult helpers (Digby and Barreto, 1993; Erb and Porter, 2017). Aside from this cooperative parental care, marmosets also show cooperative territorial defence (Lazaro-Perea, 2001), and, as mentioned, these cooperative behaviours require efficient coordination and group cohesion (Burkart and van Schaik, 2010; Massen et al., 2016). In particular, it is suggested that social skills are important (Burkart et al., 2009; Burkart and van Schaik, 2009), and common marmosets demonstrate high degrees of prosociality (Burkart et al., 2014; Martin et al. 2020), including unsolicited prosociality toward non-reciprocating and unrelated individuals (Burkart et al., 2007). Therefore, we suggest that in common marmosets, emotional contagion is essential to achieve the necessary group coordination and cohesion required for cooperation.

To empirically test emotional contagion and establish an appropriate interpretation, it is important to assess the emotional states of both the sender and the receiver, and verify whether their states match (Adriaense et al., 2020, for review of emotional contagion). An emotional state is suggested to orient on two dimensions, namely arousal (i.e. low or high intensity) and valence (positivity or negativity) (Russel, 1980; Mendl et al., 2010), and thus, matching emotional states ought to reflect similarity on both dimensions. This is an important notion, as matching arousal in two individuals does not necessarily imply matching valence, and vice versa (Briefer, 2018). For instance, increased heart rate is indicative of high arousal but not necessarily of positive (e.g. excitement) or negative (e.g. fear) valence (Edgar et al., 2012). In

that vein, matching (synchronized) behaviours or physiological expressions do not unequivocally imply matching emotional states (see Massen and Gallup, 2017, for review of yawn contagion; see Isern-Mas and Gomila, 2019, for review of the mimicry mechanism; see Adriaense et al., 2020, for review of play contagion). Moreover, measuring valence is considered more difficult than measuring arousal, and research shows that previously assumed measures of valence in fact measure arousal (Paul et al., 2005; MacDougall-Shackleton et al., 2019). Considering this, researchers in the animal domain have to be additionally cautious, as a major obstacle in this field is the absence of (human) language to provide self-report on the subjective emotional experience (Paul et al., 2005). In conclusion, empirically observing behavioural or physiological synchronization in animals cannot be taken as definite evidence for emotional contagion. This does not imply that behavioural or physiological observations do not greatly contribute to our understanding of animal emotions (Paul et al., 2005), or that mimicry does not play an important role in emotional contagion (Lakin et al., 2003) or in social relations (McIntosh, 2006), but rather that interpretations of emotional contagion should not depend on observing synchrony alone, and that additional objective indicators are needed.

Emotional contagion in common marmosets has not been directly investigated yet, though its presence has been suggested (Finkenwirth et al., 2015). Furthermore, synchronized responses have experimentally been observed in coordinated behaviour during joint action tasks (Miss and Burkart 2018), in behavioural contagion such as contagious scent-marking and gnawing (i.e. gouging) (after visual demonstration of a conspecific, Massen et al., 2016) and contagious affiliative expressions (after auditory demonstration, Watson et al., 2010), as well as in synchronized oxytocin fluctuations over time in strongly bonded dyads (Finkenwirth et al., 2015). Inferring emotional contagion should ideally be based on the

assessment of multiple indicators which allow interpretation of both dimensions of an emotion (i.e. arousal and valence) (Mendl et al., 2010). In that regard, emotions are considered adaptive, multi-componential responses to the environment, causing coordinated changes in behavioural, physiological (incl. neurological and endocrinological), cognitive, and feeling components (Paul et al., 2005; Anderson and Adolphs, 2014). This functionalist approach, in which emotions are considered central states (Adolphs and Andler, 2018), allows animal emotion research to focus on the objectively measurable components, and sets aside the conscious feeling component, allowing for systematic, comparative research across species. Usually, the behavioural and physiological component are more often studied as potential indicators of animal emotions, than the cognitive component. Yet, recent developments of the so-called cognitive bias paradigm offer a promising method to not only incorporate the cognitive component, but also provide a means to measure valence (Harding et al., 2004; Mendl et al., 2009). The paradigm is based on the emotion-cognition interaction premise (Pessoa, 2013), which finds support in neuroscience (Clore, 2018) as well as in human psychology and psychiatry. This support demonstrates that cognitive processing may alter emotional states (e.g. by means of appraisal) and that emotions may induce cognitive changes, referred to as cognitive biases (i.e., bias here implies an impact or influence, rather than error). Positive or negative emotional states bias cognitive processing in a congruent manner, so that memory, attention, or decision making will either be more positively, or negatively, biased, respectively (i.e. negative states induce e.g. negative decision making, Eysenck et al., 1991; negative future anticipation, MacLeod and Byrne, 1996; negative attention, Mathews and MacLeod, 1994; and vice versa for positive states, e.g. Eysenck et al., 1991; Nygren et al., 1996). Similarly, by analysing an animals' cognitive performance under specific conditions, we may find cognitive biases in their responses (Paul et al., 2005; Mendl et al., 2009), which may

serve as a proxy to assess the subject's emotional valence (Neville et al., 2020; Lagisz et al., 2020). The bias hypothesis predicts that animals in a positive state should show a positive or optimism bias, and animals in a negative state should show a negative or pessimism bias (note that this not implies a subjective experience of optimism or pessimism, Lagisz et al., 2020).

The judgement bias test (JBT) is one of the most frequently used cognitive bias designs, which measures biases in decision making under ambiguity. Typically, in this paradigm, animals are trained to associate one cue with a positive reward (i.e. the positive cue) and another cue with no reward or a punishment (i.e. negative cue). After successful training, animals are then presented with (an) untrained, ambiguous cue(s). Here, the animal's response to the ambiguous cue(s) is measured and whether this response *biases* more towards the response given to the positive cue (e.g. by faster response time or more responses, i.e. optimistic bias) or to the negative cue (e.g. by slower reaction time or fewer responses, i.e. pessimistic bias). The JBT has been applied across a wide range of mammalian, avian, and invertebrate species (see for reviews: Mendl et al., 2009; Bethell et al., 2016; Roelofs et al., 2016; Neville et al., 2020; Lagisz et al., 2020). The majority of these studies focused on a focal animal, and assessed whether a presumed change in affect due to, for instance, husbandry procedures (e.g. enriched environment, Douglas et al., 2012; social housing, Lalot et al., 2017), corresponds with the predicted bias in a JBT. The interaction between experimentally induced shifts in affective states and related biases in cognitive performance has also been successfully studied in a number of monkey species. Research in rhesus macaques found effects of husbandry procedures, providing evidence for associations between environmental enrichment and optimism bias, and between a veterinary visit and pessimism bias (Bethell et al., 2012). Moreover, in capuchin monkeys, stereotypical behaviour such as head twirls (but not pacing) correlated with pessimism bias, together with higher corticoids

levels (Pomerantz et al., 2012). Monkeys who show overall higher rates of scratching (which is presumably negative) also show less optimism bias (Schino et al., 2016), and individuals that generally receive more grooming and rank as alpha male, show more optimism bias (Schino et al., 2016). In common marmosets no previous work has studied the relation between experimentally induced states and cognitive bias, though, two studies used a judgement bias paradigm to assess effects of rearing (hand-reared monkeys showed no bias when compared to family-reared ones, Ash and Buchanan-Smith, 2016) and effects of handedness (left-handed monkeys showed pessimism bias and received more group aggression, Gordon and Rogers, 2015) (see also Perdue, 2017, for bias results with no experimental manipulation in rhesus and capuchin monkeys). In apes, the use of a JBT has so far been successful in one study (in terms of reaching training criterion). JBT was investigated in three chimpanzees, and whether general tendencies to expect reward or not, could potentially serve as a source to assess poor welfare when overt expression is missing (Bateson and Nettle, 2015). The study did not use an experimental manipulation, but results showed individual variance remaining stable over two weeks. The bias methodology is not always easily transferred between species, and repeated research in gorillas showed that subjects either were not able to pass the required discrimination learning (note the small sample of three subjects) or exhibited individual differences putting the findings into question (McGuire, Vonk, Fuller, Allard, 2017; McGuire and Vonk, 2018).

To our knowledge, only two studies so far have used a JBT to assess emotional states stemming from emotional contagion, namely in rats (Saito et al., 2016) and in common ravens (Adriaense et al., 2019a). Saito and colleagues (2016) used an auditory judgement bias test with a go/go design. For training, the rats were first exposed to either one of two different sounds, which represented either a sucrose solution as reward (i.e. positive

sound or cue) or white noise as punishment (i.e. negative sound or cue). After hearing one of the two sounds, the rats were trained to press either one of two available levers, where pressing lever A resulted in receiving the reward and pressing lever B resulted in avoiding the punishment. After training, rats underwent an emotion manipulation consisting of a 20-minute playback of either positive or negative calls from conspecifics, which was followed with a judgement bias test. In this test the two trained sounds were presented with in addition three intermittent, ambiguous sounds, and with each sound presentation the rats were given the option to press either lever A or B. The results of the positive and negative manipulation were compared to results of a control condition. This showed that after hearing positive calls from conspecifics, rats pressed more often lever A when presented with an ambiguous sound and, thus, perceived this sound as more rewarding. After hearing negative calls, rats pressed lever B more when hearing an intermediate-ambiguous sound, which reflects that rats perceived this sound as more punishing. Based on these judgement bias test results, this study provides evidence for positive emotional contagion, and partially for negative contagion, in rats. In the raven study (Adriaense et al., 2019a), the experiment included a spatial judgement bias test with a go/no-go design. As training, ravens were presented with a small box placed either on their left or right side, and learned that pecking the box on one side lead to receiving a piece of cheese as reward (i.e. positive side or cue), and that pecking the box on the opposite side lead to not receiving anything (i.e. negative side or cue). After learning the reward value of each of the two cues, ravens participated in an emotional contagion experiment. Here, a demonstrator raven was exposed to a two-minute positive or negative emotion manipulation, and an observer watched the demonstrator but could not see the manipulation the demonstrator was being exposed to. This was followed with a judgement bias test where a box was presented on the two trained sides with in addition a new ambiguous

location (i.e. intermittently between the positive and negative side). After the box was placed on either the left, right, or middle location, ravens had the choice to peck or not peck the box. The results of the positive and negative manipulation were compared between-condition, as well as within-condition by means of a JBT baseline measurement before the manipulation took place. Results showed that after watching the demonstrator in the negative manipulation, observer ravens pecked the box on the ambiguous location less, compared to both the positive manipulation and baseline measurement. This indicates that ravens perceived the ambiguous cue as less rewarding when the other raven was in a negative manipulation, though, no change in pecking was found in the positive manipulation. Therefore, based on the judgement bias test results in the negative condition, this study provides evidence for negative emotional contagion in common ravens.

Research question

The JBT and its fundamental theoretical cognitive bias framework provide an objective and replicable methodology, which allows for comparative emotion research between species (de Waal, 2011). For that reason, we investigated emotional contagion in common marmosets by means of a JBT, which was inspired by the emotional contagion experiment from Adriaense et al. (2019a) and the spatial judgement bias paradigm used in Hintze et al. (2018) (see details in Methods). This research thus contributes to the further validation of the bias paradigm, and the scientific investigation of affective mechanisms underlying cooperative breeding systems.

Subjects participated in dyads undergoing either a positive, negative, or control manipulation, and before and after the manipulation a spatial JBT was conducted (from here-on referred to as 'pre-JBT' and 'post-JBT'). As preparation for this experiment, animals were first trained on a stimulus discrimination task, in which they

learned that a cue presented on one side of the apparatus contained a food reward (i.e. the positive cue, referred to as P) and a cue presented on the opposite side contained no reward (i.e. the negative cue, referred to as N). After learning the different reward values of the two reference cues, resulting in an overall approach of P and avoidance of N, the subjects participated in an emotional contagion experiment with a pre- and post-JBT. During both JBTS subjects were presented with the reference cues P and N, with addition of three unknown ambiguous cues (i.e. Near Positive, NP; Middle, M; Near Negative, NN) interspersed between the positive and negative trials. NP and NN were both presented near the respective reference cues, and thus, were of intermediate ambiguity, with M being the most ambiguous.

Following the cognitive bias hypothesis, we predicted that demonstrators undergoing a positive manipulation should in the post-JBT respond to the M cue in a similar way as to the P cues (i.e., more go responses, as an indication of optimism bias). Correspondingly, after the negative manipulation, subjects should in the post-JBT respond to the M cue similarly as to the N cues (i.e. fewer go responses, pessimism bias). Through processes related to emotional contagion, we expected observers to show the same pattern of optimism bias in the positive condition, and pessimism bias in the negative condition. To follow the recommended multi-component approach in emotion research, and provide an additional validity check of the judgement bias test results, we also assessed both subjects' behaviour during the emotion manipulation and the JBTS. Specifically, to validate whether the manipulation had its intended effect on the demonstrator during the manipulation, we predicted positive-related behaviour in the positive condition, and negative-related behaviour in the negative condition (see Methods for details). Through emotional contagion, we predicted to find similar behaviours in the observers. Furthermore, we predicted that some of these behaviours would

persist in the post-JBTS, although they would likely be less present than during the manipulation, as animals should be more occupied with performing in the post-JBTS.

Methods

Sample

In total 8 common marmosets (four females, four males) participated in this study. An additional five marmosets participated in the discrimination training (see Methods), but did not reach criterion within the designated study timeframe. All animals were born in captivity and housed at the Department of Behavioral and Cognitive Biology, UZA 1, University of Vienna, Austria (see SI Table S1 for subject details; see SI for housing details).

Procedure

The overall procedure of one test session went as follows. Subjects participated in dyads consisting of a demonstrator ($n = 8$) and an observer ($n = 7$, three females, four males), and each subject took on the role of demonstrator or observer per test session (see for more info under 'Total test sessions'). Each subject was first tested with a pre-JBT, then they underwent an emotion manipulation, and were then again tested with a second JBT (i.e. post-JBT). During both JBTS, the subjects were tested individually and the visual access to their dyadic partner was blocked, whereas during the emotion manipulation, the subjects received visual access to each other (by use of a moveable door, see Fig. 1 and SI Fig. S1). The pre-JBT served as baseline measurement (average time per JBT: 10 min). Afterwards, the demonstrator was exposed to an emotion manipulation, while the observer was exposed to the demonstrator's behaviour only, and thus, could not see the stimuli used for the manipulation. The manipulation had three conditions, namely positive, negative, and

control, with one condition per test session (presentation time: 2 min). This was followed by a post-JBT, using the same procedure as the pre-JBT. During the emotion manipulation and the two JBTs the behavioural responses from both subjects were quantified. This design allowed us to assess the emotion manipulation effect (i.e. by means of the demonstrator's behaviour and judgement bias data), as well as to assess potential emotional contagion (i.e. by means of the observer's behaviour and judgement bias data). After the post-JBT the subjects were free to join their social groups again (average time per session: 22 min) (see SI for dyad details and details on welfare and habituation).

Total test sessions. Each subject (excl. Aurora, see SI for dyad details) participated in total in 12 test sessions; namely, twice as demonstrator and twice as observer in all three conditions (i.e. positive, negative, control). These repeated measures (i.e. labelled 'period 1', 'period 2' in our variables, see SI) of testing twice were introduced as we were interested in how this would impact JBT results, and whether the emotion manipulation would have stronger or weaker effects over time. We only conducted period 2 testing once the subjects had completed all testing of period 1 (i.e. once as demonstrator in all three conditions and once as observer in all three conditions).

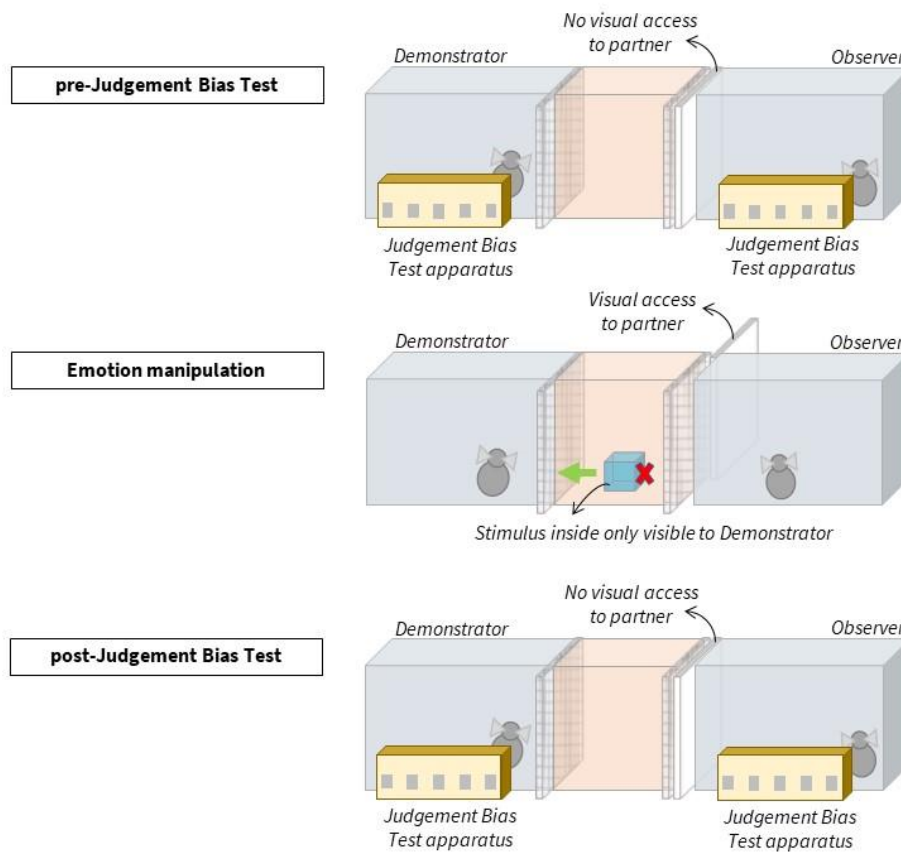


Fig. 1: Experimental design. Study subjects always participated in dyads consisting of a demonstrator and an observer. In each session, the subjects were first tested on a pre-Judgement Bias Test (i.e. pre-JBT) during which they had no visual access to one another (i.e. the white door was closed). Then an emotion manipulation followed, in which the two monkeys had visual access to one another (i.e. the white door was opened). Here, each demonstrator saw either a positive, negative, or control stimulus in a box with only one opening which was directed to the demonstrator. The observer had no visual access to the content of the box, but was able to see the behavioural responses of the demonstrator. Lastly, the visual access between subjects was again blocked (i.e. the white door was closed) and both subjects were tested on a post-Judgement Bias Test (i.e. post-JBT) (see also SI Fig. S1 and S2).

Emotion manipulation. In the positive condition the demonstrator was presented with a bowl of banana pieces (i.e. preferable food item, to induce a positive state), in the negative condition with an artificial large rubber spider (i.e. threatening item, to induce a negative state), and in the control condition with nothing (for between-condition comparison) (see SI Fig. S3). The stimuli were presented inside of a white foam box with only one opening, which was oriented toward the demonstrator, so that the content of the box was not visible to the observer (see Fig. 1). During test sessions we controlled for potential banana odour cues by placing a small container filled with banana pieces on top of the middle testing compartment before subjects entered the testing room (see SI Fig. S2). Therefore, the observer was presumably naïve to the manipulation stimuli aside from watching the demonstrator's responses. Between each test session all three compartments were cleaned with a vinegar-water solution.

Judgement bias paradigm. We used a spatial JBT to assess the emotional valence of the demonstrator and observer, before and after the emotion manipulation. Generally, a judgement bias paradigm consists of a discrimination training, followed by the actual judgement bias test. Due to the nature of this paradigm and the use of ambiguous cues, various elements of the methodology are important to consider when designing a bias test. When these elements are not efficiently or appropriately incorporated, they may inflate findings of either pessimism or optimism biases, or the test may measure other variables (e.g. response to novelty) rather than response to ambiguity. Below we describe how we incorporated these key requirements into our judgement bias training and testing (based on the review by Roelofs et al., 2016).

Judgement bias training: Trial initiator. A key element mentioned by Roelofs et al. (2016), is the choice of either a go/no-go or a go/go design. The former is a popular design choice in JBT studies and refers to the animal either actively

approaching a cue (P cue) or not (N cue). However, a limitation to this design is the requirement for response suppression as subjects need to actively inhibit their behaviour when being exposed to the N cue, which is known to be difficult (Mendl et al., 2009). As a result, such inhibition issues may during testing either lead to (seemingly) optimistic or pessimistic responses, which in reality may be either failures to inhibit, or to react, respectively. The go/go design obligates the animal to make active choices for both P and N cues and, thus, the design does not require behavioural inhibition. Still, a major limitation of the go/go design is the extent of training before the actual JBT takes place, as this design is more cognitively demanding and often demands more time to reach training criterion (Roelofs et al., 2016; Lagisz et al., 2020). For this reason, we used a new hybrid go/no-go design which includes a third choice serving as opt-out alternative (originally designed by Hintze et al., 2018). When facing either one of the presented cues during testing, subjects have the choice to either approach the cue or not, and when they do not approach, they have the choice to opt-out and start the next trial, or do nothing. Such opt-out alternative (labelled 'trial initiator') gives animals a second active choice, limits the requirement for behavioural inhibition, and moreover, puts the animal in control of the trial progress. Therefore, the training prior to the experimental study consisted of two main training stages, namely apparatus training and discrimination training.

Judgement bias training: Apparatus training.

The judgement bias test apparatus was custom built (84 x 20 x 40 cm) and had five wooden doors (i.e. from left to right) as cues. The doors could be opened and closed by a researcher, by holding and pulling a small screw sticking out. When pulling, the doors hit a small object on their upper left to additionally create an auditory cue. We implemented this simultaneous visual and auditory cue when the door opened, to increase saliency, and thus, to ensure that subjects were attentive to all door cues. On the right side of the

apparatus was a string which connected to the trial initiator (i.e. a white plastic object, 20 x 4 x 1 cm), placed on the opposite side of the apparatus (i.e. distance between apparatus and initiator: 100 cm) (see SI Fig. S4, S5, and S6 for details). During apparatus training, animals were trained to touch the trial initiator as necessary requirement before any of the JBT cue doors would be opened. Concretely, the subject would touch the initiator and subsequently, on the opposite side of the cage, one of the two reference doors (i.e. the positive and negative cue) of the JBT apparatus would be opened which the subject had to approach within 10 s. Therefore, touching the initiator meant the start of a next trial, and, thus, if animals did not want to approach a certain cue, they could re-touch the initiator and start the next trial (see SI for training details; SI Table S2 for training schedule).

Judgement bias training: Discrimination training. After apparatus training, subjects followed a discrimination training of the reference cues P and N (i.e. positive cue and negative cue). Each trial began when subjects touched the trial initiator opposite of the apparatus, upon which one of the apparatus' doors opened (during training only the P and N cues were used, and later during testing all five cues were used). After touching, the trial initiator went out of view for 3 s and subjects had three options within this trial: either they approached the open door within 10 s (coded as go response), either they did not approach the open door within 10 s (coded as no-go response), or they touched the trial initiator again after it was lowered for 3 s (coded as no-go and active choice) (see SI Table S3 for ethogram). With this third choice a new trial began immediately, in which the previous door closed and a new one opened, and again 10 s would be given to make a choice. If within these 10 s the subjects did not approach the open door and did not touch the initiator for a new trial, the open door would be closed after 10 s and a new trial would only start when the subject touched the initiator. On P trials, the correct choice was a go response, and thus, to approach the open P

door within 10 s. On N trials, the correct choice was a no-go response, either by not approaching the open N door within 10 s or by initiating a new trial. To achieve this discrimination training, P trials were always rewarded after subjects sat in front of the open door, and N trials were never rewarded. The criterion to pass spatial discrimination training was set at 80% go response for P trials and 80% no-go response for N trials (i.e. 8/10 trials each cue), calculated per day, over three consecutive days (See SI Table S2 for training details).

Judgement bias test. After successful training, subjects took part in the experiment. Importantly, the ambiguous cues now presented during the JBT should be equally related to the reference cues P and N (Roelofs et al., 2016). Therefore, we chose a gradual, horizontally oriented, spatial design going from the reference cue P to a near positive cue (NP), a middle cue (M), near negative cue (NN), and the reference cue N (see SI Fig. S6). Furthermore, a well-known problem is that multiple measurements over time may lead to animals learning the true reward value of the ambiguous cues NP, M, and NN. This learning effect may cause a loss of ambiguity, eventually resulting in an increased go-response to either of these cues when they are rewarded, or a decreased go-response when they are not rewarded. Consequently, such learning effects may inflate findings of optimism or pessimism bias, respectively. We incorporated four solutions in our design to prevent a potential learning effect. First, we used a 1 trial per ambiguous cue per test session, as a lower amount of ambiguous trials decreases the possibility of learning their true reward value (Roelofs et al., 2016). This gives in total for period 1 12 trials for each ambiguous cue per subject, and thus 24 trials after repeated measures and for the whole study. This is in line with the number of ambiguous trials used in other judgement bias studies (e.g. Pomerantz et al., 2012; Bateson and Nettle, 2015; Bethell et al., 2016). Second, we added a control manipulation (with respect to the emotion manipulation) and a pre-JBT to provide baseline

results. Both serve the idea of testing the response to ambiguity in the absence of experimental manipulation, in which no change in response to the ambiguous cues is expected. Adding a control condition allows us to rule out alternative effects on responses to ambiguous cues, and adding pre-JBTs offers to compare within-condition results in addition to between-condition responses. As third solution we followed the reward schedule by Hintze et al. (2018), in which NP, M, and NN trials were rewarded when animals approached these cues. So far, the main issues with learning have been in regard to inflated findings of pessimism biases, potentially due to the saliency of unrewarded ambiguous cues. Though our design may still inflate optimism bias, using a reward schedule is potentially less salient, and thus, may lead to less problems with a learning effect. As final option to counter potential learning effects, we added responses to each of the ambiguous cues in a synchronized order, and as such, statistically accounted for this effect in our model and give more accurately represented results. One JBT consisted of 13 trials (i.e. 5 P; 1 NP; 1 M; 1 NN; 5 N) and per test session two JBTs were conducted per subject (i.e. one pre- and one post-JBT), resulting in 26 trials per session (i.e. 20 P; 2 NP, 2 M, 2 NP, and 20 N) (see SI Table S4 and S5 for total trials and order of testing).

Behavioural responses. Overall, results from a judgement bias test should be further validated with other variables which are assumed to assess affect (Roelofs et al., 2016). Therefore, we quantified behaviour shown during the emotion manipulation and the pre-and post-JBTs. Specifically, during the positive emotion manipulation, we predicted to observe positive state-related behaviour, such as vocalisations related to food anticipation (from here on labelled 'positive calls'). Here, we paid particular attention to "chirp" and "food-beg" calls, as these often occur in food anticipatory context (e.g. Epplé, 1968; Watson et al., 2010). We also predicted a greater proportion of subjects positioning themselves in front of the stimulus

(labelled 'position'), as we assume that taking a position directly in front of the stimulus indicates increased interest. In particular, we predicted this for both demonstrators and observers, because demonstrators had visual access to the stimulus in front of them, and thus, we expected increased positioning in front within the positive condition. For observers we predicted a greater positioning in front in this condition as well, though they had no visual access to the stimulus, but through emotional contagion we expected them to approach (or avoid in the case of the negative condition) the area directly in front of the presented stimulus box. During the negative emotion manipulation, we predicted negative state-related behaviour, namely the presence of a pilo-erected tail ('pilo-erect tail'), scratching ('scratching'), predator or alarm calls ('negative calls'), and more positioning elsewhere in the cage. In marmosets, pilo-erected tail is often used as behavioural indicator of general arousal, with some findings in negative contexts (e.g. Ermatinger et al., 2019; Šlipogor et al. 2016, under review), and scratching is frequently a measure of (negative) stress (e.g. Bassett et al., 2003; Šlipogor et al. 2016, under review). For negative calls we looked at "tsik", "tsik-egg", "cough", and "seep" calls, which are described as mobbing or alarm calls in reaction to threat or predation (Bezerra and Souto, 2008). During both pre- and post-JBTs, we predicted increased scratching in the post-negative test, but we had no further predictions as for the majority of the time subjects were expected to be involved in responding to the test. For overall additional exploratory purposes, we looked at other behaviours shown during the manipulation and the JBTs, such as scent-marking, gnawing, contact calls (i.e. "phee", "shrill", and "whirr"), egg calls, defecating, urinating, and self-grooming (see SI Table S3 for ethogram).

Recording. The entire study was video recorded and afterwards the files were re-named to ensure blinding of the data. An independent researcher (LM) used the re-named files to code for the responses during JBT, including all go/no-go

responses and behaviour. LM was unaware of the research questions at the time and no cues of the emotion manipulation were present on the actual video footage. JA used the re-named files to code the behaviour shown during the emotion manipulation. All videos were coded using Solomon Coder software (Péter, 2017).

Results: Descriptive statistics

Training JBT

On average, marmosets reached criterion for discrimination training in 6 days and 128 trials (range days: 3-9; range trials: 60-180) (see SI Table S6 for training results).

JBT

Each subject completed a maximum of 12 test sessions, resulting in 24 JBTs per subject in total (see SI Table S4 for total test trials per subject). Subjects correctly exhibited a higher proportion of go responses to the P cues (sample mean = $0.93 \pm \text{SD} = 0.09$), with a gradual decrease between the intermediate cues NP (0.81 ± 0.14), M (0.52 ± 0.18), and NN (0.33 ± 0.17), to the expected lowest proportion of go responses to the N cues (0.08 ± 0.1). This gradual decline in the proportion of go responses shows the monotonic graded response curve ideally observed in JBT results (Gygax, 2014) (see Fig. 2 for group-level results, and SI Fig. S7 for individual-level results). The use of the trial initiator showed a similar monotonic response pattern, resulting in a low proportion to opt out for the P cue (4%), followed by a gradual incline between the intermediate cues NP (10%), M (26%), NN (42%), to a higher proportion opting out when presented with N cues (70%). This confirms the use of the trial initiator as active choice aside from a go response. On average during testing, the responses to P cues had a 6.7% error rate (i.e. performing an incorrect no-go response) and to the N cues 8.4% (i.e. performing an incorrect go response), which is in line with others reporting that more mistakes tend to occur toward N cues

(e.g. Hintze et al., 2018).

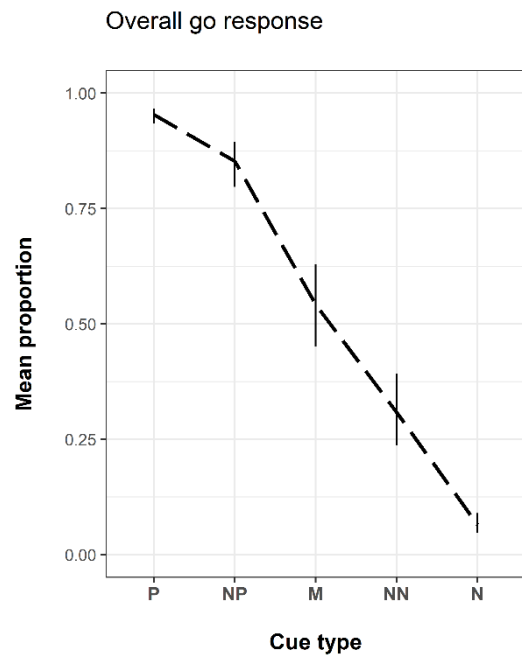


Fig. 2: Mean predicted proportion (bars indicate SE) of go responses to the five cues of the JBT. Plot shows overall result of all subjects, across all conditions, confirming a successful discrimination training between the different reference cues and their reward values, and the required monotonically graded response. P=positive, NP=near positive, M=middle, NN=near negative, N=negative.

Results: Statistical analyses

Model comparison

All statistical analyses were done in R 3.6.2 statistical environment (R Core Team, 2013) and we used generalized linear mixed models (GLMM's), using the 'lme4' package (Bates et al., 2015). We chose GLMM's as they account for repeated measures within subjects, enhance statistical power, and avoid artificial reduction of the variability in the dataset (Gygax, 2014). For all models, we used a likelihood ratio test and the Akaike's information criterion (AIC) as model selection procedure to identify the best model

explaining variation in the dependent variables, go response and behaviour. The likelihood ratio test verifies whether two models significantly differ from each other, and when no significant difference is shown, the least complex model is chosen. If a significant difference exists, the AIC values of the two models are compared, and when the difference is less than 2, both models are considered sufficient and again the least complex model is chosen, and when the difference is 2 or higher than 2, the model with the lowest AIC is considered better (Symonds and Moussalli, 2011).

Based on the variability observed between individuals for overall go responses in the JBT (see SI Fig. S7), we included subject as random variable in all our subsequent analyses, as well as date. For our main research question (i.e. optimism or pessimism bias) and, thus, to assess differences in go responses between (i.e. between positive, negative, control) and within (i.e. between pre- and post-JBT) each condition, the model was specified with a binomial distribution using logit transformations. We included test nested within cue nested within condition as this specific interaction was expected to show differences in the go response. Due to our repeated measures study design we expected different results in the repeated measures, so we included period (i.e. period 1, period 2) as predictor. For theoretical reasons regarding emotional contagion we included role (i.e. demonstrator, observer), and for exploratory purposes we included researcher (i.e. VS, JA) and time (i.e. testing in the AM, testing in the PM) as predictors as well. A likelihood ratio test and AIC comparing this full model to a reduced model (i.e. without the main or interaction effects of period, role, researcher, and time), supported a model with researcher, role, and period each as main effect, and condition/test/cue as interaction.

Each basic behaviour model included condition (positive, negative, control) as predictor and during model comparison this was compared to a full model with either predicted or exploratory

variables (see SI for details of each dependent variable). To verify differences in subjects' behaviour during emotion manipulation, the model was specified with a Poisson distribution using log link transformations for behaviour counts (i.e. all vocalisations, scratching, scent-marking, gnawing) and a binomial distribution with logit transformation (i.e. pilo-erected tail). We also coded position during emotion manipulation, for which we performed a logit transformation on the proportion of time spent in front. For behaviour during emotion manipulation we compared mean behaviour counts between and within conditions. To assess differences in subjects' behaviour during JBT, we included condition/test as interaction effect, and the model used a Poisson distribution for behaviour counts (i.e. scratching, scent marking, gnawing), with comparisons made between and within conditions (see SI for final models for each behavioural parameter).

JBT paradigm checks

Discrimination training success

We performed statistical tests to verify the success of discrimination training and the monotonically graded response pattern as a means of internal validity (Hintze et al. 2018). To this end, we ran a model with cue as independent variable (with subject and date as random variable) and found that subjects had significantly higher proportion of go responses to the P cues (compared to M: $\beta = 2.854$, $z = 12.602$, $P < 0.001$), and significantly lower proportion of go responses to the N cues (compared to M: $\beta = -2.836$, $z = -12.893$, $P < 0.001$). Subjects also responded to the intermediate cues as being (gradually) different from M with a significant higher proportion for NP (compared to M: $\beta = 1.586$, $z = 5.885$, $P < 0.001$), and a significant lower proportion for NN cues (compared to M: $\beta = -0.973$, $z = -3.960$, $P < 0.001$). These proportional results confirm that the marmosets successfully learned to discriminate between the P and N cues, and confirms that NP, M, and N were

perceived as intermediate (see Fig. 2).

Learning or order effect of ambiguous cues

Then we verified whether the go response to the ambiguous cues changed over time, potentially indicating a learning effect of its reward value. We added order as independent variable (with subject and date as random variables), and we found that over time there was no significant change in go responses to specifically the ambiguous cues (for NP; $\beta = -0.026$, $z = -0.608$, $P = 0.543$; for M; $\beta = -0.017$, $z = -0.552$, $P = 0.581$; for NN: $\beta = -0.061$, $z = -1.728$, $P = 0.084$). This confirms that subjects did not learn the reward value of either ambiguous cue, and that a potential optimism bias would not have been due to an order effect. For that reason, we did not add order as control variable in our subsequent analyses.

Go responses during JBT

Responses to the ambiguous cues

We predicted that responses to the M cues would show an optimism bias after the positive manipulation, and a pessimism bias after the negative manipulation, for both demonstrators and observers. Our analysis did not support either prediction: After experiencing the positive manipulation, demonstrators did not show a significant increase in go responses to the M cues (compared to pre-test: $\beta = -0.318$, $z = -0.398$, $P = 0.691$), neither did they show a significant decrease in go responses after the negative manipulation (compared to pre-test: $\beta = 0.685$, $z = 0.823$, $P = 0.411$). Observers did not show a significant increase in go responses to the M cues after positive manipulation to the demonstrator (compared to pre-test: $\beta = -0.322$, $z = -0.400$, $P = 0.689$), or a significant decrease after the negative manipulation (compared to pre-test: $\beta = 0.846$, $z = 0.911$, $P = 0.362$) (see SI for details) (see Fig. 3).

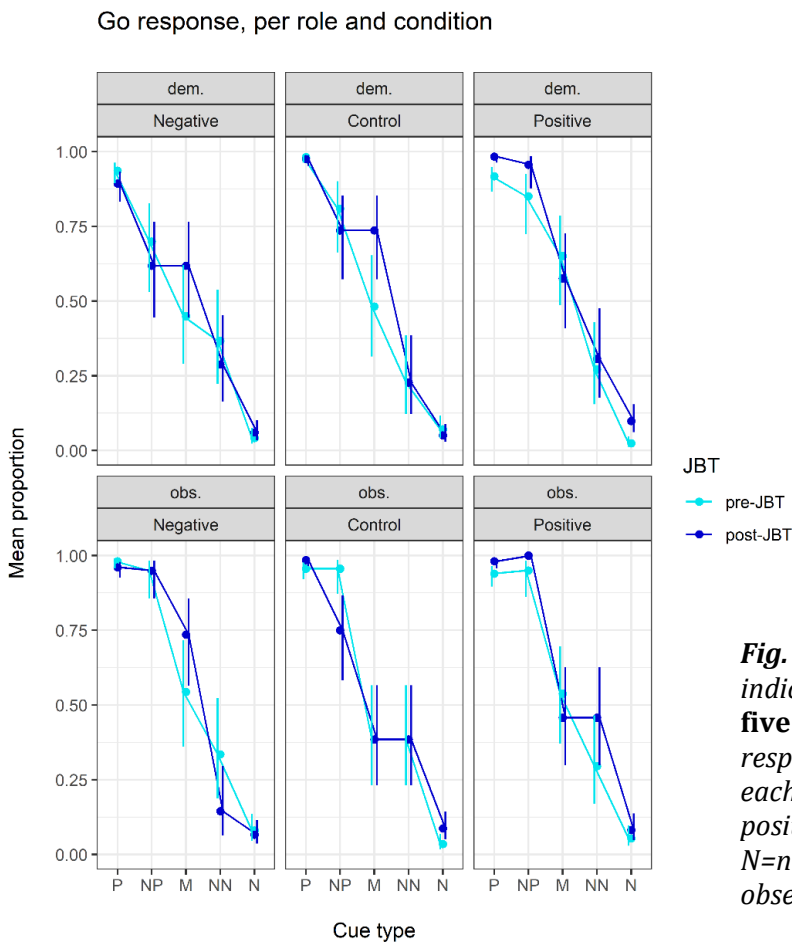


Fig. 3: Mean predicted proportion (bars indicate SE) of go response to each of the five cues of the JBT. Plots show go responses between conditions and roles, for each pre- and post-JBT. P=positive, NP=near positive, M=middle, NN=near negative, N=negative; dem.= demonstrator, obs. = observer.

Regarding the other ambiguous cues, subjects significantly increased their go response to the NP cue in the post-positive test (compared to post-control: $\beta = 2.711$, $z = 2.398$, $P = 0.016$; post-negative: $\beta = 2.416$, $z = 2.127$, $P = 0.034$), and more specifically, this concerns the demonstrators (compared to post-negative: $\beta = 2.605$, $z = 2.145$, $P = 0.032$). Note that model comparison did not support a model with role included, though based on our theoretical question of emotional contagion, we decided to include role as interaction variable to further explore this result.

Responses to the reference cues

We found an unexpected significant effect of condition in response to the reference cues. In the post-positive test, subjects significantly increased their go response to the reference cues P and N (compared to pre-positive test, for P: $\beta = 1.452$, $z = 2.487$, $P = 0.013$; for N: $\beta = 1.003$, $z = 2.102$, $P = 0.036$), and in the post-negative test, they significantly decreased their go response to the P cue (compared to post-positive: $\beta = -1.481$, $z = -2.507$, $P = 0.012$; compared to post-control: $\beta = -1.315$, $z = -2.443$, $P = 0.015$). Further, we found that specifically the demonstrators showed an increased response to cue P and N in the post-positive test (compared to pre-positive, for P: $\beta = 1.665$, $z = 2.052$, $P = 0.040$; for N: $\beta = 1.500$, $z = 2.164$, $P = 0.030$), and a decreased response to the P cue in the post-negative test (compared to post-positive: $\beta = -1.947$, $z = -2.415$, $P = 0.016$; compared to post-control: $\beta = -1.533$, $z = -2.328$, $P = 0.020$) (note: role as interaction effect was not supported by the model comparison). Results also showed that over time, subjects significantly decreased their go response to all cues (i.e. P, NP, M, NN, and N) (compared to period 1: $\beta = -0.603$, $z = -3.267$, $P = 0.001$).

Exploratory analyses

For exploratory purposes, we analysed additional factors with a potential impact on the go response. We found a significant main effect of

researcher showing overall more go responses when tested by researcher VŠ (compared to JA, $\beta = 0.492$, $z = 3.146$, $P = 0.002$).

Behaviour during emotion manipulation

Negative condition

As predicted, demonstrators vocalized significantly more negative calls in the negative condition (compared to the control condition: $\beta = 3.422$, $z = 6.228$, $P < 0.001$; to the positive condition: $\beta = 1.254$, $z = 6.509$, $P < 0.001$; to the observers in the negative condition: $\beta = 4.773$, $z = 7.809$, $P < 0.001$).

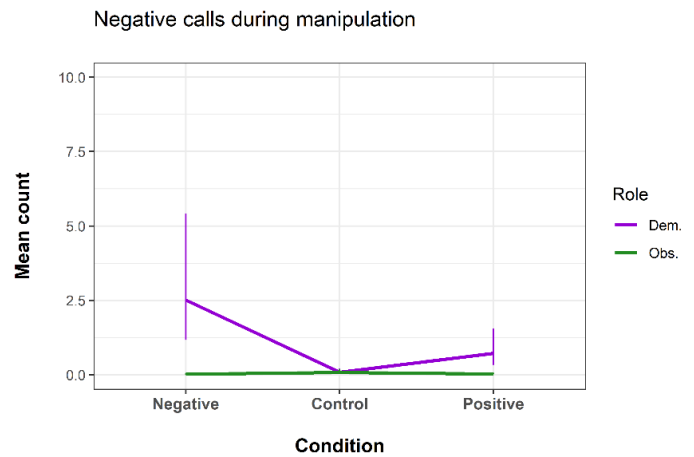


Fig. 4: Mean predicted count (bars indicate SE) of negative calls given during the three experimental conditions. Dem.= demonstrator; Obs.= observer.

Observers showed no significant difference in negative calls between conditions (Fig. 4; see SI for details). Demonstrators also showed significantly more pilo-erected tail in the negative condition (compared to the control condition: $\beta = 3.548$, $z = 2.523$, $P = 0.012$; to the positive condition: $\beta = 3.242$, $z = 2.67$, $P = 0.008$; to the observers in the negative condition: $\beta = 2.585$, $z = 2.173$, $P = 0.03$). Observers showed no significant difference between conditions (Fig. 5; see SI for details). In contrast to our predictions,

demonstrators did not show a significant difference in scratching between conditions (see SI for details). On average, observers scratched significantly more than demonstrators ($\beta = 1.222$, $z = 2.663$, $P = 0.008$), and specifically, observers scratched more, although not significantly, in the negative condition (compared to the positive condition: $\beta = 1.275$, $z = 1.896$, $P = 0.058$). (note: role as interaction effect was not supported by the model comparison).

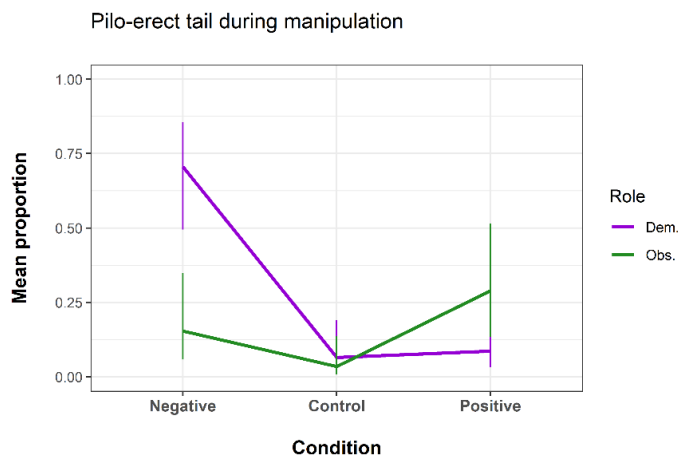


Fig. 5: Mean predicted proportion (bars indicate SE) of pilo-erect tail during the three experimental conditions. Dem.= demonstrator; Obs.= observer.

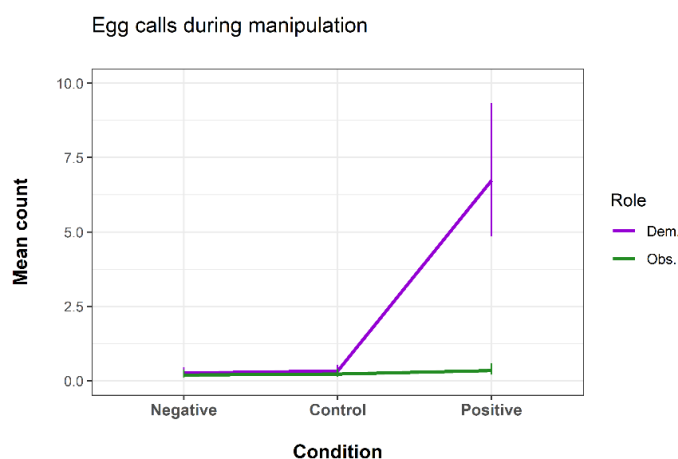


Fig. 6: Mean predicted count (bars indicate SE) of egg calls given during the three experimental conditions. Dem.= demonstrator; Obs.= observer.

Positive condition

As predicted, demonstrators vocalized significantly more positive calls in the positive condition, compared to the control condition ($\beta = 4.927$, $z = 5.800$, $P < 0.001$) and to the negative condition, where no positive calls were given. Overall, observers emitted fewer positive calls in the positive condition (compared to demonstrators: $\beta = -2.671$, $z = -11.402$, $P < 0.001$), but they showed no significant difference between conditions (see SI for details). Per exploratory analysis, we found that demonstrators vocalized significantly more egg calls in the positive condition (compared to the control condition: $\beta = 3.010$, $z = 7.915$, $P < 0.001$; to the negative condition: $\beta = 3.268$, $z = 6.893$, $P < 0.001$; to the observers in the positive condition: $\beta = 2.986$, $z = 6.579$, $P < 0.001$). Observers showed no significant difference in egg calls between conditions (see Fig. 6) (see SI for details).

Overall, observers spent more time in front of the stimulus than demonstrators ($\beta = 0.860$, $t = 2.165$, $P = 0.033$), but in contrast to our predictions, animals did not spend more time positioned in front of the stimulus in the positive condition (compared to the control condition: $\beta = 0.432$, $t = 0.904$, $P = 0.369$; to the negative condition: $\beta = -0.066$, $t = -0.138$, $P = 0.891$) (see SI for other results).

Behaviour during JBT

Scratching

Overall, subjects showed more scratching in the post-positive test (compared to the post-negative: $\beta = 0.666$, $z = 2.090$, $P = 0.037$; compared to pre-positive: $\beta = 0.601$, $z = 2.016$, $P = 0.044$) (see SI Fig. S8). Specifically, observers increased scratching in the post-positive test (compared to the pre-positive: $\beta = 0.847$, $z = 2.152$, $P = 0.031$), and demonstrators decreased scratching in the post-negative test (compared to the pre-negative: $\beta = -1.099$, $z = -1.927$, $P = 0.054$) (note: adding role as interaction effect was not

supported by the model comparison) (see SI for more results; see SI Fig. S9).

Scent-marking

Demonstrators showed significantly less scent-marking in the post-control test (compared to pre-control: $\beta = -0.871$, $z = -4.404$, $P < 0.001$; compared to post-negative: $\beta = -0.562$, $z = -2.560$, $P = 0.010$; compared to post-positive: $\beta = -0.692$, $z = 3.346$, $P < 0.001$). Observers showed significantly less scent-marking in the post-negative test (compared to post-positive: $\beta = -0.551$, $z = -2.937$, $P = 0.003$; compared to pre-negative: $\beta = -0.524$, $z = -2.796$, $P = 0.005$) (see SI for more results; see SI Fig. S10).

Gnawing

Demonstrators gnawed significantly less in the post-positive test (compared to pre-positive: $\beta = -1.158$, $z = -4.775$, $P < 0.001$) and observers gnawed significantly more in the post-positive test (compared to post-negative: $\beta = 0.544$, $z = 2.711$, $P = 0.006$; compared to post-control: $\beta = 0.408$, $z = 2.008$, $P = 0.044$), while gnawing less in the post-negative test (compared to pre-negative: $\beta = -0.447$, $z = -2.199$, $P = 0.028$) (see SI for more results; see SI Fig. S11).

Discussion

Our main research question focused on emotional contagion in common marmosets, where we predicted that specific emotional states induced in the demonstrator would transfer to an observer. To this end, we assessed behavioural and cognitive responses, the latter by a judgement bias test. We predicted that demonstrator marmosets exposed to either a positive or negative stimulus, would show an optimism or pessimism bias, respectively, in their responses to the ambiguous middle cue on a judgement bias test. Furthermore, we predicted that an induced positive state would correlate

with emitting positive calls and by bodily positioning in front of the shown stimulus, and that an induced negative state would correlate with emitting negative calls, and showing more pilo-erected tail, scratching, and less positioning in front of the stimulus. We further investigated emotional contagion in the observer, and predicted to find an optimism or pessimism bias in the positive or negative condition, respectively. Further, we predicted positive or negative state-related behaviours, similar to the expressions seen in the demonstrator. Although our emotion induction in the demonstrator seemed successful, at least based on the behavioural assessment, our emotional contagion hypothesis was not confirmed, and we did not find predicted behaviours in the observer that would be reflective of the experimental condition. Moreover, neither animal showed an optimism or pessimism bias in the judgement bias test. We further analysed the responses to other cues in the JBT and performed an exploratory analysis of additional effects, to verify whether the JBT results occurred due to inherent issues with the paradigm, or general lack of manipulation effect. We will now first discuss the cue responses in the JBT, followed by a discussion of the behaviour shown during emotion manipulation, and lastly behaviour shown during the JBT.

Cue responses in the JBT

To verify the JBT paradigm we performed two manipulation checks, namely discrimination training success and order effect of the ambiguous cues. Subjects showed successful discrimination between the reference P and N cues, including an intermediate valuation of the NP, M, and NN cues, resulting in a typical monotonically graded response curve (Gygax, 2014). Subjects also showed no learning effect of the NP, M, or NN cues, a necessary prerequisite for further interpretation of the test results. Nevertheless, despite a potential successful emotion manipulation effect in the demonstrator, the effect may not have been strong enough to either temporally last until, or be detected by, the

post-JBT. Accordingly, we found no congruent optimism or pessimism bias in the M cue response, in the positive or negative condition, respectively. Furthermore, demonstrators showed an increased go response to the NP cue in the post-positive JBT, as well as to the reference P and N cues, while showing a decrease in go response to the P cue in the post-negative JBT (as we noted before, an interaction with role was unsupported by model comparison, but due to theoretical reasons regarding emotional contagion we did examine certain results further). In addition, our study shows a researcher-dependent effect on the JBT, with a higher go response when tested with one of the two researchers involved in data collection.

Previous studies have considered a response change to the intermediate ambiguous cues NP and NN as evidence for a change in affective state (e.g. Saito et al., 2016). Based on this assumption, our result would provide evidence for a positive emotional state in the demonstrator. However, we are convinced this may be an inaccurate interpretation. Due to the presence near the reference cues (i.e. NP to P and NN to N), the reward value of NP and NN is less ambiguous and more certain than the middle cue M. This emphasizes a pivotal element of a judgement bias test, and the ambiguous cue should be truly ambiguous before we are able to infer the meaning of its potentially found bias (Gygax, 2014; Roelofs et al., 2016). More importantly, our results also show a change in response to the reference cues, which puts into question the validity of our task design and the interpretation of any of our JBT results, including the response to NP. Generally, no bias effects are expected at the reference cues, as the reward values of these cues have been established during training, and thus, have more certainty than the ambiguous cues (Gygax, 2014; Neville et al., 2020). Still, other studies have reported effects at the reference cues as well (Lagisz et al., 2020), with in particular changed responses to the N cue (Neville et al., 2020). One suggestion is that effects at the reference cues are either due to

ineffective training or interference with the emotion manipulation (Lagisz et al., 2020). Considering our strict training criterion and its following discriminatory success during testing, the effects found on the P and N cues are more likely to have happened due to potential conflict with the emotion manipulation. Indeed, this is supported by the finding that specifically demonstrators changed their response to the P and N cues, as these subjects were directly exposed to the food reward in the positive condition. Potentially the use of food, rather than non-food, as positive stimulus, altered the demonstrators perceived reward value of P and N, and this potential confound should be considered in further research. Alternatively, a general increase in motivation to perform could have driven these results, yet, this should have also prompted more responses to the ambiguous M and NP cues, which is not the case. Therefore, it seems that there is a specific change potentially due to the used food reward for the positive manipulation. This pattern is perhaps also observed in the effects of researcher identity. Here, the higher response potentially indicates a change in reward expectation, where a higher reward is anticipated when the test is conducted by VŠ. We assume this is due to researcher VŠ having worked in the marmoset lab for more years than researcher JA, in a variety of experimental set-ups which often included food rewards. Despite our extensive efforts to standardize the protocol, in which both researchers were trained to operate the apparatus and to interact with the subjects identically, it seems the more familiar researcher had a stronger reward expectation effect on the subjects, which was then detectable through the judgement bias test. Another study on marmosets investigated researcher identity and found that it may impact participation, but not performance (Schubiger et al., 2015), and we are unaware of any judgement bias study showing a researcher effect. To conclude, these results of response changes to other cues, rather than solely to the middle ambiguous cue, highlight the importance of including all cues to the statistical analyses

(Gygax, 2014), as well as adding the full dataset with other, potentially important variables such as researcher identity, to increase the analyses' power (Lagisz et al., 2020).

In recent years, the use of the cognitive bias paradigm, and specifically the judgement bias design, has risen in popularity, resulting in a plethora of studies applying the test. Nevertheless, several reviews have raised important concerns regarding methodological and theoretical questions (Mendl et al., 2009; Bethell et al., 2015; Roelofs et al., 2016). A first meta-analysis concluded that, when controlling for potential drug side-effects, the judgement bias paradigm is a valid measure to assess the positive or negative association of pharmacologically induced states in animals (Neville et al., 2020). A second meta-analysis focussing on non-pharmacological affect manipulations (Lagisz et al., 2020) also found general support for the judgement bias paradigm as a valid measurement of affect in animals. Importantly, the authors emphasize the need for more and continued validation of the paradigm, as there is great variability in effect sizes between studies and in the extent that experimental design details are reported, as well as the need for more empirical research in regard to different design types, including species-relevant setups and cues. Indeed, in the human emotion field, where the cognitive bias hypothesis originates from, investigation of the paradigm is ongoing to understand all different aspects of the decision-making process and how affect may play a role (Ilgaya et al., 2016). In this vein, there are very few studies on the use of the judgement bias paradigm in primates, which is potentially indicative of (methodological) difficulties inherent to the bias paradigm's requirements. In particular for the primate group, more empirical research is required to validate the paradigm.

Further, these results might also, or in addition, be due to a lack of manipulation effect and our study (and subsequent JBT results) could have benefitted from a more realistic intervention

rather than by using static objects (e.g. a simulation procedure, as in Adriaense et al., 2019b). Still, other studies have successfully used artificial toy predators as manipulation (see Neal and Caine, 2016, for examples). Moreover, most studies on cognitive bias focus on long-term moods through environmental changes (e.g. enrichment in pigs, Douglas et al., 2012) or social behaviours (e.g. long-term grooming behaviour and optimism bias in Schino et al., 2016), but effects of short-term social behaviour may show different results (e.g. immediate grooming behaviour shows no bias, in Schino et al., 2016; though see e.g. Adriaense et al., 2019). Others have also raised concerns regarding the success rate of affect induction in cognitive bias tests, calling for further validation of its paradigm (Košťál et al., 2020).

Behaviour during emotion manipulation

As predicted, during the positive manipulation, demonstrators gave more positive calls, and during the negative manipulation, they emitted more negative calls and showed pilo-erected tail. The observation that types of calls given by the demonstrator reflect the positive or negative condition, is congruent with previous findings of these calls in contexts of either food anticipation or high vigilance and predator mobbing (e.g. Epple, 1968). Further, pilo-erected tail is often used as behavioural indicator of arousal in both captive and wild conditions (Schubiger et al., 2015; Šlipogor et al. 2016, under review), and is also observed in negative-related conditions (Ermatinger et al., 2019). This is consistent with the observation of increased pilo-erected tail in our negative condition, and together with the negative calls this indicates a negative, aroused state in the demonstrator. Interestingly, demonstrators showed no distinction in terms of staying in front of the stimulus instead of elsewhere in the experimental cage. This latter result calls into question the fear-inducing aspect of the negative manipulation, as in a fear context we would expect an avoidance rather than an approach response. Furthermore, demonstrators

gave more egg calls during the positive manipulation. Independent egg calls are often observed when facing a threat or aggression (Bezerra and Souto, 2008; Epplé, 1968) and thus, probably reflect vigilance and negative context. We are unaware of studies observing egg calls in positive contexts, though, a food context may not necessarily be positive as it may elicit food competition, which is potentially stress inducing (e.g. Tardif and Richter, 1981, see discussion below). Additionally, a food context may lead to frustration in the demonstrator because the food is inaccessible, and as such, the egg calls may reflect frustration. This shift from positive anticipation to frustration is often discussed in emotion research (Briefer et al., 2015; also mentioned as argument for the positive condition in Adriaense et al., 2019a). In this case, it could be that the observer picked up this state in the demonstrator, and subsequently showed congruent frustration-related scratching in the post-positive JBT. Despite that the other predicted behaviours of staying in front of the stimulus and scratching during the manipulations were not supported in our sample, the remaining observed behaviours provide evidence for a distinction between the two manipulations. Therefore, in conclusion, demonstrators show distinct behaviours between the two manipulations, with contrasting vocalizations and pilo-erected tail, confirming their general positive and negative inducing effect. Yet, the demonstrator's response to stay in front of the negative stimulus, rather than moving away, potentially warrants against a more precise interpretation and raises the question whether the manipulation indeed induced a fear-related state. Further, and despite the apparently successful manipulation effect, upon seeing the demonstrators, the observers showed no predicted or manipulation-related behaviour, aside from increased scratching during the negative condition (note: role interaction was not supported by model comparison). Therefore, based on the observable behavioural expressions of the observers, we cannot conclude that emotional contagion occurred. This result is

consistent with other studies, where for instance marmosets exposed to food calls do not show overt changes in behavioural expressions, but exhibit variation in nasal temperature (Ermatinger et al., 2019). It would thus be interesting to use thermography for our particular judgement bias test and emotional contagion design in further studies.

Behaviour during JBT

To assess the emotion manipulation effect, we analysed behavioural responses during JBT as well. Due to the subjects' simultaneous occupation with the JBT, the overall frequencies of these additional behaviours were low, yet, they may help to clarify whether the manipulation was either not strong enough to last until, or be detected by, the JBT. After the positive manipulation, demonstrators showed no change in scent-marking and they decreased gnawing, and observers showed more scent-marking, gnawing, and scratching (note: role interaction not supported by model comparison). After the negative manipulation, demonstrators decreased scratching (note: role interaction not supported by model comparison), and observers decreased scent-marking and gnawing. The significance of each of these behaviours and their changes is challenging to interpret without other specific measurements, and our results from the judgement bias test do not facilitate interpretation. Still, each of these behaviours has been studied in relation to a variety of social contexts in other studies and we will discuss our results in light of these.

Scratching

Scratching is commonly observed in primates in negative situations, for instance in occurrences of social conflict (Aureli and van Schaik, 1991), contradicting motivations (Troisi et al., 1991), or predatory threat (see Neal and Caine, 2016, for overview). Depending on the specific circumstances, scratching may thus reflect negative stress or anxiety, and therefore,

scratching has been suggested as general indicator of a negative emotional state (Maestriperi et al., 1992; Troisi, 2002). In marmosets this is supported by, for example, observations of increased scratching during mildly stressful husbandry procedures (Bassett et al., 2003), and decreased scratching when animals are given anxiety-reducing drugs (Cilia and Piper, 1997) or after positive interaction with human caretakers (Manciocco et al., 2009). In our study, subjects showed an increase in scratching in the post-positive condition, and specifically, demonstrators decreased scratching in the post-negative condition, and observers increased scratching in the post-positive condition. This result is in contrast to our prediction, as we expected to find more scratching in the negative condition, both during manipulation and during post-JBT. The decreased scratching in the demonstrator may perhaps support the interpretation that, despite the negative manipulation apparently being successful, the effect was not strong enough to last until the post-JBT. However, demonstrators did not increase scratching during the negative manipulation and, moreover, observers showed an increase in scratching in the post-positive JBT. Therefore, we suggest that scratching in this study, particularly in the post-positive test, may not necessarily reflect anxiety, but perhaps indicates a negative state similar to frustration or conflicting motivations. Indeed, scratching has been proposed to reflect mild anxiety, yet with increasing anxiety the relation with scratching follows an inverted U-shape (Troisi et al., 1999). Emotional contagion has been suggested to facilitate a variety of social behaviours, such as food competition, in which an initially assumed positive context, and perhaps state, changes into a more negatively associated context, and thus, potentially also negative state. Our demonstrator-observer design does not exclude these other social elements. Seeing a group mate in a seemingly positive state may put the observer in a conflicting state due to not being able to get the same context as the demonstrator. This seems a plausible hypothesis as watching the

other group member in a beneficial context may induce food competition, which is known to be stress-inducing (e.g. Clay and de Waal, 2015), and also appears in common marmosets (Tardif and Richter, 1981). For that reason, the increased scratching in the post-positive JBT potentially reflects a negative state in the observer.

Scent-marking and gnawing

Scent-marking is often observed when common marmosets are in new environments (Epple, 1970) and functionally serves territorial defence and reproductive status advertisement (Harrison and Tardif, 1988; Lazaro-Perea et al., 1999). Yet, in our study, only social group members took part in the experiment, which excludes territorial defence, and the composition of pairs did not include any adult female-male pairs, which excludes status signalling. Furthermore, marmosets usually gnaw holes in trees to extract gum, which is a behaviour often observed as fixed action-pattern with scent-marking after the gnawing is completed (Lazaro-Perea, 1999; Massen et al., 2016). Interestingly, scent-marking and gnawing are suggested to be arousal related behaviours (e.g. both are part of the arousal cluster in Martin et al., 2019). In that vein, our data may indicate that the different manipulations were not sufficiently arousal-inducing to have a lasting temporal effect until the post-JBT. During the negative manipulation, demonstrators showed more pilo-erected tail, and thus, it could be expected that this greater arousal would be reflected in the other behaviours during JBT. Yet, demonstrators showed no change in scent-marking in either post-positive or -negative JBT, and even showed a decrease in gnawing after the positive manipulation. Interestingly, observers exhibited a condition-dependent pattern in which more scent-marking and gnawing occurred in the post-positive JBT, and less scent-marking and gnawing in the post-negative JBT. If these behaviours are indeed related to arousal, then this indicates that watching the demonstrator specifically during the positive manipulation was more arousal-

inducing for the observers than the negative manipulation. Interestingly, some have suggested that scent-marking may be a (negative) stress-related behaviour, though perhaps less sensitive than scratching (Cilia and Piper, 1997; Bassett et al., 2003). In regard to our results, this would indicate that watching the demonstrator in a positive food context, induces both a higher arousal and negative state in the observer.

Emotional contagion?

When combining all results, namely the results of the judgement bias test, and the behaviours during manipulation and JBTs, we find further support for our post-hoc food competition hypothesis. In the post-positive condition, observers showed more scent-marking and gnawing, which is proposed to reflect high arousal and to some extent negative stress, while also displaying more scratching, which is assumed to indicate negative affect. This combination suggests that watching the demonstrator in the positive condition generated a context of high arousal and negative affect for the observer. Perhaps our specific design prompted an unintended food competition, where the observer was not able to directly experience the positive manipulation itself, yet picks up on the food cues from the demonstrator. This interpretation is consistent with the finding of positive food calls and egg calls in the demonstrator in the positive condition, as these calls combined may be indicators of a positive, but also a vigilant state, and thus, these calls are also potentially indicative of a competitive setting. Our argument of competition in the positive condition, rather than strict emotional contagion, is consistent with the post-negative results, showing decreased arousal-related behaviours in the observer, indicating that watching the demonstrators here was not arousal inducing. The competition hypothesis is further supported by reduced scent-marking in the observer and the lower rates of scratching in the demonstrator, which both may reflect the absence of a negative state in the post-negative

condition. Moreover, the judgement bias results provide additional tentative support, as demonstrators showed increased responses for the P and N cues in the post-positive manipulation. As discussed previously, this may be indicative of a higher reward expectancy, and if indeed the increased responses to P and N reflect this expectancy, then this confirms the efficacy of the positive manipulation effect, which then again may explain the observer's behaviour in the post-positive condition. However, it is important to point out that in the case of a higher reward expectancy, we would expect to find an increased response to the ambiguous middle cue, and no change toward the reference cues (Gygax, 2014). In the study of Ermatinger et al. (2019) they found a stronger presence of food competition in females, so we were interested in further exploration of our competition hypothesis and potential sex effects, but due to the low sample size of females as observers ($n = 3$), this was not feasible.

Importantly, a small number of studies report that scratching as indicator of a negative state is perhaps not as empirically supported as initially assumed (see Neal and Caine, 2016, for overview). For instance, Barbary macaques show increased scratching after (assumably positive) grooming bouts, which potentially puts the assumed negative valence of scratching into question (see Semple et al., 2013 for discussion, but see contrasting results in Ueno et al., 2015 for evidence of decreased scratching after grooming; see Berthier et al., 2018 for decreased scratching after observing others groom). Studies in common marmosets find that subjects undergoing anxiety-inducing manipulations of social isolation, food competition, and predatory threat, show a decrease in scratching during these manipulations (Neal and Caine, 2016). Moreover, after manipulations of social isolation, predatory threat, and administration of anxiogenic drugs, marmosets do not increase scratching (Kato et al., 2014; but see Cilia and Piper, 1997). Accordingly, researchers have called for awareness about the assumed

emotional state underlying scratching, thereby suggesting that scratching may be associated with a general arousal level, or even positive arousal, depending on the context (Neal and Caine, 2016). Though a direct examination of the correlation between scratching and positive arousal is missing in current research (Neal and Caine, 2016), it remains an interesting notion in light of our study. It is possible that the observer's scratching relates to socio-positive behaviour reminiscent of positive excitement. Watching the demonstrator in a rewarding or beneficial context may induce a positive state, because that reward may eventually be beneficial to the observer, or may induce a general positive affect (Nakahashi and Ohtsuki, 2018). The latter notion is supported by the evidence that common marmosets are highly prosocial (Burkart et al., 2007, 2014), and thus, observers may experience seeing the other in a beneficial context as rewarding to themselves. In a thought-provoking conclusion by Neal and Caine (2016), they mention that scratching has perhaps been too easily assumed to be negative. Accordingly, a priori expecting an all-or-nothing relation between negative circumstances and scratching may have unwanted consequences to the progress of this research topic, as it may result in a lack of alternative explanations, further investigation, or even the publication of null results.

The potential presence of a competitive context also highlights the difficulty of investigating emotional contagion. The concept itself may underpin a variety of social behaviours (e.g., predator mobbing or conflict management) which result in various combinations of similar and/or differing emotional states (e.g., a matching state would work counterproductive in situations of consolation or helping, Adriaense et al., 2020), which additionally depends on the specific actors and context (Dezecache et al., 2015). This may explain the relatively low number of experimental studies on emotional contagion, despite its popular status due to its relevance for empathy, and despite the growing

interest in animal emotions in social settings such as in animal welfare (Baciadonna et al., 2018). Moreover, the study of emotions and their induction in a laboratory setting is challenging, even in humans, and, for instance, positive or low arousal states remain particularly difficult to assess in animals (Mendl et al., 2009). This may explain why the research field has been primarily dominated by research on high arousal, and intense negative states such as pain (Boissy, 2007; Meyza, 2016).

Conclusion

Although common marmosets' social lifestyle in extended family groups demands complex social skills, including the need for efficient communication and coordination, we did not find evidence of emotional contagion through a judgement bias paradigm in this study. Yet, it is unclear whether this was due to our study design, or a general absence of emotional contagion in common marmosets. Based on some of the behavioural parameters, the demonstrators' emotional states were seemingly successfully manipulated in the study, yet, this effect was potentially not strong or long-lasting enough to be detected by the post-JBT. As JBTs usually assess mood, they may be less sensitive to detect affective changes in short-term emotion manipulation designs. Moreover, it remains unclear whether potential confounds of the judgement bias paradigm also (partially) impacted this result. Therefore, more empirical research on the relation between long- and short-term social behaviours and judgement bias is needed, as well as a better understanding of different emotion manipulations, and potential external effects leading to measurement bias such as researcher identity. Further, we find an interesting combination of increased scent-marking and scratching in the observer after watching the demonstrator undergoing a positive manipulation. Nevertheless, it remains unclear how to interpret these particular condition-dependent changes, and the difficulty to infer the specific emotional states relevant to our

contrasting hypotheses (i.e. emotional contagion and food competition) emphasizes one of our main arguments on measuring animal emotions, which is that without additional objective investigation, it remains particularly challenging to interpret valence from overt, behavioural observations. Therefore, further research is required to explore our post-hoc food competition hypothesis, and to verify the presumed state of scent-marking and scratching in different contexts. Importantly, future work should consider the facilitating effect of emotional contagion, and aim at more precisely analysing its information transmission function.

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Supplemental Information

1. Methods

Housing

The 8 subjects were housed in four separate social groups (Group 1: Aurora; Group 2: Oli and Luna; Group 3: Fimo and Locri; Group 4: Smart, Simba, and Nala). Group 2 and Group 4 were housed with other family members, which included a breeding pair and their offspring, Group 1 was housed with other unrelated conspecifics, and Group 3 were the only members of this social group. The four social groups were within visual, acoustic, and olfactory range from each other. Each group was housed in wire mesh indoor home enclosures (approx. 250 x 250 x 250 cm) with access to outdoor enclosures (approx. 250 x 250 x 250 cm), and to the experimental enclosures through a tunnel system with moveable doors. Animals had free access to both indoor and outdoor enclosures during warmer periods of the year, and outdoor access was restricted in winter, when outside temperature fell below 5°C, or during necessary husbandry procedures. The rooms had windows for natural light, indoor temperature was kept between 21°C and 29°C, humidity between 30% and 60%, and additional lamps provided a 12:12 h light:dark cycle. Heating lamps were provided for each group to optimize well-being of the animals. Every home enclosure consisted of various enrichment objects (branches, ropes, platforms, blankets, sleeping baskets) with wood pellets as floor bedding. All animals were fed twice daily (i.e. they received breakfast around 7:00 and lunch around 12:00) with a varied diet of marmoset pellets and jelly, fruits, vegetables, grains, milk products, protein and vitamin supplements, and insects. Water was available *ad libitum* for each group. The housing conditions were in accordance with institutional guidelines, Austrian legislation and the European Association of Zoos and Aquaria husbandry guidelines for Callitrichidae.

Dyads

Dyads were formed with an individual from the same housing group, making for a total of 8 study subjects (Aurora, Luna, Oli, Fimo, Locri, Smart, Nala, Simba) and 5 dyads (Luna & Oli, Fimo & Locri, Smart & Nala, Smart & Simba, Nala & Simba). Each subject took on the role of demonstrator and observer at least once and maximum twice. One subject (Aurora) was tested as single demonstrator throughout the entire study as her designated testing partners did not reach discrimination training criterion within the set time period (we decided to not exclude her to increase sample size for verifying the emotion manipulation).

Apparatus training

Before discrimination training, subjects underwent an apparatus training, consisting of an initiator and door training. During initiator training, we first trained subjects to touch the trial initiator by holding the initiator in one hand and rewarding the subject with the other hand, after which we gradually increased the spatial distance between touching and receiving reward. The end result of this training was achieved when subjects touched the trial initiator and then crossed the cage to its opposite side to receive a reward (total distance: 100 cm). The trial initiator was then attached to a string on one side of the cage, which could be manipulated by the researcher while standing on the other side of the cage (see SI Figures S3, S4, and S5). This part included the same training steps in which subjects had to touch the trial initiator, after which it was pulled up and out of view of the subject, and then subjects were expected to cross the cage over to the researcher to receive a reward.

This training was followed by door training, which refers to the five doors placed in the JBT apparatus

(see SI Figure S5). Subjects were trained to touch the trial initiator, then cross the cage and sit in front of the door that was opened by the researcher. This step was done to make sure the subjects kept using the trial initiator to actively start the next trial. The doors used in this training step represent the reference P and N cues. In this door training step, both doors were equally rewarded to ensure that animals were attentive to both cues. Some of the criticism of the judgement bias paradigm is the potential issue that animals learn to neglect the N cues, as these are often unrewarded from the start of the discrimination training (also noted by Hintze et al., 2018). Such learned disregard for certain cues, and their related cue characteristics (e.g. spatial orientation), may lead to disregard of any other cues similar to this characteristic later during testing. Concretely, the most left or right cue is trained as the N cue, and when animals learn to avoid N, they may apply a strategy to visually or auditorily neglect this side of the spatial test. During testing the additional NN, or even M, cues may also be ignored as they visually are fully, or partially, in the disregarded area. A potentially found pessimism bias may partially be due to disregard of these cues, rather than a negative judgement of their ambiguity. To counter this potential neglect, we followed the proposed training schedule by Hintze et al. (2018). Subjects were first presented with 20 rewarded N trials and after reaching training criterion, the N trials remained unrewarded (criterion was set at 80% go response to 15 P and 15 N cues, within 10 s of touching trial initiator, see SI Table S4 for details). In addition, when a cue door opened, both a visual element as well as an auditory one was present. This way, even if animals did not immediately look at the opened door, the auditory element added a second salient effect to increase their attention.

Trial presentation

Trials were presented in semi-random order with the first trial always being P, and NP, M, and NN followed P or N in a balanced order between test sessions.

Welfare

To ensure our subjects' wellbeing during training and testing, we only continued testing when the animals showed no overt signs of distress. We terminated the session if we observed any of the following: repeatedly moving back and forth to the compartment's exit door, remaining at the exit door (for longer than 10 s), staying in one location of the compartment without moving or ignoring the experimental apparatus (for longer than 15 minutes), quickly jumping back and forth in the compartment with jerky movements and/or emitting lots of 'phee' calls.

Habituation

Judgement bias testing is often done in isolation, rather than in the animal's social group. Such isolation may increase levels of stress and decrease willingness to participate in the experimental testing (Roelofs et al., 2016). We incorporated an extensive habituation protocol for all tested subjects to enter and stay in experimental cages alone, and the training was done in the same locations where the actual study took place. At all times, the subjects' family group members remained in the tunnels in the experimental room and were within auditory reach. Our subjects were also already familiar with the experimental cages due to participation in previous studies.

2. Results

Variables

The following variables were either predicted or used for exploratory purpose. All were used for model

comparison with AIC, and depending on the likelihood ratio test and AIC value, the variables were used for further analyses.

The response or dependent variables were: go response (yes, no), behaviour during JBT (scratching, scent marking, gnawing), behaviour during emotion manipulation (negative calls, positive calls, egg calls, contact calls, pilo-erect tail, scratching, scent marking, gnawing, position).

Predicting or independent variables were: researcher (VŠ, JA), role (demonstrator, observer), period (period 1 or 2), condition (positive, negative, control), cue (P, NP, M, NN, N), test (pre-JBT, post-JBT), subject (Aurora, Luna, Oli, Fimo, Locri, Smart, Nala, Simba), date (date of testing), and time (AM, PM).

Cue responses during JBT: additional results

We verified whether the go response to the M cue would change between pre- and post-JBT, within the different conditions, and for each role (which we added in interaction for theoretical reasons). For this we used a model including researcher and period as main effects, and role/condition/cue/test as interaction effect. Additional results showed that there was no change in response to the M cues in the post-JBT of the control condition (compared to pre-control, for demonstrators: $\beta = 1.100$, $z = 1.267$, $P = 0.205$; for observers: $\beta = 0.000$, $z = -0.000$, $P = 1$).

Behaviour during manipulation: model comparison

Based on a likelihood ratio test, comparing the basic model with a full model, and the AIC, the best model for negative vocalizations included time as predictor; for positive vocalizations time (in the observer subset) and period (in the demonstrator subset); for egg calls period as main effect and role/condition as interaction effect; for contact calls role/condition as interaction effect; for pilo-erect tail time as main effect and role/condition as interaction; for scratching role as main effect; for scent-marking period as main effect and role/condition as interaction effect; for gnawing period as main effect; and for front position role as main effect. Each of these models included subject and date as random variables, except front position with only subject as random variable.

Behaviour during manipulation: additional results

Negative calls

Overall, marmosets showed a significant small increase of negative calls when tested in the afternoon ($\beta = 0.455$, $z = 2.151$, $P = 0.032$). Demonstrators gave significantly more negative calls in the positive condition, compared to the control condition ($\beta = 2.167$, $z = 3.953$, $P < 0.001$) and compared to the observer in the positive condition ($\beta = 3.343$, $z = 6.400$, $P < 0.001$). Observers showed no significant difference in negative calls between conditions (between negative and control condition: $\beta = 1.264$, $z = 1.593$, $P = 0.111$; between negative and positive condition: $\beta = 0.176$, $z = 0.239$, $P = 0.811$).

Positive calls

As demonstrators showed no positive calls in the negative condition, we subset the data by role (dataset 1: demonstrators, positive and control; dataset 2: observers, all conditions). Over time, demonstrators showed a significant decrease in positive calls (compared to period 1: $\beta = -2.406$, $z = -2.563$, $P = 0.010$). Observers showed a significant decrease in positive calls when tested in the afternoon ($\beta = 2.148$, $z = 2.239$, $P = 0.025$), and showed no significant difference between conditions (between negative and

control condition: $\beta = -0.930$, $z = -1.070$, $P = 0.285$; between negative and positive condition: $\beta = -0.654$, $z = -0.786$, $P = 0.432$).

Egg calls

Over time, subjects showed a significant decrease in egg calls (compared to period 1: $\beta = -0.704$, $z = -2.595$, $P = 0.009$). Observers showed no significant difference in egg calls between conditions (between positive and control condition: $\beta = -0.400$, $z = -0.673$, $P = 0.552$; between positive and negative condition: $\beta = -0.571$, $z = -0.782$, $P = 0.434$).

Pilo-erect tail

Overall, marmosets showed a significant increase of pilo-erect tail when tested in the afternoon ($\beta = 2.001$, $z = -2.557$, $P = 0.011$). Observers showed no significant difference in pilo-erect tail between conditions (between negative and control condition: $\beta = -1.639$, $z = -1.026$, $P = 0.305$; between negative and positive condition: $\beta = 0.807$, $z = 0.706$, $P = 0.480$).

Scratching

Demonstrators showed no significant increase in scratching in the negative condition (compared to control condition: $\beta = 0.419$, $z = 0.445$, $P = 0.656$; to positive condition: $\beta = 0.397$, $z = 0.428$, $P = 0.669$).

Additional exploratory analyses

Demonstrators gave more contact calls (i.e. phee, shrill, and whirr) in the positive condition (compared to the negative condition: $\beta = 0.894$, $z = 3.626$, $P < 0.001$) and in the control condition (compared to the negative condition: $\beta = 0.669$, $z = 2.239$, $P = 0.025$). Observers emitted less contact calls in the positive condition (compared to the negative condition: $\beta = -0.470$, $z = -2.049$, $P < 0.001$), and when compared to demonstrators in the negative condition, observers gave more contact calls ($\beta = 0.998$, $z = 3.870$, $P < 0.001$). Furthermore, all subjects showed a significant increase of scent-marking over time (compared to period 1: $\beta = 1.741$, $z = 3.355$, $P < 0.001$), and demonstrators showed more scent-marking in the control condition (compared to the positive condition: $\beta = 1.387$, $z = 2.338$, $P = 0.019$). Over time, subjects also showed a significant increase in gnawing (compared to period 1: $\beta = 2.641$, $z = 2.310$, $P = 0.021$). Subjects only occasionally showed self-grooming, defecation, and urinating, so no further analyses were performed for these behaviours.

Behaviour during JBT: model comparison

The best model for scratching included time as main effect, condition/test as interaction effect, and subject as random variable; for scent-marking and for gnawing each model included period as main effect and role/condition/test as interaction.

Behaviour during JBT: additional results

Scratching

On average, subjects scratched significantly less when tested in the afternoon (compared to the morning: $\beta = -0.469$, $z = -2.301$, $P = 0.021$). All subjects showed less scratching in the pre-control test (compared to the pre-negative: $\beta = -0.934$, $z = -2.273$, $P = 0.023$; post-control: $\beta = -0.965$, $z = -2.351$, $P = 0.019$). After adding role as interaction effect, we found that observers increased scratching in the post-control test (compared to the pre-control: $\beta = 1.299$, $z = 2.017$, $P = 0.044$).

Scent-marking

Over time, subjects showed a significant small increase in scent marking (compared to period 1: $\beta = 0.252$, $z = 3.069$, $P = 0.002$).

Gnawing

Overall, subjects showed more gnawing in period 2 (compared to period 1: $\beta = 0.809$, $z = 5.453$, $P < 0.001$). Demonstrators gnawed more in the pre-positive test (compared to pre-negative: $\beta = 0.546$, $z = 2.502$, $P = 0.012$) and more in the pre-control test (compared to post-control: $\beta = 1.059$, $z = 3.794$, $P < 0.001$). Observers also showed a significantly higher count of gnawing in all post-tests (compared to demonstrator data, for post-negative: $\beta = 0.876$, $z = 3.195$, $P = 0.001$; for post-positive: $\beta = 1.596$, $z = 6.653$, $P < 0.001$; for post-control: $\beta = 1.434$, $z = 5.207$, $P < 0.001$).

Supplemental Tables

Table S1. Subject details

Subject	Sex	Age at time of study	Social group*	Relatedness
Aurora	F	5	1	NA (i.e. single testing)
Oli	F	12	2	Mother
Luna	F	4	2	Daughter
Locri	M	14	3	Siblings
Fimo	M	15	3	
Smart	M	8	4	Father
Simba	M	2	4	Son of Smart + sibling of Nala
Nala	F	2	4	Daughter of Smart + sibling of Simba

*Social group refers to the group the subject is housed in, and with which other study subjects they share their housing

Table S2. Training schedule

Training steps				Criterion
1. Apparatus training	1. Initiator training	1. Trial initiator (by hand)	1. Reward placed on top of trial initiator	Open end
			2. Reward given after touching trial initiator	Open end
			3. Reward given at increasing distance (from 10 cm to 100 cm)	Open end
		2. Trial initiator (by string)	1. Reward given after touching trial initiator and coming to the opposite side of the cage	20 trials
	2. Door training	1. Shaping P door	1. Reward given after touching trial initiator and coming to the P* door.	Min. 20 trials
		2. Shaping P and N doors	1. Reward given after touching trial initiator and coming to either the P or N door	15 P, 15 N; 80% correct Go; within 10 s.
2. Discrimination training		Reward given after touching trial initiator and coming to the P door. No reward was given when coming to the N door.	10 P, 10 N; 80% correct Go per cue/per day; within 10 s; 3 consecutive days	

*P= positive cue or door; N= negative cue or door

Table S3. Ethogram of behavioural variables.

Behaviour	Description
Go response	Subject sits directly in front of the open apparatus door within 10 seconds after touching the trial initiator.
No-go response	Subject does not sit in front of the open apparatus door within 10 seconds after touching the trial initiator, or they sit in front of a closed (i.e. wrong) door.
Active choice	Subject touches the trial initiator again, within 10 seconds after touching it previously, without first going to the open door. This response also codes as “no-go response”.
Wrong choice	Subject either performs a go response in an N trial or a no-go response in a P trial.
Scent marking	Marmoset rubs sternal or anogenital area over surface.
Gnawing	Marmoset gnaws at wood with teeth (i.e. also known as “gouging”).
Scratching	Marmoset repeatedly moves hand or foot with claws drawn rapidly across fur.
Pilo-erected tail	Brushed or raised fur on tail.
Position	The position refers to the subject either staying directly in front of the presented stimulus, or away from it
Positive calls	Combination of “chirp” and food-beg calls
Negative calls	Combination of “tsik”, “tsik-egg”, “cough”, and “seep” calls
Egg call	Also called eck or ek calls in literature
Contact call	Combination of “phee”, “shrill”, and “whirr” calls

Table S4. Total test trials per subject

Subject	Test period¹	Total trials p²	Total trials NP	Total trials M	Total trials NN	Total trials N	Total trials³
Aurora	1	30	6	6	6	30	78
	2	30	6	6	6	30	78
Oli	1	60	12	12	12	60	156
	2	60	12	12	12	60	156
Luna	1	60	12	12	12	60	156
	2	60	12	12	12	60	156
Fimo	1	60	12	12	12	60	156
	2	50	10	10	10	50	130
Locri	1	60	12	12	12	60	156
	2	50	10	10	10	50	130
Smart	1	58	12	12	11	59	152
	2	50	10	10	10	50	130
Simba	1	60	12	12	12	59	155
	2	60	12	12	12	60	156
Nala	1	50	10	10	10	50	130
	2	50	10	10	10	50	130

¹Test period= refers to testing in time period 1 or 2, in which period 2 is repeated measures testing of period 1 (see also info under Methods in main paper). ²P= positive cue; NP= near positive cue; M= middle cue; NN= near negative cue; N= negative cue. ³Number of test trials differs between animals as not all subjects finished testing within the designated timeframe of our study.

Table S5. Chronological order of testing per subject

Subject	Test period	Demonstrator			Observer		
		Positive condition	Negative condition	Control condition	Positive condition	Negative condition	Control condition
Aurora	1	1	5	2	NA		
	2	3	6	4			
Oli	1	3	1	5	4	2	6
	2	7	12	10	9	8	11
Luna	1	4	2	6	3	1	5
	2	9	8	11	7	12	10
Fimo	1	4	3	1	2	10	5
	2	8	9	6	11	NA	7
Locri	1	2	10	5	4	3	1
	2	11	NA	7	8	9	6
Smart	1	3	1	4	2	8	5
	2	10	6	NA	7	11	9
Simba	1	3	6	1	4	5	2
	2	12	11	9	7	10	8
Nala	1	3	8	1	2	7	6
	2	4	10	5	9	NA	NA

Table S6. Training data per subject (see Table S2 for description of training steps)

Subject	1. Initiator training (total trials)		2. Door training (total trials)		3. Discrimination training		
	1. Initiator by hand	2. Initiator by string	1. Shaping P door	2. Shaping P and N doors	Number of trained days before reaching criterion	Number of trained trials	% correct response per cue (results of correct 3 consecutive days shown)
Aurora	99	108	24	90	5	100	100% P, 93% N
Oli	77	154	30	58	9	180	93% P; 90% N
Luna	103	130	25	86	5	100	95% P; 90% N
Fimo	144	85	29	50	8	160	100% P; 100% N
Locri	179	124	20	92	5	100	90% P; 95% N
Smart	150	130	27	60	8	160	95% P; 95% N
Simba	157	91	20	74	8	160	100% P; 93% N
Nala	150	68	34	62	3	60	95% P; 90% N

Supplemental Figures



Figure S1. Experimental design. From left to right: demonstrator's compartment, stimulus presentation compartment, (white) sliding door, and observer's compartment. The sliding door remained closed during the judgement bias tests, and was only opened during the emotion manipulation. Both demonstrator's and observer's compartment had a judgement bias test apparatus placed in front. Both compartments were designed identically (same size: 100 x 100 x 200 cm, same distance to trial initiator: 100 cm, same judgement bias apparatus). The tunnels with moveable doors at the top of the experimental cage provided access to the compartments.



Figure S2. Experimental design. The design allowed for two researchers to conduct the judgement bias test at the same time with the two participating subjects, namely the demonstrator (left compartment) and the observer (right compartment). The red container placed on top of the middle compartment (i.e. where the emotion manipulation took place after the pre-judgement bias test) was filled with food pieces to control for odour cues.



Figure S3. Stimulus presentation. Left: negative condition, large artificial rubber spider. Middle: control condition, empty box. Right: positive condition, preferred food cut into pieces. The box opening is oriented toward the demonstrator's compartment.



Figure S4. Side view of demonstrator's compartment. On the left is the trial initiator (out of view) and on the right is the judgement bias test apparatus. To go from the initiator to the test, subjects had the option to jump across, use the left or right side of the wire mesh cage, or use two branches attached to the wire mesh. In front of the judgement bias test apparatus a platform was attached on which subjects could land and move during the test.

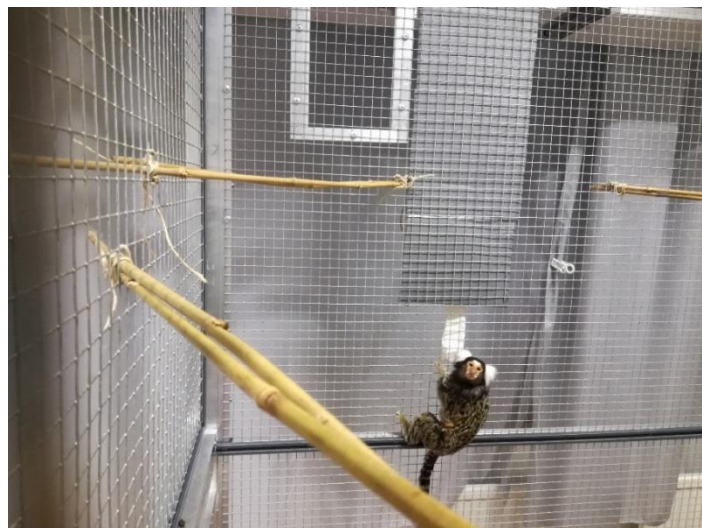


Figure S5. Side view of demonstrator's compartment. The subject is touching the trial initiator (white object), which can then be pulled up by a string, after which the initiator disappears behind a (grey) view blocker.



Figure S6. Front view of demonstrators' compartment. The judgement bias apparatus with 5 wooden door cues representing the positive P cue, near positive NP cue, middle M cue, near negative NN cue, and the negative N cue.

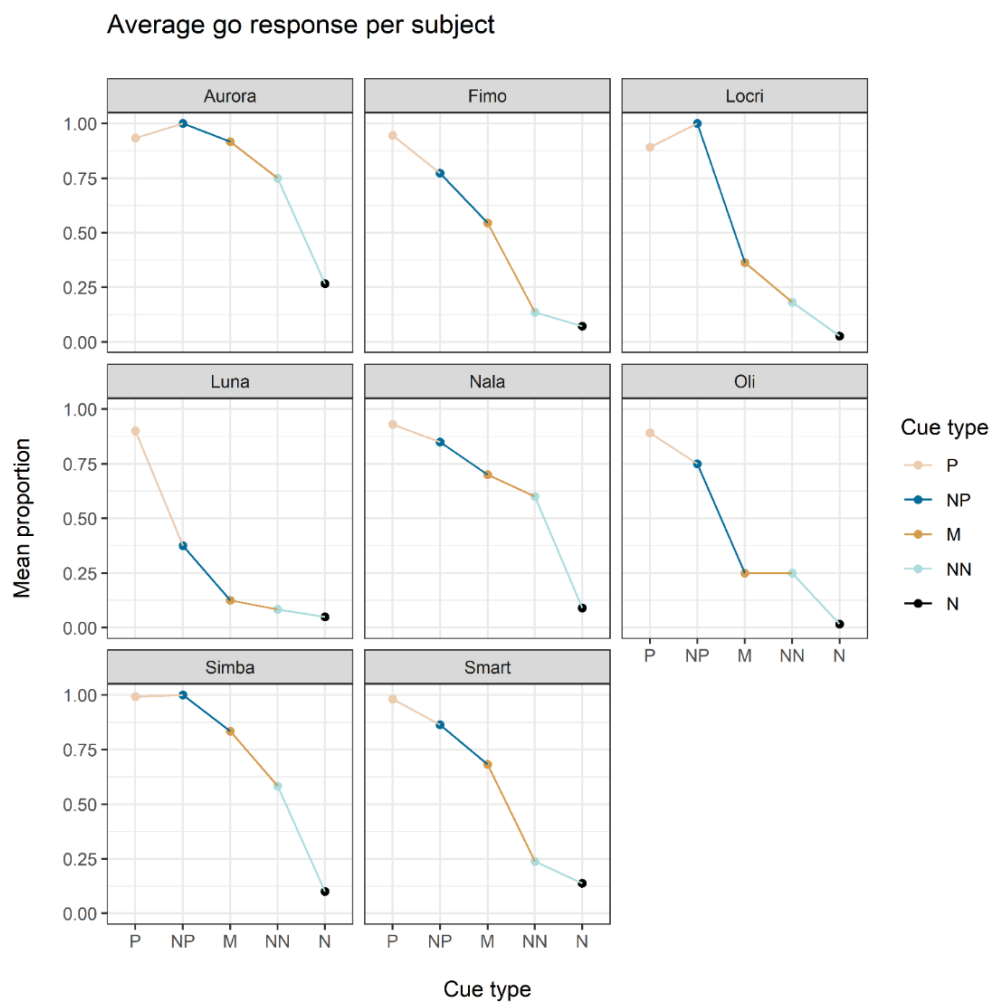


Figure S7. Average raw proportion of go responses per subject showing a monotonic graded curve. P= positive cue; NP= near positive cue; M= middle cue; NN= near negative cue; N= negative cue

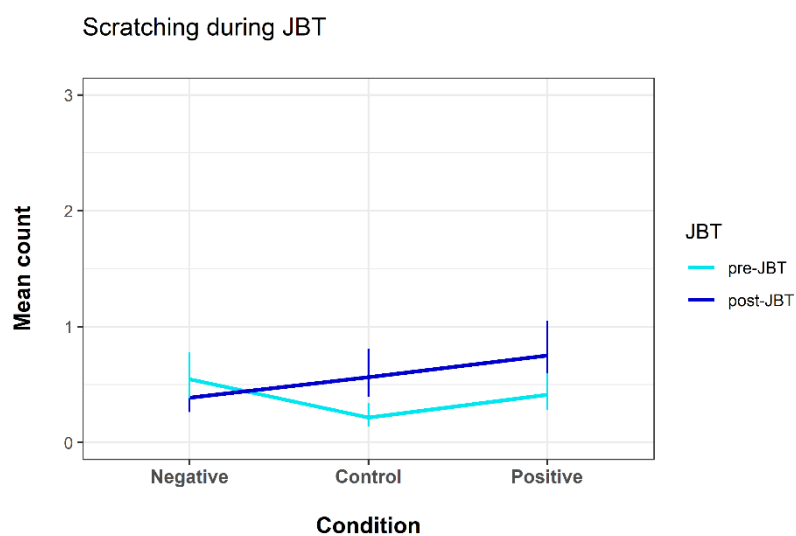


Figure S8. Mean predicted count scratching (bars indicate SE).

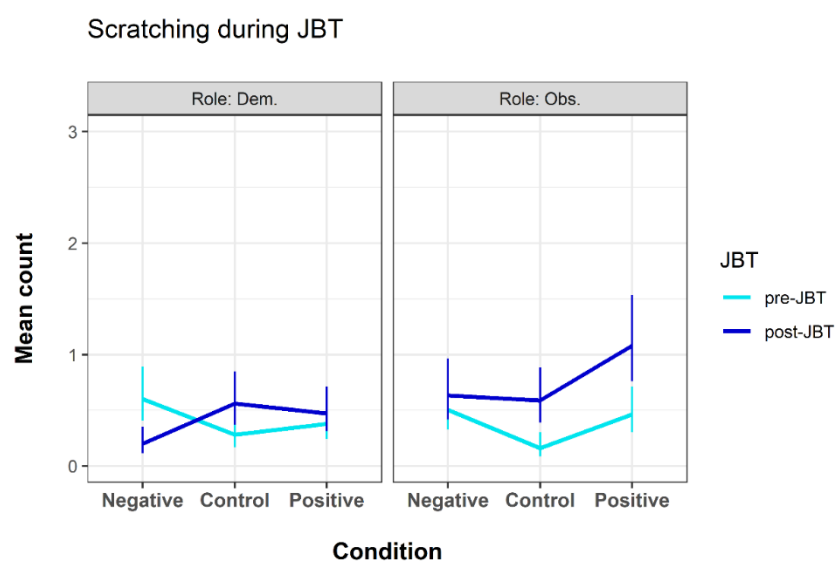


Figure S9: Mean predicted count scratching (bars indicate SE): between roles (demonstrator, observer) and across conditions (negative, control, positive), for each judgement bias test (pre-JBT and post-JBT).

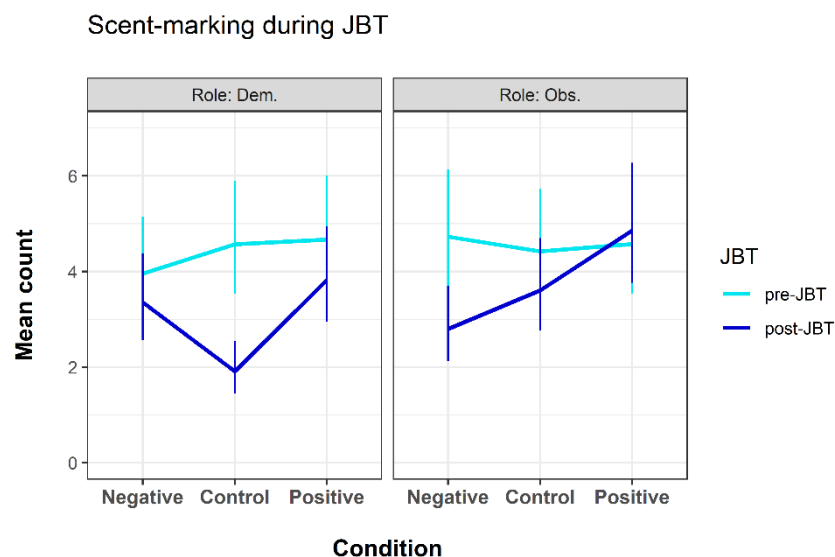


Figure S10. Mean predicted count scent marking (bars indicate SE): between roles (demonstrator, observer) and across conditions (negative, control, positive), for each judgement bias test (pre-JBT and post-JBT).

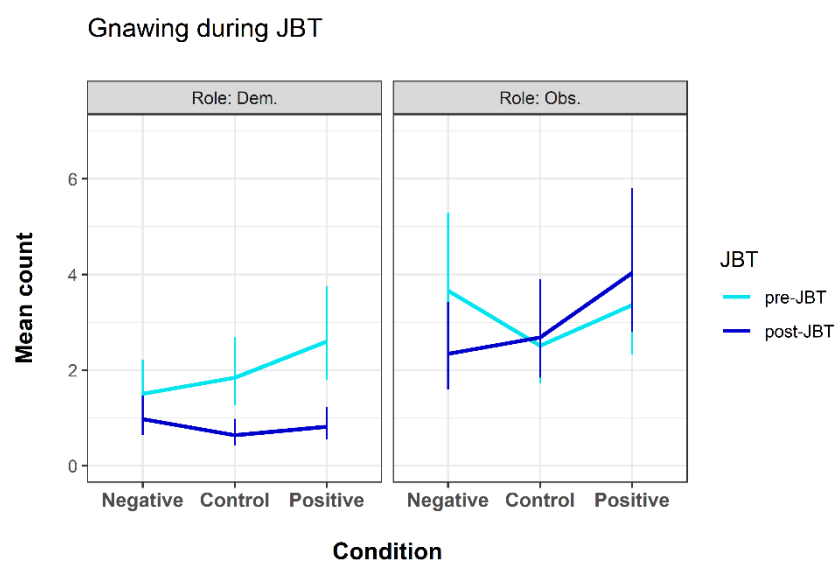


Figure S11. Mean predicted count gnawing (bars indicate SE): between roles (demonstrator, observer) and across conditions (negative, control, positive), for each judgement bias test (pre-JBT and post-JBT).

References – Chapter 4

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Chapter 5.

Wer mit Ungeheuern kämpft, mag zusehn, dass er nicht dabei zum Ungeheuer wird. Und wenn du lange in einen Abgrund blickst, blickt der Abgrund auch in dich hinein.

Whoever fights with monsters, had better see that it does not turn him into a monster. And when you gaze long into an abyss, the abyss also gazes into you.

— Friedrich Wilhelm Nietzsche

(Jenseits von Gut und Böse/Beyond Good and Evil, 1886)

Integration and overall discussion

Summary of research

With this thesis I aimed at answering whether other non-human species exhibit emotional contagion, with an important emphasis on how we measure emotional contagion. I approached this aim by first analyzing and discussing the current literature on comparative animal empathy research (Chapter 2). In this publication, my collaborators and I concluded that researchers ought to acknowledge the complexity of studying (animal) empathy, certainly when it is used as a broadly defined construct. We can do so by disentangling the different and distinct concepts, and by empirically investigating each concept systematically for its function(s), mechanism(s), and interlinkage with other empathy-related concepts. Further, we emphasize the need for more cross- and within-species research, including species outside the primate and rodent taxa groups, especially when it is plausible from a socio-ecological perspective that empathy-related phenomena have emerged in these species. As a general red thread resulting from this review, we found an overall lack of emotion-focused methods, or specifically, techniques that assess emotions aside from the observational method. For that reason, we recommended a greater focus on the emotional basis of the different empathy-related phenomena.

This review paper set the foundation for my further empirical PhD work in which I incorporated a cross-species perspective to study the emotional basis of emotional contagion (Chapter 3 and 4). Overall, both empirical studies had a semi-similar experimental design in which I measured behavior and cognition to assess emotional contagion. I used a demonstrator-observer procedure, with the demonstrator being directly exposed to either a negative or positive intervention, and the observer was exposed to the demonstrator's behavior only. During this intervention I analyzed the behavior of both animals, as well

as before and after the intervention during a judgment bias test (only in the marmoset study as ravens showed no additional behavior during their bias tests). The judgment bias paradigm was used to assess valence of their potential emotional states. Therefore, the demonstrator's behavioral and bias test results served as verification whether the experimental intervention was efficient, and whether any behavioral changes would be detected by the bias test. Then, the observer's behavioral and bias test results would indicate whether the demonstrator's behavior during the intervention had any influence on the observer, and whether this facilitated emotional contagion (i.e. by similar behavior and/or bias results), or perhaps lead to other socio-positive or -negative outcomes. Concretely, I predicted that in the negative intervention, both species would show (assumed) negative-related behavior and a pessimism bias in the judgment bias test, and that in the positive condition, animals would show (assumed) positive-related behavior and an optimism bias.

In chapter 3, I reported my first published PhD study on emotional contagion in common ravens. Together with my collaborators, I showed that in particular the negative condition had an intervention effect, as supported by the demonstrator's (assumed) negative related behavior. More importantly, we demonstrated negative emotional contagion in the observer, as confirmed by a pessimism bias in the observer's responses in the judgment bias test. In chapter 4 I reported the submitted version of my second empirical PhD study, which investigated emotional contagion in common marmosets. Similarly to the raven study, the demonstrator behavior in the different conditions was congruent with the emotion manipulations, thereby confirming the intervention effect. Yet, in contrast to the raven study, we found no response bias in the observers, therefore potentially ruling out emotional contagion as measured by the judgment bias test. Interestingly, the observer's behavior shown during the bias test, and in particular in the positive condition, indicated a social impact on the observer (though unclear whether positive or negative). Through exploratory analyses we found additional results in the bias test, including evidence for unexpected environmental effects (i.e. researcher identity). These two empirical studies will now be discussed for their scientific contributions, as well as their limitations, followed by how future research may help to clarify remaining ambiguities.

Discussion of research: Insights and Contributions

My PhD research advances our scientific understanding of animal emotional contagion, and to a broader extent empathy, by four main contributions.

Measuring valence. First, my work highlights a novel experimental approach to study the transfer of animal emotions. Based on the results of the raven study, the judgment bias paradigm is a promising method to investigate emotional contagion, and specifically its valence dimension. Therefore, this thesis lays the foundation for further studies interested in objectively measuring valence in the context of

empathy-related, or other social, phenomena. This is in particular of great importance as a major obstacle hampering progress in these domains is the experimental investigation of animal emotions and valence. When we cannot with certainty conclude whether an animal's (behavioral or physiological) expression is of positive or negative valence, it becomes a challenging task to interpret what we are really observing (Paul et al., 2005), and this gives rise to the question whether that observation is evidence for an empathy-related phenomenon. For instance, some of these questions are: *When animals show consolation after conflict, is that based on similar emotional states with the victim? Is affiliative bonding driven by (positive) emotional mechanisms or perhaps also, or only, by cognitive ones? When there is a transfer of emotions, does the other have the same state or does the transfer bring about a contrasting state? Is prosocial behavior such as food sharing or rescuing conspecifics driven by emotional mechanisms, and if yes, are they congruent with the other's state?* This notion of measuring valence is in particular of relevance to my study in marmosets (Chapter 4). Here, we found that observers show increased scratching after seeing the demonstrator in the positive condition. Yet, without additional data on its valence, the interpretation of scratching is problematic. Indeed, several studies provide evidence for a link between negative circumstances and scratching in primates (e.g. Kaburu et al., 2012), which has led to the widely accepted use of self-scratching as indicator of negative emotions (Mastripietri et al., 1992). In that vein, watching a group member in a seemingly rewarding context may induce food competition (which is known to be stress-inducing, e.g. Clay & de Waal, 2015), and so, it seems a plausible hypothesis that the observer's scratching reflects a negative state, reminiscent of frustration or conflict. However, other studies report contrasting results, either showing no increased scratching in negative situations (Dubosq et al., 2014), increased scratching in assumed positive contexts (Semple et al., 2013; but see Ueno et al. 2015), or even decreased scratching during and after negative manipulations (Neal & Caine, 2016; Kato et al., 2014). Further, physiological research in olive baboons showed no association between behavioral measures of anxiety, including self-scratching, and faecal glucocorticoid levels (i.e. used as indicator of stress) (Higham et al., 2009). Consequently, aside from the idea that scratching is not necessarily indicative of an intense negative state, and perhaps also of a low-level stress state (Higham et al., 2009), some scholars suggest now that scratching is not automatically *only* indicative of a negative state (Neal & Caine, 2016). In that regard, perhaps the increased scratching in my study reflects socio-positive behavior in line with (positive) excitement. This seems an alternative, plausible hypothesis, as observing the other in a beneficial situation may eventually lead to the observer acquiring those benefits as well (Nakahashi & Ohtsuki, 2018), or may induce a general positive affect. To conclude, both the negative (i.e. food competition) and positive (i.e. socio-positive behavior) interpretation are plausible, at least based on the available empirical evidence. To be able to interpret the findings with more certainty, we need to additionally measure valence through other means than observable behavioral changes. Admittedly, studying animal emotions and their valence is incredibly challenging, and has been the topic of long-standing debates between and within different disciplines (e.g. Mendl et

al., 2010). Nonetheless, these disagreements should not prevent scientific progress, and through integrating different disciplines, such as psychology, ethology, and animal welfare in the case for the cognitive bias test, we are equipped with the appropriate methods to continue to take on the challenge of studying animal emotions.

The cognitive approach. In that vein, the second contribution of my thesis is that the cognitive approach allows to disentangle behavioral or physiological matching from emotional matching. As discussed in the review paper (Chapter 2), emotional contagion research in animals often relies on findings of synchrony in behavioral expressions or in physiological variables, yet, the current evidence does not unanimously support the notion of synchrony automatically leading to emotional convergence. Moreover, as recent research shows, synchronized physiological responses may perhaps merely reveal a synchronized arousal level, and thus, behavioral or physiological matching between subjects does not necessarily imply emotion matching (Massen & Gallup, 2017; Neilands et al., 2020). By applying a multicomponent approach, including assessment of the cognitive component, we are able to collect more information beyond (potential) findings of synchronization. Furthermore, we showed in our raven study that the observer did not display any matching behavior when watching the demonstrator during the intervention, nor during the observer's bias test. This emphasizes that the scientific measurement of emotional contagion relies not necessarily, or solely, on observations of synchrony, and highlights the benefits of adding a cognitive method.

Social systems. Another strength of this thesis is the inclusion of two species who share similarity in their social systems with the social life of humans, and hence, this makes their results relevant to eventually understanding emotional contagion in humans. Common ravens are known for their diverse social bonds with others, leading to groups characterized by these social relations and thus, fission-fusion dynamics within these groups, which requires specific mechanisms to deal with this challenging, diverse social life (Aureli et al., 2008; Bugnyar, 2013). Emotional contagion is suggested to be one of the potential affective mechanisms, due to its information transmission function facilitating group life. Furthermore, common marmosets are cooperative breeders (Burkart et al., 2009), and this specifically requires coordination and group cohesion, which in turn may also be facilitated by emotional contagion. Though this thesis does not study emotional contagion in humans, nor does it directly investigate the functional contribution of emotional contagion to each of these two social systems, it sets the groundwork for further and more extensive research of why emotional contagion potentially emerged in these specific socio-ecological circumstances.

Avian emotional contagion. As final major contribution, my thesis, and in particular the study on ravens, pushes forward the field of avian emotions and emotional contagion. The result of negative emotional contagion provides us with the opportunity to further explore avian social behavior and empathy-related phenomena, as well as investigate its evolutionary drivers. This contribution is extremely

important as the current research on emotional contagion, and empathy, is mainly driven by work in mammals (but see e.g. Edgar et al., 2011). Yet, as discussed in the introduction of this thesis, various avian species show extensive parental care, which has been hypothesized to be a main evolutionary driver for empathy, and thus, it leads to the question whether empathy and emotional contagion play an equally important role in avian parental care and other social behavior. Furthermore, this then facilitates the overall study on the biological relevance of emotional contagion, as a wider cross-species scope allows us to investigate this question on a deeper level.

Discussion of research: Limitations

This thesis has contributed in different ways to the scientific development of animal emotional contagion and emotion research, yet, there are three main limitations that are important to consider in future research.

Demonstrator bias results. A first limitation of my work is the absence of cognitive bias test results for the demonstrator, and this is especially relevant for the raven study (Chapter 3). The demonstrators did participate in the bias test, yet, due to an unforeseen, but substantial, confound in the procedure, the bias data of the demonstrator were probably impacted, and hence, not reliable for interpretation. Indeed, emotion induction is a highly peculiar and sensitive task, which is supported by human emotion research showing various effects between induction procedures (Zhang et al., 2014), as well as the difficulty of designing appropriate neutral conditions, and controlling for the unintended induction of additional emotions (Siedlecka & Denson, 2019). Considering that in (emotion) research with animals we face additional challenges, it is even more likely that emotion induction, without invasive intervention, is a delicate task. Future research on emotional contagion using a demonstrator-observer design should consider our potential procedure confounds and create an experimental setup which allows to rule out these unwanted effects.

Validation judgment bias test. The second limitation relates to the use of a judgment bias paradigm to measure emotions. Two recent meta-analyses (Neville et al., 2020; Lagisz et al., 2020) conclude that there is considerable support for the judgment bias test as a valid method for assessing affective states. Still, the authors underline that more validation is required. For instance, in general it is expected to find a (potential) change in response to the ambiguous cues, though a change should not be observed to the trained cues (Gygax, 2014). However, some research has reported changes in response to these cues as well, though unfortunately, not all studies report whether there were these changes (Lagisz et al., 2020). In our marmoset study we unexpectedly found changed responses to the trained cues after the demonstrator had seen the positive stimulus, which could indicate a change in reward expectation, and in turn, this would be a congruent effect with the positive condition (i.e. increased go response). Still,

what exactly led to a higher response to these cues is unclear. Furthermore, our study revealed a researcher identity effect, and marmosets showed an increased response when one of the two researchers was testing. This effect was most likely due to the close bond between this person and the subjects, though extensive training was introduced to reduce any difference in conducting the judgment bias test. Nevertheless, this researcher effect may form a plausible confound in judgment bias research, as reward expectation is the main factor guiding the interpretation of optimism or pessimism bias (Burman et al., 2008). For that reason, further validation of the bias paradigm and potential external effects is required. As a final note, we found (partially) predicted behavior of the demonstrator in both positive and negative condition, still, this effect was not picked up by the judgment bias test. In contrast to the raven study, our marmoset design should not have had confounding set-up effects, so the absence of either an optimism or pessimism bias in the demonstrator is surprising. In conclusion, based on the demonstrator's behavior, the manipulation effect was seemingly successful, and so, together with the response change to the trained cues and the researcher effect, the judgment bias test in this particular study was perhaps not measuring what it should have measured. This conclusion is again supported by the behavior of the observer in the positive condition, though again, the underlying state of this behavioral expression was not detected by the bias test. All this together calls for further investigation of the judgment bias paradigm, and validation between different interventions and species.

Disentangling emotional contagion. A final, important limitation regards the empirical study of emotional contagion. Notably, emotional contagion is difficult to measure, not only due to the great challenge of measuring animal emotions, but also because the transferred state may be caused by other sources (i.e. the contagion needs to come from another subject's state, and not from the source that induces this state in the other subject). Moreover, researchers ought to be cognizant of the facilitating effect of emotional contagion, and thus, aim at disentangling emotional contagion from other social behaviors. For instance, the transfer of emotions may lead to counter-states (Dezecache et al., 2015), such as anger evoking fear (Wrobel & Olszanowski, 2019) or fear evoking prosocial helping (Preston & de Waal, 2002; Wrobel & Imbir, 2019). This is specifically relevant to both my experimental studies and its positive intervention, as emotional contagion may bring about a competitive context when observers recognize that the other is in a highly beneficial situation. Interestingly, in the raven study we found no optimism bias, and the marmoset observers expressed behavior that potentially indicated a negative response (though the meaning of scratching may be debated, see discussion above). Both study results exhibit effects that were not predicted by the positive contagion hypothesis and are potentially indicative of a counter-state, such as the tentative interpretation that the positive intervention induced a food competition context (as discussed above). To conclude this interpretation with more certainty, further emotional contagion research including positive emotions and different types of positive induction is needed. Nonetheless, the overall results of the positive conditions in my PhD work

emphasize the notion that emotional contagion may facilitate other social behaviors, and thus, supports the idea that a precise assessment is often difficult to achieve. In terms of the negative manipulation, the raven study provides support for its hypothesis, though, the marmoset study shows unexpected results in which both demonstrator and observer show less negative-related behavior overall. This was a very surprising result, yet, I believe that this particular manipulation could be improved in future studies. In contrast to the raven study, where I manually held and split food pieces, and simulated as if I would hand them over to the demonstrator, we used a static and immobile object in the marmoset study (i.e. toy tarantula). During the exposure of this toy, the demonstrator did show some negative-related behavior, though, its effect may not have been strong enough to induce longer lasting states in either animal. In conclusion, aside from further investigating positive emotional contagion, future research should explore different negative emotion induction procedures.

Future research

In conclusion of this discussion, I would like to elaborate on research I've been working on as follow-up to the discussed limitations above. These studies are additional projects I conducted after my PhD research and are not official part of my dissertation, though, each of them serves as empirical extension to this thesis, and therefore might be of interest to this discussion.

First, in light of measuring emotional contagion experimentally, I designed and conducted a study on emotional contagion in another avian species, namely chickens (*Gallus gallus domesticus*). This work was supported by the Marietta-Blau exchange grant and done in collaboration with Dr. Michael Mendl, Dr. Elizabeth Paul, and Dr. Christine Nicol, at the Langford Veterinary School of the University of Bristol (U.K.). The study had 72 subjects which I raised by hand until they reached 6 weeks (step 1: habituation and training) and 12 weeks of age (step 2: experimental study). All (laying) hens were tested with a between-subjects design following a demonstrator-observer procedure, in which the demonstrator was either exposed to a distressing stimulus (i.e. air-puff) or nothing. Here I measured behavior of both animals, body temperature by means of infrared thermography (e.g. Stewart et al., 2005; Herborn et al., 2015), the observer's approach or avoidance response to the distressing location after the intervention (Paul et al., 2018), and social behavior within the dyads upon reunion (Burkett et al., 2016). The first two measurements were used to assess emotional arousal, and the observer's response to the distressing location specifically taps into the signaling function of emotional contagion (Nakahashi & Ohtsuki, 2018). Considering the need for more empirical research on the biological relevance of emotional contagion, this study will make an important contribution to this topic. At the moment of thesis submission, this work is at the stage of video coding the behavior and data analyses.

Second, to address the need for further validation of the cognitive bias paradigm, I performed a study on positive and negative affective states in capuchin monkeys (*Cebus [Sapajus] apella*) as measured by

a judgment bias test. This study is done in collaboration with Dr. Sarah Brosnan from the Comparative Economics and Behavioral Studies lab, at Georgia State University (U.S.). Dr. Brosnan's lab, in which animals are trained to use computer set-ups, offers the ideal location to explore the bias paradigm with a specific focus on its methodology. Concretely, I aimed at further investigating the following 3 design specifics: the type of cues used (by using both a spatial and a shape judgment task in which the location or the size of the cue varies), the number of cues presented (one automatized bias test includes 100 trials versus the average of 20 trials in manual tasks), and the option to opt-out from a trial (similar use as in the marmoset study where animals are in control of the start of new trials). Moreover, the automaticity that comes with using computerized set-ups allows to rule out researcher identity effects. Currently, all data has been collected and data analyses are ongoing.

Conclusion

My PhD research contributes to the intriguing study of animal emotional contagion and empathy, including the experimental investigation of animal emotions. After all, if we want to get a full grasp of why and how humans evolved empathy, and each of the empathy-related phenomena such as emotional contagion, we ought to take on a comparative perspective, and take a closer look at the other beings we share our planet with. Furthermore, in order to perform such research, it is essential to continue the development and exploration of new methods to assess the key components playing a role in empathy and emotional contagion, and thus, investigate which appropriate means will bring us closer to the emotional basis. In this regard, my thesis contributes to a new experimental approach to measure social emotions in animals, with in particular an emphasis on emotional valence, by investigating species with similar social systems as humans do, as well as contributing to a more profound understanding of the emotional life of birds. Nonetheless, this work has undoubtedly also opened up additional questions. In regard of emotional contagion research, how can we further study its functional relevance, and which study-species would be most appropriate to answer this question? In terms of proximate mechanisms, how can we creatively disentangle the suggested mimicry mechanisms from other mechanisms? In relation to using the bias paradigm to measure emotional states, to what extent can the pessimism bias found in ravens be replicated in other assumed negative circumstances, such as negative social situations (e.g. isolation) or non-food stimuli (e.g. threat)? Can we apply the same design to study underlying emotions in ravens' parental care, affiliative pair-bonding, or other empathy-related phenomena such as perspective taking? These behaviors have previously been suggested to be driven by affective mechanisms (Preston & de Waal, 2002), similarly to cooperation in marmosets (Massen et al., 2019), and thus, it seems appropriate for future research to empirically investigate these claims. Furthermore, will these findings appear in other avian species, such as in crows (Wascher et al., 2019)?

And how can we bridge the gap between captive studies and work done in the field, especially in terms of integrating the bias design into natural environments (see e.g. Brilot et al., 2009)? Empirical studies with captive animals allow for greater experimental control of its design, involved subjects, and stimuli used for manipulation. As consequence, captive research provides the opportunity to disentangle different effects and achieve a more precise interpretation. On the other hand, field studies with wild animals permit to investigate the scientific topic in the context of everyday life, including the various dynamics between animals and their environment, and therefore provides the benefit of being ecologically more valid. Specifically, for emotional contagion it would allow for natural events to unfold and, thus, provide information on why emotional contagion is important. And finally, in regards of (animal) emotions, what is the extent of various emotions and is there (functional) resemblance between human and animal emotions? And are emotions discrete, as is more traditionally assumed (i.e. a fixed set of distinguishable, basic emotions, Panksepp, 2007), more dimensional (Barrett, 2006), or a combination of the two (e.g. Mendl et al., 2010)? A final key, but difficult to answer, question remains, which is what does the bias paradigm really measure, and is it really affect that drives the response change, or are we measuring the outcome of another, for now still unknown mechanism (Neville et al., 2020)? In that vein, further comparative research on emotional contagion with the cognitive bias paradigm would benefit greatly from the inclusion of human subjects, as this would not only contribute to a broader comparative perspective, but would allow us to assess the emotional basis of emotional contagion in alternative ways not possible in animals. These are just a number of important questions for further scientific work on emotions and emotional contagion, many of which will hopefully stimulate interest and lead to new, creative research avenues for the future. To conclude, I hope the reader of this thesis finds my research to be contributing in adding some of the puzzle pieces we need to complete the bigger picture of emotional contagion and empathy.

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Appendix

1. General abstract

Empathy is a remarkable skill which plays a vital role in our human existence. It allows us to feel the emotions of others and to understand them, and as such, improves the quality of our lives. One of the suggested fundamental phenomena related to empathy is emotional contagion, defined as a matching of emotions. For long it was assumed that emotional contagion, and empathy, were restricted to mammalian species, yet, observations in other animal taxa puts this notion into question. Therefore, this thesis investigated emotional contagion by applying a comparative approach. The thesis starts with a review paper, followed by two empirical studies with an avian (common ravens, *Corvus corax*) and a primate species (common marmosets, *Callithrix jacchus*), each characterized by their own social system potentially driving the evolution of emotional contagion. The review paper examined the current comparative empathy literature, with as main conclusion that a profounder focus on the emotional basis of empathy is needed, as well as the requirement for more between- and within-species research, and objective methodology. To follow up the review paper's main recommendation for more emotion-oriented research, the two empirical studies focused specifically on measuring emotions and their transfer in an affiliative dyad set-up. Here, a demonstrator was exposed to an emotion manipulation, and an observer could only see the demonstrator's reaction to the manipulation. Emotional states of demonstrators, and of observers as induced through emotional contagion, were quantified by means of behavioral assessment and a cognitive bias test. The latter taps into the cognitive approach of measuring emotions in animals, as it offers a way to assess emotional valence rather than emotional arousal. The first experimental study in common ravens provided evidence for negative emotional contagion, though, we found no evidence for positive contagion. The second study in common marmosets did not find any evidence of emotional contagion, at least not based on the cognitive bias test results, or in the strict sense of matching emotions. Still, it is unclear why marmosets seemingly showed no emotional match, and whether this is due to the study design, or a general absence of emotional contagion in common marmosets. These findings are combined and further discussed in terms of their scientific contributions and limitations in the closing discussion chapter.

1. Zusammenfassung

Empathie ist eine bemerkenswerte Fähigkeit, die eine wichtige Rolle in unserer menschlichen Existenz spielt. Sie ermöglicht uns andere um uns herum zu verstehen, und verbessert als solches die Qualität unseres Lebens. Eines der vorgeschlagenen fundamentalen Phänomene im Zusammenhang mit Empathie ist die Stimmungsübertragung („emotionale Ansteckung“), definiert als Übereinstimmung von Emotionen zweier Individuen. Lange Zeit wurde angenommen, dass emotionale Ansteckung und Empathie auf Säugetierarten beschränkt waren, doch Beobachtungen in anderen Tier-Taxa stellen diese Annahme in Frage. In dieser Doktorarbeit wurde daher die Emotionale Ansteckung anhand eines vergleichenden Ansatzes untersucht. Die Arbeit beginnt mit einem Übersichtsartikel, gefolgt von zwei empirischen Studien mit einer Vogel- (Kokkraben, *Corvus corax*) und einer Primatenspezies (Weißbüschelaffen, *Callithrix jacchus*), die jeweils durch ihr eigenes soziales System gekennzeichnet sind, das möglicherweise die Entwicklung der Emotionalen Ansteckung antreibt. Der Übersichtsartikel befasste sich mit der aktuellen Literatur im Bereich der vergleichenden Empathieforschung und führte zu den Schlussfolgerungen, dass ein schärferer Fokus auf die emotionalen Grundlagen von Empathie gelegt werden muss und dass mehr vergleichende Forschung sowie objektive Methoden erforderlich sind. Um der Empfehlung des Übersichtsartikels mehr emotionsorientierte Forschung zu betreiben zu folgen, konzentrierten sich die beiden empirischen Studien speziell auf die Messung von Emotionen und deren Übertragung zwischen zwei befreundeten Individuen. Hierbei wurde ein Demonstrant einer Emotionsmanipulation ausgesetzt, und ein Beobachter konnte nur die Reaktion des Demonstranten auf die Manipulation sehen. Die emotionalen Zustände von Demonstranten und Beobachtern, wie sie durch Emotionale Ansteckung hervorgerufen wurden, wurden mittels Verhaltensbewertung und einem kognitiven Bias-Test quantifiziert. Letzterer greift auf den kognitiven Ansatz der Messung von Emotionen bei Tieren zurück, da dieser Test eine Möglichkeit bietet, die emotionale Wertigkeit und nicht die emotionale Erregung zu bewerten. Die erste experimentelle Studie an Kokkraben lieferte Hinweise auf eine Übertragung negativer Emotionen, wir fanden jedoch keine Hinweise auf eine Übertragung positiver Emotionen. Die zweite Studie an Weißbüschelaffen ergab keine Hinweise auf eine emotionale Ansteckung, zumindest nicht basierend auf den Ergebnissen des kognitiven Bias-Tests oder im strengen Sinne der Übereinstimmung von Emotionen. Es ist jedoch unklar, warum die Affen scheinbar keine emotionale Übereinstimmung zeigten und ob dies auf das Studiendesign oder auf das generelle Fehlen einer emotionalen Ansteckung bei Weißbüschelaffen zurückzuführen ist. Diese Ergebnisse werden kombiniert und im Hinblick auf ihre wissenschaftlichen Beiträge und Einschränkungen im abschließenden Diskussionskapitel weiter diskutiert.

2. Additional publication

Published in Proceedings of the National Academy of Sciences of the United States of America

REPLY TO VONK: Disentangling emotional contagion from its underlying causes

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We thank Vonk (2019) for her interest in our paper (Adriaense et al., 2019) in PNAS. We appreciate her concerns; however, several comments in her Letter are already discussed and supported by data in our paper. We thus respectfully disagree with her claims about the limitations of our study and theoretical interpretation. Vonk argues that we should distinguish between “responding to others’ internal states rather than to behaviors” before claiming emotional contagion in animals. While we appreciate the importance of disentangling these mechanisms, we disagree that “to experience emotional contagion implies that observers perceive others’ emotions.” Emotional contagion refers to the transfer of emotional states, which does not necessarily imply representation of, or concern for, the other’s emotional state. We have repeatedly argued for a clear distinction on this matter (Singer & Lamm, 2009), and thus in our paper we refrain from speculating about the mechanism facilitating emotional contagion. Moreover, Vonk suggests that our contagion findings reflect “expectation of reward” rather than emotion. Yet sensitivity to reward forms the foundation of the bias hypothesis: The expectation of reward is influenced by the emotional state, and so the observed evaluation of ambiguous stimuli reflects the underlying emotional valence (Burman et al., 2008; Mendl et al., 2009). In addition, Vonk’s description of our experimental methodology and results seems misleading and might (partially) be based on an incomplete reading of our paper. While Vonk states that “results of cognitive bias tests are open to interpretation,” multiple studies have confirmed

a priori predictions of environmental effects on cognitive bias (Mendl et al., 2009). Indeed, the purpose of the bias test is to facilitate identification of “phenomena . . . not easily detectable by . . . behavioral measures” (Adriaense et al., 2019). Nonetheless, as we repeatedly state in our paper, we agree that bias tests are “best used in conjunction with other measures of emotional state.” While it is correct that the ratio of ambiguous to other cues is relatively high, the total amount of ambiguous cues is similar to past research and was selected to avoid false-positive findings (Roelofs et al., 2016). Although our subjects continued to respond to negative cues, we also disagree that “they did not fully learn when they would not receive a reward.” This interpretation would require dismissing the evidence that animals often exhibit difficulty inhibiting their responses in go/no-go tests (Roelofs et al., 2016). We therefore analyzed response latencies, to provide a more nuanced measure of reward expectation. Thus, our interpretation of ambiguous responses is based upon more than the fact that “birds continued to respond to [ambiguous cues].” Similarly, while the experience of the observer may influence their vicarious reaction (Atsak et al., 2011), we show in the paper’s supplement that prior exposure had no effect on the observer’s bias test. Finally, although Vonk argues that the demonstrator bias data “did not support the manipulation,” we describe as well why interpretation of these responses was inhibited by unforeseen confounds, and that future research needs to overcome these limitations. To conclude, we appreciate Vonk’s claim that our study presents a promising methodology, but we think she overstates its limitation.

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3. Curriculum Vitae

Jessie E.C. Adriaense

Nationality: Belgian

Current position & Education

- 2014 - present **PhD candidate in Psychology**, Social, Cognitive, and Affective Neuroscience Unit & Department of Behavioral and Cognitive Biology, University of Vienna (Austria).
- 2019 **Visiting scholar**, Comparative Economics and Behavioral Studies lab & Language Research Center, Georgia State University (U.S.). Collaboration with Prof. Dr. Sarah Brosnan.
- 2018 **Visiting scholar**, Animal Welfare and Behaviour Research group, Langford Veterinary School, University of Bristol (U.K.). Collaboration with Prof. Dr. Michael Mendl, Dr. Elizabeth Paul, & Prof. Dr. Christine Nicol.
- 2012 - 2014 **MSc degree** in Experimental Psychology, Ghent University (Belgium) *cum laude*
- 2013 **Internship**, The Social Brain lab at the Netherlands Institute for Neuroscience, Amsterdam (the Netherlands). Supervision by Dr. Maria Carrillo, Dr. Filippo Migliorati, & Prof. Dr. Christian Keysers.
- 2010-2012 *personal travel & temporary work*
- 2008 - 2010 **MSc degree** in Industrial Psychology, Ghent University (Belgium), *cum laude*
- 2004 - 2007 **BSc degree** in Industrial Psychology, Ghent University (Belgium)

Funding & awards

- 2019- 2020 **Dissertation completion grant** (€6000, University of Vienna, Austria)
- 2018 - 2019 **Marietta Blau Exchange grant** (€18 000, OEAD & BMWFW - the Austrian Ministry of Education, Science, and Research), for international research. Host: University of Bristol, U.K.
- 2017 **Cross Disciplinary Research grant** (€7500, Vienna Doctoral School Cognition, Behavior, and Neuroscience, Austria), for the project "Empathy and personality in common marmosets: a multi-method approach"
- 2017 **Travel grant** (€400, University of Vienna, Austria)
- 2017 **Best Poster** award, Comparative Affective Sciences workshop, Leiden (the Netherlands)
- 2016 **Research grant** (€3000, University of Vienna, Austria)
- 2016 **Travel grant** (€400, University of Vienna, Austria)
- 2016 **Best Talk** award, Vienna Doctoral School kick-off meeting, University of Vienna (Austria)
- 2016 **Best Talk** award, 8th European Conference of Behavioral Biology, Vienna (Austria)

- 2014 **Cognitive Science Platform Fellowship** (3-year payed PhD position, University of Vienna, Austria)
- 2013 **Erasmus Fellowship** (6-months payed internship abroad, by the European Union)

Publications

- 2020 **Adriaense, J.E.C.**, Koski, S., Huber, L., Lamm, C. Challenges in the comparative study of empathy and related phenomena in animals. *Neuroscience & Biobehavioral reviews*, 112, 62-82
- 2019 **Adriaense, J.E.C.**, Martin, J.S., Schiestl, M., Lamm, C., Bugnyar, T. Reply to Vonk: Disentangling emotional contagion from its underlying causes. *Proceedings of the National Academy of Sciences*, 201910556
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- Norman, K., **Adriaense, J.E.C.**, Nicol, C. The impact of early structural enrichment on spatial cognition in layer chicks. *Behavioural processes*, 164, 167-174

Conference participation

- 2020 **Adriaense J.E.C.**, “*The experimental investigation of avian emotions*”. **Invited talk** at the Avian Cognitive Neuroscience meeting in Bochum (Germany), March 2020, *Cancelled due to COVID-19*
- 2019 **Adriaense J.E.C.**, Koski S., Lamm C., Bugnyar T. “*The experimental investigation of emotions in primates*”. **Talk** at the European Federation of Primatology meeting, Oxford (U.K.)
- 2018 **Adriaense J.E.C.**, Norman K., Paul L., Mendl M., Nicol C. “*The effect of negative emotional contagion on learning and social interaction in layer pullets*”. **Poster** at the ASAB winter meeting ‘Animal Behaviour and Welfare’, London (U.K.)
- Adriaense J.E.C.**, Norman K., Paul L., Mendl M., Nicol C. “*The investigation of empathy and emotional contagion in hens*”. **Talk** at the Animal Behaviour, Welfare, and Ethics walks & talks workshop, Leeds (U.K.)
- Adriaense J.E.C.**, Lamm C., Bugnyar T. “*Comparative empathy research in animals*”. **Poster** at the European Conference for Behavioral Biology, Liverpool (U.K.)
- 2017 **Adriaense J.E.C.**, Martin J.S., Schiestl M., Lamm C., Bugnyar T. “*Negative emotional contagion and cognitive bias in common ravens (Corvus corax)*”. **Poster** at the ‘Comparative Affective Sciences’ workshop, Leiden (the Netherlands)
- Adriaense J.E.C.**, Rütgen M., Lamm C. “*Placebo empathy analgesia: an indirect effect of trial design?*”. **Poster** at the Society for Interdisciplinary Placebo Studies conference, Leiden (the Netherlands)
- Adriaense J.E.C.**, Rütgen M., Lamm C. “*Placebo empathy analgesia and potential mediation by trial design: an EEG study*”. **Poster** at the International Convention of Psychological Science, Vienna (Austria)
- 2016 **Adriaense J.E.C.**, Martin J.S., Schiestl M., Lamm C., Bugnyar T. “*Emotional contagion in common ravens*”. **Talk** at the Vienna Doctoral School ‘Kick-off meeting’, Vienna (Austria)

Adriaense J.E.C., Martin J.S., Schiestl M., Lamm C., Bugnyar T. “*Your pessimism brings me down, but does your optimism lift me up? Emotional contagion in common ravens*”. **Talk** at the 8th European Conference for Behavioural Biology, Vienna (Austria)

Adriaense J.E.C., Rütgen M., Lamm C. “*Placebo empathy analgesia: an indirect effect of trial design?* “. **Poster** at the European Society of Cognitive and Affective Neuroscience conference, Porto (Portugal)

Adriaense J.E.C., Martin J.S., Schiestl M., Lamm C., Bugnyar T. “*Emotional contagion in common ravens*”. **Poster** at the Human and Animal Emotions meeting, Erice (Italy)

2015 **Adriaense J.E.C.** “*Empathy in birds*”. **Poster** and **speed talk** at the Aegina Summer School ‘The social self: how social interactions shape body and self-representations’, Aegina (Greece)

Adriaense J.E.C. “*Studying emotions in ravens*”. **Talk** at the Cognition and Communication Workshop, Vienna (Austria)

Seminars & invited lab talks

2016 “*Scientific integrity*”, at the Annual meeting of the Vienna Doctoral School, Cognition, Behavior, and Neuroscience, University of Vienna (Austria)

“*Emotional contagion in animals*”, at the Behavioral Ecology Lab meeting (PI: Prof. Dr. Adrian Jäggi), Emory University, Georgia (U.S.)

“*An empathy paradigm in ravens*”, at the Social Brain Lab (PI: Prof. Dr. Christian Keysers), the Netherlands Institute for Neuroscience, Amsterdam (the Netherlands)

2015 “*Implications and restrictions of research data*”, at the Ph.D. seminar of the faculty of Psychology, University of Vienna (Austria) (together with Freya Acar from Ghent University)

Mentoring experience

2016-2017 Supervision Master thesis, University of Vienna (Austria)

2016 Supervision Bachelor internship of 3 students, University of Vienna (Austria)

Professional service

2015-2016 Organizer Journal Club in the Cognitive Biology department, University of Vienna

2014-2017 Start-up and organizer Journal Club in the Social, Cognitive, and Affective Neuroscience Unit, University of Vienna

Media coverage (selection)

My research has also been covered in other languages such as Spanish, Portuguese, Hungarian, Russian, and Chinese.

Interview for radio show: Nieuwe feiten, Radio 1 (Belgium) (May, 2019)

Online press with interview: RiffReporter - Die Flugbegleiter (July, 2019), Cottage life (June, 2019), PBS Nova (May, 2019), Science News (May, 2019)

Online press without interview: FaunAlytics (August, 2019), Psychology Today (June, 2019), Die Welt (May, 2019), Ars Technica (May, 2019), Radio Canada (May, 2019), New York Post (May, 2019), ZME Science (May, 2019), VICE (May, 2019), Der Standard DE (May, 2019), Neue Zürcher Zeitung (May, 2019), Phys.org (May, 2019), Dailymail (May, 2019), Science ORF (May, 2019), Wiener Zeitung (May, 2019), IFL-Science (May, 2019), MyScience (May, 2019; October 2016), National Geographic Russia (May, 2019)

Podcasts: STEM Fatale Podcast (May, 2019)

Acknowledgments

In 2011, I made a decision that broke all expectations of my life at the time. I quit a business job, finished a new degree, moved countries, and ended up finding myself surrounded by MRI-scanners and bird aviaries. It was the most inconceivable thing I had ever done, and although *follow your guts* may truly be the corniest advice, to me it's one of the most important ones. At the start of my PhD, I initially set out to understand the neurological basis of human empathy, but my work in ravens dramatically changed that, and it eventually drove me deeper into the behavioral domain of animal empathy. And so, the PhD path I carved out for myself over the last 6 years turned into an intriguing adventure, and as many others have probably felt at this point, bringing this enormous task to an end feels rather surreal. For that reason, I'd like to dedicate these final pages to a concluding reflection and express my gratitude to some important people.

During my PhD, and all the decisions and changes, ponderings and doubts, I had two of the sweetest, most generous, and most supportive people by my side: my parents. If not for them pushing me forward and cheering me on, this whole PhD would've been pretty unrealistic to begin with. Thanks for teaching me perseverance, independence, and a very intense perfectionist mindset. Bedankt mama en papa voor alles, "Aan de meet delen ze de prijzen" en bij deze is die marathon nu ook echt gedaan.

Halfway into my PhD I found my grounding as a researcher and around that time I met a peculiar person. Whether it is science that brought us together, his stay in Vienna, our overlapping study topics, or just his wonderful persona – my (now) husband is by far the best thing this PhD has given me. Jordan, thank you for taking life as serious as you do, for being the most intense, deep, and caring soul, for continuously overwhelming me (and others) with love and warmth, for reigniting my creative side, for sharing your imagination, and for showing me that life can be really good. You are my shining joy every single day, and thanks to you I am a better person and researcher.

Despite its demanding nature, impostor-inducing challenges, and often nerve-wrecking pressure, this PhD exposed me to an amazing hidden treasure as well: the pleasure of having a job that allows you to think and read, and then think some more. Therefore, a thank you to my supervisors for providing me with this treasure and believing in me from the very start. Further, a particular huge thank you to my psychology supervisor, Claus, who flexibly let me be in charge of my own scientific route, and whose support and encouraging words provided a tremendous buffer against the rougher side of the past years. You offered solutions when I spent my entire 2nd year on what turned out to be a failed study, and your empathic mindset is exemplary. Also, a thank you to my biology mentor, Thomas, who allowed a psychologist to roam his department, and offered the chance to study one of the most fascinating species in the world.

Furthermore, what is an adventure if one cannot share it with others? So thank you to all the others around me, all of you left great warm marks on my heart: my godparents who relentlessly show tremendous interest and care (Eddy, Christa), my supportive Belgian and American family, my Viennese science/music/crafters crew (Lisa, Jasminka, Sabrina, Clio, Tina) and my numerous psychology and biology colleagues, my Belgian supporters (Vicky, Katrien, Margo, Margot, Lieve), my previous mentors whose support still resonates with me (Lize, Filippo, Maria), my awesome science friends (Sonja, Jorg, Sara, Luisa, Erik), and our loving companion and forever family member, Shiva.

On a final note, my first real exposure to animal emotion research was through the work of the late Professor Dr. Jaak Panksepp. Admittedly, when I signed up in 2013 for an internship at the Social Brain Lab in Amsterdam, I had not even heard of his name before, though this is perhaps no surprise considering my mainly human-focused psychology background. Still, once I dug deep into the lab's work as preparation for my upcoming project on rat empathy, Dr. Panksepp's writing and research took hold of my brain. On top, during my very first week at the lab in September 2013, Dr. Panksepp happened to be in Amsterdam for a visit and a scientific talk. Only about 10 people were present in the room, which in my personal opinion is now hard to believe, and I raised some particularly non-clever comments, but his studies with rats and his discovery of similar brain structures involved in the emotional experience of both humans and other animals left a great impression on me. I've always had a huge interest in how the social lives of humans work, but I had no clue that I would end up studying animals and trying to figure out how *their* social lives work. It was Dr. Panksepp who instigated a curiosity in me, and an admiration and respect for other species. It truly is a position of privilege and honor to work with the beings around us, and I symbolically want to thank Dr. Panksepp for his insights and knowledge, which he so passionately shared with the rest of the world.