



Review article

Emotion recognition in nonhuman primates: How experimental research can contribute to a better understanding of underlying mechanisms

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ARTICLE INFO

Keywords:

Nonhuman primates
Emotion recognition
Cognitive empathy
Emotional contagion
Affect

ABSTRACT

Recognising conspecifics' emotional expressions is important for nonhuman primates to navigate their physical and social environment. We address two possible mechanisms underlying emotion recognition: *emotional contagion*, the automatic matching of the observer's emotions to the emotional state of the observed individual, and *cognitive empathy*, the ability to understand the meaning and cause of emotional expressions while maintaining a distinction between own and others' emotions. We review experimental research in nonhuman primates to gain insight into the evolution of emotion recognition. Importantly, we focus on how emotional contagion and cognitive empathy can be studied experimentally. Evidence for aspects of cognitive empathy in different nonhuman primate lineages suggests that a wider range of primates than commonly assumed can infer emotional meaning from emotional expressions. Possibly, analogous rather than homologous evolution underlies emotion recognition. However, conclusions regarding its exact evolutionary course require more research in different modalities and species.

1. Introduction

Being able to recognise the emotional expressions of others is essential in providing appropriate responses to conspecifics and events in the environment and is a pivotal skill for all social animals (Ferretti and Papaleo, 2019). We define emotion recognition as the ability to form an internal representation of the emotions of others based on the perception of their emotional expressions. Two possible, non-mutually exclusive mechanisms underlying this ability are *emotional contagion* and *cognitive empathy*. *Emotional contagion* is a relatively low-level bottom-up process in which the state of the perceiver of an emotional signal is automatically matched to the state of the sender. It is defined as the tendency to automatically mimic and synchronize emotional expressions with those of others, resulting in emotional convergence (Hatfield et al., 1994). In other words, emotions of others unconsciously evoke a basic internal representation of the emotion in the perceiver (de Waal and Preston, 2017; Morimoto and Fujita, 2011; Preston and de Waal, 2002). A more cognitively demanding way of recognising emotions is through *cognitive empathy*. This is the capacity to understand the

meaning or the cause of an emotion without necessarily experiencing the same emotion (de Waal and Preston, 2017; de Waal, 2008; Preston and de Waal, 2002). This process results in a more cognitive representation of the perceived emotion and entails a clear self-other distinction in the observer of the emotion.

Cognitive empathy has been hypothesised to be phylogenetically younger than emotional contagion. De Waal (2008) compares emotional contagion and cognitive empathy to different parts of a Russian doll. The inner doll represents emotional contagion: a basic and early evolutionary mechanism to form internal representations of others' emotions. Cognitive empathy, presented as the next step in evolution, is built around this core without fully replacing it. Cognitive empathy is a controlled top-down process related to enhanced prefrontal functions such as inhibition and goal-directed behaviour (Preston and de Waal, 2002). As these prefrontal functions emerged relatively recently in evolution (Ardila, 2008), this suggests that emotional contagion might be phylogenetically older.

To gain a better insight into the evolutionary development of emotion recognition and its underlying mechanisms, conducting

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comparative research is of utmost importance. Both observational and experimental studies comparing responses to emotional displays in different species can help to disentangle at what point in evolution emotional contagion and cognitive empathy emerged as mechanisms of emotion recognition, under which environmental pressures, and whether aspects of emotion recognition may have evolved in a homologous or analogous way.

In the past decades, much research has been conducted on nonhuman primates' (hereafter: primates) responses to emotional expressions. Primates are evolutionary close to humans and known for their complex emotional behaviours. In this review, we discuss observational and experimental studies on emotion recognition in different primate species in light of the different aspects of cognitive empathy and emotional contagion, with an explicit focus on experimental research and the visual and auditory domain.

Our first aim is to provide an inter-species comparison between different primate lineages to come closer to conclusions on which mechanisms are shared and which are different, thereby shedding light on the evolutionary origins of emotion recognition. Because we believe that experimental research is a key addition to observational studies in unravelling the underlying mechanisms of emotional behaviour, the second contribution of this review is a critical discussion of the experimental methods used in the literature discussed. Importantly, we provide suggestions for experimental designs in future studies.

It should be noted that several researchers have highlighted the importance of emotional communication through signal types other than the extensively studied topic of facial expressions (Fröhlich and van Schaik, 2018; Hobaiter et al., 2017; Schirmer and Adolphs, 2017). Therefore, we also included vocal expressions, bodily expressions and physiological responses to emotion in this review. Outside the scope were the – more indirect – olfactory expressions of emotion (Laska and Salazar, 2015) and emotional expression via touch (Schirmer and Adolphs, 2017). Although these modalities may be relevant for emotion recognition research, too little research has been conducted to be able to draw meaningful conclusions from.

The structure of this review is as follows. In Section 2 we elaborate on emotional contagion and we discuss research on various contagious emotional expressions and behaviours and how these can be linked to emotion recognition. Section 3 describes the mechanism of cognitive empathy and discusses evidence of different primate species inferring meaning from emotional expressions. In Section 4 we reflect on the conclusions and their importance for future research. A detailed overview of the key literature discussed can be found in the Appendix. Fig. 1 provides a schematic overview of primate phylogeny, to be used as reference in the following sections.

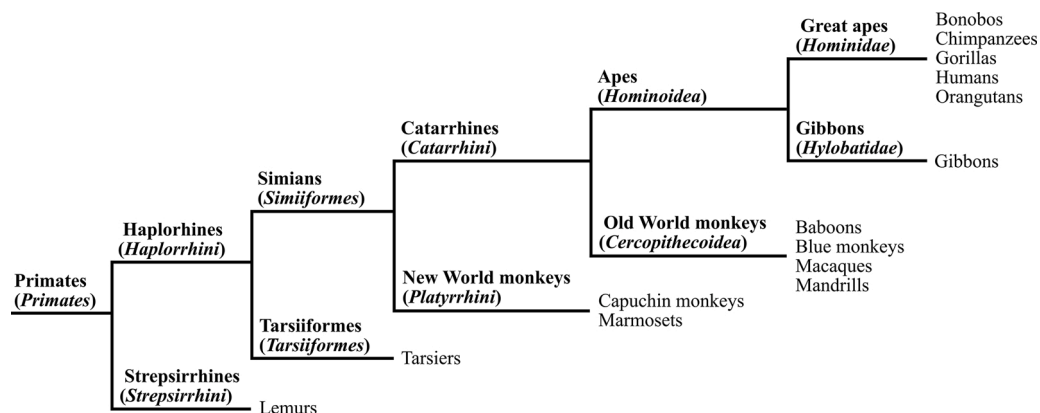


Fig. 1. Schematic overview of primate phylogeny with examples of species.

2. Emotional contagion: recognising emotions through state matching

Emotional contagion is the emotional synchrony between an individual expressing an emotion and the perceiver of that emotion. This process is thought to arise from automatic mimicry (Hatfield et al., 2014, 1994). Automatic mimicry is the phenomenon where emotional expressions automatically elicit identical emotional expressions in the observer of an emotion. It may occur on a motor level (e.g. facial expressions and body movements) and on an autonomic, physiological level (e.g. synchrony of heartbeat rhythm, breathing and pupil size) (Prochazkova and Kret, 2017).

Even in humans, emotions can be recognised automatically with little involvement of cognitive processes (Lima et al., 2019). According to Perception-Action Model by Preston and de Waal (2002), perceiving emotional expressions automatically activates internal representations of the same emotion, leading to a shared emotional experience. The Neurocognitive Model of Emotional Contagion by Prochazkova and Kret (2017) elaborates on this view. In this model, the perception of both motor and physiological expressions of emotion in another individual activates neural representations of this emotion (also termed neural resonance, e.g. Anders et al., 2011), which in turn lead to automatic mimicry. Through both physiological and motor feedback, this mimicry can help to induce an emotional experience in the perceiver.

Mimicry does not always necessarily lead to a transmittance of the underlying emotion. It has been suggested that mimicry can be seen as an evolutionary 'building block' for emotional contagion (Davila-Ross et al., 2008) and automatic mimicry on multiple levels can lead to convergence of the emotional experience (Kret, 2015; Prochazkova and Kret, 2017).

In this section, we review experimental evidence of different types of automatic mimicry in primates. We discuss to what extent these findings implicate the convergence of emotions and if so, to what extent emotional contagion enables primates to recognise the emotional expressions of others.

2.1. Facial mimicry

We start our discussion of emotional contagion with evidence for facial mimicry in different primate species. Facial mimicry is the process where facial emotional expressions induce identical expressions in an observer. A distinction is made between relatively slow voluntary facial mimicry and rapid facial mimicry, which occurs within one second and is considered an elementary and unconscious mechanism (Hatfield et al., 1993). Since emotional contagion does not involve conscious processing of the emotion (e.g. Tamietto et al., 2009; see also the review by Palagi et al., 2020, published in the current special issue), we are mostly interested in experimental evidence of involuntary, rapid facial mimicry

in primates.

Convincing evidence of rapid facial mimicry in primates has been found in Bornean orangutans (*Pongo pygmaeus*) (Davila-Ross et al., 2008). When play bouts of 31 captive orangutans were analysed, they were found to mimic each other's open mouth displays, an expression associated with positive emotion. This happened rapidly, within one second, indicating that this mimicry resulted from an unconscious and involuntary process. However, nine orangutans did not show rapid facial mimicry of their playmate's open mouth displays. The authors propose the influence of socio-emotional factors such as familiarity and social closeness as possible explanations for these individual differences, but these variables were not included in their analysis. Alternatively, the lack of facial mimicry in some individuals could imply that orangutans do not rely heavily on communication through facial expressions. Forests are orangutans' primary habitat (Cawthon Lang, 2005) and since the environment in which primate species have evolved may have affected the modalities of their emotional communication (Fröhlich and van Schaik, 2018), we may speculate that orangutans rely more on emotional expression through for example vocalisations or larger gestures such as scratching (e.g. Laméris et al., 2020).

Rapid facial mimicry has also been reported in gelada baboons (*Theropithecus gelada*), an Old World monkey species (Mancini et al., 2013a, b). Observations of play bouts in a group of captive geladas revealed that both immature (one month–four years old) and adult individuals mimicked play faces of their playmates. Also, the highest levels of rapid facial mimicry and the fastest responses were found between infants and their mothers, as compared to infants with other individuals. The latter finding may suggest that facial mimicry and contagious emotions are facilitated by social closeness. However, the authors did not explicitly control for visual attention, an important possible confound in determining the social factors influencing motor mimicry (Massen and Gallup, 2017).

Scopa and Palagi (2016) investigated and compared rapid facial mimicry between two different macaque species: the socially tolerant Tonkean macaque (*Macaca tonkeana*) and the relatively intolerant Japanese macaque (*Macaca fuscata*). Interestingly, only Tonkean macaques were found to mimic play faces during social play. In this species, play sessions accompanied by facial mimicry also had a longer duration than play sessions without facial mimicry. Possibly, the social nature of Tonkean macaques favours rapid facial mimicry, which in turn improves emotional communication and cooperation between conspecifics. This type of feedback loop appears to be absent in the less tolerant Japanese macaques. The difference in facial mimicry between closely related species reported in this study highlights the importance of comparative research between different species within one taxon.

Altogether, studies on facial mimicry provide initial evidence for the presence of motor mimicry of emotions in catarrhines. However, studies investigating facial mimicry in primates mainly focused on the play face, and the mimicry of different facial expressions such as fearful or angry displays has yet to be investigated. Also, a systematic comparison of facial mimicry between different primate species, including New World monkeys, is necessary. The evidence so far is limited. We learned that even within-taxon differences in social tolerance may have an influence on facial mimicry, emphasising the need for comparative inter-species studies to provide a better evolutionary account of facial mimicry in relation to emotional contagion.

2.2. Contagious yawning: a special case of motor mimicry

A type of behaviour that is remarkably contagious in many species is yawning. The function of yawning is a highly debated topic, with proposed explanations ranging from the communication of boredom (Guggisberg et al., 2010) to cooling the brain by changing the blood temperature (Gallup and Gallup, 2007). Even though yawning may not come across as emotional behaviour at first sight, yawning has been associated with distress and arousal in primates (Maestripieri et al.,

1992; Troisi, 2002). For example, chimpanzees tend to yawn after perceiving vocalisations in neighbouring groups, a situation that often leads to anxiety (Baker and Aureli, 1997). The emotional and/or empathic nature of contagious yawning is subject to debate (for a recent review, see Massen and Gallup, 2017). Regardless of its exact relation to emotion, contagious yawning is an obvious and reflexive type of motor mimicry and therefore informative of evolutionary basic forms of contagious emotional facial expressions.

Various studies have examined contagious yawning in primates, either in observational settings where yawns in response to perceived yawns of group members were scored (Baenninger, 1987; Demuru and Palagi, 2012; Laméris et al., 2020; Massen et al., 2016; Massen et al., 2012; Palagi et al., 2019; Palagi et al., 2009; Palagi et al., 2014a), or in experimental setups where contagious yawning was tested in response to video stimuli of conspecifics (Amici et al., 2014; Anderson et al., 2004; Campbell et al., 2009; Campbell and de Waal, 2011; 2014; Massen et al., 2012; Palagi et al., 2019; Paukner and Anderson, 2006; Reddy et al., 2016; Stevens et al., 2017; Tan et al., 2017; van Berlo et al., 2020) or in response to a human demonstrator (Amici et al., 2014; Madsen et al., 2013).

With respect to great apes, most evidence has been collected in chimpanzees (*Pan troglodytes*) (Anderson et al., 2004; Campbell et al., 2009; Campbell and de Waal, 2011; 2014; Massen et al., 2012; Madsen et al., 2013). As far as we know, there are no studies that report overall null-findings in chimpanzees, apart from some individual differences. In bonobos (*Pan paniscus*), one study failed to find contagious yawning (Stevens et al., 2017), but convincing evidence for this phenomenon in bonobos was found in studies including larger samples (Demuru and Palagi, 2012; Palagi et al., 2014b; Tan et al., 2017). In a recent study, evidence was found for contagious yawning in Bornean orangutans (*Pongo pygmaeus*) (van Berlo et al., 2020). In contrast to the findings for chimpanzees, bonobos and orangutans, a study in Western gorillas (*Gorilla gorilla*) failed to find contagious yawning in this species (Palagi et al., 2019). Interestingly, the only study so far that directly compared contagious yawning between four ape species (Amici et al., 2014) also found contagious yawning in response to videos of yawning conspecifics in chimpanzees, but not in bonobos, Western gorillas or Sumatran orangutans (*Pongo abelii*). We must note that the sample size for chimpanzees was also larger than for the other three species (for further details on sample sizes see the Appendix).

Less is known about contagious yawning in monkeys. An early study failed to find contagious yawning in mandrills (*Papio sphinx*), an Old World monkey species (Baenninger, 1987), but in later studies, contagious yawning has been reported in stump-tailed macaques (*Macaca arctoides*) (Paukner and Anderson, 2006) and in gelada baboons (Palagi et al., 2009). Moving even further away from humans in the primate phylogeny, a recent study examined contagious yawning in common marmosets (*Callithrix jacchus*), a New World monkey species, but did not find contagious yawning because of the scarcity of yawn observations (Massen et al., 2016).

Finally, contagious yawning has been studied in two species of lemurs (*Varecia rubra* and *Lemur catta*), belonging to the strepsirrhine primates. Despite extensive study in individual and group settings, contagious yawning in response to video stimuli was not found for these species, even though the lemurs were shown to be able to understand emotional video content (Reddy et al., 2016).

Together, the findings on contagious yawning in primates give a far from conclusive image on the evolutionary development of this phenomenon. Whereas chimpanzees, bonobos and orangutans as well as some monkey species appear to yawn contagiously, initial evidence points toward an absence of this behaviour in gorillas. Possibly, contagious yawning evolved in an analogous, rather than a homologous way, meaning that species from different taxa evolved this capacity independently from each other. This is supported by the finding that contagious yawning also evolved in budgerigars (*Melopsittacus undulatus*) (Miller et al., 2012) and dogs (*Canis lupus familiaris*) (Madsen and

Persson, 2013), species evolutionary distant from primates. Possibly, the most social of the social species show this behaviour (but see van Berlo et al., 2021 for evidence in orangutans). Clearly, more comparative research on contagious yawning in primates is needed before we can draw firm conclusions about its evolutionary path (Massen and Gallup, 2017).

Studies on contagious yawning in primates have revealed interesting parallels between different species. In a study with gelada baboons, contagious yawning appeared to be affected by social closeness. Individuals that groomed each other tended to show more contagious yawning (Palagi et al., 2009). This is in accordance with findings in chimpanzees yawning more in response to videos of familiar conspecifics than to unfamiliar individuals (Campbell and de Waal, 2011). However, a follow-up study did not support the influence of social closeness of contagious yawning in chimpanzees (Campbell and de Waal, 2014). Contagious yawning was equally frequent in response to familiar and unfamiliar humans and in-group conspecifics, even though it did not occur in response to videos of yawning gelada baboons, a species they were not familiar with. Cross-species contagious yawning in chimpanzees was further demonstrated in another study in response to human yawns (Madsen et al., 2013). Also, research investigating the factors influencing contagious yawning in chimpanzees did not find any effect of relationship quality (Massen et al., 2012). Instead, in this latter study a sex effect was observed, with male yawns being more contagious than female yawns. Possibly, instead of social bonding, dominance and influence (usually higher in chimpanzee males) stimulate yawn contagion. A sex effect was also found in bonobos: female yawns were demonstrated to be more contagious than male yawns (Demuru and Palagi, 2012). As females are the dominant sex in bonobos, this parallels with the findings in chimpanzees. Interestingly, socially bonded bonobos were also observed to show more contagious yawning (Demuru and Palagi, 2012; Palagi et al., 2014a) but an experimental examination of the influence of social closeness on contagious yawning in bonobos found no support for this suggestion (Tan et al., 2017).

In addition to social and sexual biases, an interesting finding is that contagious yawning in both chimpanzees (Anderson et al., 2004; Madsen et al., 2013) and gelada baboons (Palagi et al., 2009), just as in humans, is not present from birth but develops later in life. It should be noted that the target stimuli in one study (Madsen et al., 2013) were not chimpanzees but human models, which possibly influenced the likelihood of yawn contagion. Ontogenetic differences may suggest that yawn contagion requires more cognitive resources than other instances of motor mimicry such as facial mimicry.

A final remarkable observation is that in both stump-tailed macaques (Paukner and Anderson, 2006) and gorillas (Palagi et al., 2019), yawning was accompanied by increased levels of stress-related self-directed behaviour such as scratching. This could be explained by distress caused by the visibility of canine teeth in the yawning conspecifics (Paukner and Anderson, 2006). It is also possible that the observing individuals contagiously experienced the same emotional arousal that is associated with yawning (Maestriperi et al., 1992). From this perspective, the scratching that accompanied the contagious yawning seems to support the relation between contagious yawning and emotional contagion, as it illustrates transference of the negative emotional state. In the next section, we discuss contagious scratching in more detail.

2.3. Contagious scratching: another possible indicator for emotional contagion?

Scratching is a form of self-directed behaviour that is usually driven by the sensation of itch. Itch serves as a signal of possibly harmful stimuli to the skin and is common in many species (Sanders et al., 2019). Scratching can be contagious and this is thought to have the evolutionary benefit of profiting from others' danger signals (Sanders et al., 2019). In primates, scratching is associated with a negative emotional

state (Maestriperi et al., 1992; Palagi and Norscia, 2011; Troisi, 2002). Interestingly, contagious scratching adds a focus on bodily expressions to our discussion of emotional contagion. Also, scratching may have an auditory component which can have an advantage in certain habitats where the visual transmission of emotional expressions is limited.

Japanese macaques have been found to scratch themselves more when they observe a target monkey scratching in response to a potentially alarming situation (i.e. the presence of a strange monkey) (Nakayama, 2004). The possibility that the increased scratching in the observing monkeys was caused by the presence of the strange monkey was ruled out in this study by having the target monkey observe the stranger through a peephole. The scratching was not caused by vocalisations of conspecifics either, because no contagious scratching was found when the observers' view on the target monkey was occluded. Even though the sample size in this study was rather small (four observing monkeys), all observing monkeys scratched contagiously, suggesting that negative emotions in this species can be transferred through the synchrony of scratching behaviour.

This was further supported by two experiments in rhesus macaques (*Macaca mulatta*) (Feneran et al., 2013). In the first experiment, the authors observed scratching behaviour of pair-housed rhesus macaques. They found that the monkeys started scratching when their cage mates scratched. In the second experiment, subjects observed videos of scratching conspecifics. Scratching behaviour was significantly more frequent during scratching videos than in response to neutral videos or images, indicating that also video stimuli can evoke contagious emotions in rhesus macaques.

In contrast with these findings, when six Barbary macaques (*Macaca sylvanus*) were presented with videos of scratching conspecifics, their attention toward scratching behaviour increased, as compared to neutral behaviour, but they did not increase their own scratching (Whitehouse et al., 2016). The authors explain this lack of contagious scratching as compared to the presence in rhesus and Japanese macaques (Feneran et al., 2013; Nakayama, 2004) as an indication that Barbary macaques differ from other macaques with respect to their social capacities. They are thought not to passively copy the negative emotion, but instead to perceive it as information which can be used to form an appropriate response. This is an interesting hypothesis, because it would reflect a more cognitively advanced response to emotions of others resembling cognitive empathy: understanding the meaning of the emotions of others without copying them – a topic we will discuss later. However, the study does not provide any evidence that the Barbary macaques showed an understanding of the emotions related to scratching. Alternatively, the lack of contagious scratching in Barbary macaques can be explained by the use of video stimuli, rather than natural observations. This is however unlikely, given previous results obtained with video stimuli in rhesus macaques (Feneran et al., 2013). It remains to be tested further to what extent this socially tolerant macaque species is capable of more complex cognitive processing of emotions.

Contagious scratching in apes has only been addressed recently in great apes (Laméris et al., 2020). Observations revealed that Bornean orangutans showed more scratching behaviour when they saw conspecifics scratching, compared to baseline. To a lesser extent, this effect also occurred when the apes only heard their group mates scratch. Interestingly, scratch contagion occurred more between low-quality bonded individuals, which is in contrast to findings that social closeness promotes different kinds of contagious behaviours in some primate species (Campbell and de Waal, 2011; Palagi et al., 2009; Mancini et al., 2013a, 2013b; Demuru and Palagi, 2012; Palagi et al., 2014b). Very little is known about emotional contagion in orangutans, but these preliminary results seem to suggest contagion of emotional expressions at work in this semi-solitary living ape species. This is especially interesting because of their evolutionary environment, which is rich in vegetation (Cawthon Lang, 2005) and may therefore select for more obvious bodily emotional communication over and beyond subtle facial expressions.

All in all, contagious scratching is an interesting topic for future research on emotional contagion, because of the emotional nature of scratching behaviour and the fact that it involves larger bodily movements than facial expressions. So far, contagious scratching has been demonstrated in some monkey species (Nakayama, 2004; Feneran et al., 2013) and in orangutans (Lam  ris et al., 2020), but also appeared to be absent in one macaque species (Whitehouse et al., 2016). More research, especially in apes and New World monkeys, is needed to examine whether scratching is contagious in all primates, and which factors determine its contagion.

2.4. Physiological responses to emotional stimuli

In the previous sections we have considered motor mimicry and behavioural contagion. In research on emotional contagion it is however important to investigate whether, besides the emotional expression, the underlying emotional state is also transferred to the observer. Considering emotional contagion as a multilevel phenomenon comprising both motor and autonomous synchrony (Hatfield et al., 1994; Prochazkova and Kret, 2017), assessing whether contagion occurs at the level of physiological arousal is an important addition to research on motor mimicry. A physiological response to an emotional display of a conspecific may indicate that this emotion induces signs of emotion in the perceiver, which is an indication of a contagiously experienced emotion. In this section, we review evidence from physiological experiments on emotion perception in primates.

Various physiological measures of emotion have been used in primates (e.g. heart rate, Berntson and Boysen, 1989; and skin conductance, Laine et al., 2009). However, these measurements require highly controlled lab environments and allow for little movement by the subject, which creates an unnatural (Dezecache et al., 2017) and possibly stressful situation for the animals.

A promising, non-invasive way to measure the contagion of physiological arousal is the measurement of pupil mimicry. Pupil dilation is an involuntary, autonomous response associated with increased attention and arousal (Bradley et al., 2008). Pupil mimicry is paired with activity in social brain regions (Prochazkova et al., 2018). Chimpanzees as well as humans have been found to mimic each other's pupil-size (Kret et al., 2014). Subjects from both species observed videos of human and chimpanzee eyes in which the pupils either dilated or constricted. Both humans' and chimpanzees' pupils dilated more when they observed a member of their own species with dilating pupils, as compared to constricting pupils. However, the chimpanzee sample size was small, as were the effects.

Another important contribution to the study of emotion in primates is the ability to measure emotional responses contact-free by using infrared thermography. Nakayama et al., 2005 were the first to use this technique in primates. The authors measured facial skin temperature in rhesus macaques in response to a human demonstrator, dressed in a lab coat and holding a catching net to look threatening. A decrease in nasal skin temperature was found as compared to a baseline period, accompanied by other behaviours that reflect a negative emotional state. In a second study, rhesus macaques were presented with videos of different emotional expressions (Kuraoka and Nakamura, 2011). Nasal skin temperature decreased in response to expressions of aggressive threat and screams, as opposed to coos (a neutral expression). The authors also reported that combined audio-visual stimuli evoked a larger drop in nasal skin temperature than auditory and visual stimuli alone.

The thermo-imaging technique has also been used to measure emotional responding in chimpanzees (Kano et al., 2016). When chimpanzees were presented with sounds and videos of fighting conspecifics, their nasal skin temperature decreased in response to these stimuli, in contrast to control sounds of allospecific display calls and videos of resting conspecifics. This drop in nasal skin temperature also related to changes in behaviour and in heart rate variability, confirming activity of the sympathetic nervous system. Infrared thermography has also been

used to measure emotional states in wild chimpanzees (Dezecache et al., 2017). Nasal temperature was found to decrease in response to aversive calls such as screams and out-group pant hoots, associated with distress, but not in response to neutral vocalisations such as resting and travel vocalisations. Temperature in the ear region did not change significantly during aversive vocalisations but increased during non-aversive vocalisations, which indicates that different body parts have different responses in response to emotional signals. Altogether, both rhesus macaques and chimpanzees appear to have measurable changes in facial temperature in response to emotional stimuli and importantly, in response to emotional expressions of conspecifics. These findings emphasise the possibilities for thermo-imaging as a physiological measure of emotional contagion in primates.

However, a problem with these initial thermo-imaging studies for emotional contagion research is that it is often not clear whether the emotional responses originate from contagious processes, or from the subject's own fear evoked by the stimuli used. For example, when chimpanzees were presented with playback fights of conspecifics (Kano et al., 2016), it is likely that their fear response was evoked by the risk and danger associated with these scenes, rather than with contagious emotions evoked by the emotions of the chimpanzees in the videos. The same applies to the studies that used aggressive vocalisations (Dezecache et al., 2017; Kuraoka and Nakamura, 2011), which are associated with stressful situations and personal risk. On a sidenote, in studies with humans it is also often difficult to pull these two apart.

Experiments specifically addressing the synchrony of physiological arousal between observer and demonstrator (or video stimulus), such as studies on pupil mimicry (Kret et al., 2014), lack this confound. Many physiological displays of emotion are involuntary (e.g. blushing, breathing) and may therefore be studied without interference of a more conscious evaluation of the valence of the stimulus (Kret et al., 2020, this issue).

Another way to address this issue is to design experiments with conditions containing emotional stimuli such as predators and aversive out-group vocalisations, as well as conditions with emotional expressions from conspecifics in response to these stimuli. If emotional responding is tested in both conditions, we might be able to distinguish responses to emotional situations from contagiously experienced emotions.

One study using different stimulus conditions indeed found a possible indication for contagious processes underlying physiological responding (Parr, 2001). Skin temperature was measured in chimpanzees with a temperature transducer on their left hand while they were presented with different videos. When chimpanzees watched videos of conspecifics being injected with darts and needles, their skin temperature dropped. Interestingly, their skin temperature did not decrease in response to scenes of conspecifics displaying general agonism. This possibly indicates that the decrease in skin temperature was caused by empathic processes: the chimpanzees felt the arousal associated with the injection with needles, even though they were not injected themselves. It is possible that this drop in skin temperature was not found in response to agonistic displays because the observation of pain evoked a strong contagious response, whereas the agonistic videos did not.

In conclusion, contact-free physiological methods such as thermo-imaging and measures of pupil dilation are a useful tool in the study of emotional contagion. However, this field needs more research focused on the synchrony of autonomous responses. It should also be noted that, apart from assumed associations between certain types of physiological arousal and negative affect (e.g. decreased skin temperature; Parr, 2001), many physiological measures are currently unable to index exact emotional valence. Furthermore, studies should separate emotionally contagious expressions from responses of fear of the situation displayed in the stimuli. Lastly and importantly, because the presence of one type of mimicry may not be the same as emotional contagion (Prochazkova and Kret, 2017), a combination of measures of autonomous and motor responses is needed to be able to conclude whether a perceived emotion

is actually internalised through emotional contagion.

2.5. Manipulating mimicry: does emotional contagion facilitate emotion recognition?

So far, we have discussed how a combination of contagious expressions and synchronised emotional arousal can point toward emotional contagion: matching of the emotional state. Importantly, this review aims to address emotional contagion as one of the mechanisms underlying emotion recognition. We defined emotion recognition as the formation of an internal representation of the emotion of another individual. When an emotion is experienced contagiously, one may argue that the emotion is internally encoded in the perceiver of the emotion and therefore recognised. But, reasoning the other way around, how do we know that when an individual recognises a perceived emotion, emotional contagion is the (only) mechanism at play? To investigate whether emotional contagion underlies emotion recognition in a certain animal in a certain situation, it would be interesting to manipulate individuals' access to emotional contagion and then test their emotion recognition. This could provide insight into which primates rely on emotional contagion for their emotion recognition and to what extent.

In this section we discuss several experimental methods that test primates' ability to recognise emotional expressions. These methods could be extended with ways to physically manipulate the ability to mimic emotional expressions. For example, facial mimicry could be blocked by having the subject drink through a plastic straw. Also, contagious behaviours such as scratching could be prevented by giving the subjects a task with their limbs (e.g. holding something). This compares to emotion recognition research in humans when mimicry is prevented by for example Botox (Neal and Chartrand, 2011), biting on a pen or chewing gum (e.g. Oberman et al., 2007; Borgomaneri et al., 2020; but see Wagenmakers et al., 2016) or using a pacifier (Niedenthal et al., 2012). A second option would be to manipulate individuals' baseline emotion and then test whether this affects their emotion recognition. A similar approach was adopted in a study in humans where subjects performed an emotion detection task after their emotional state was manipulated using videos and sounds. It was found that participants' mood facilitated the detection from one emotional expression to another (Niedenthal et al., 2001).

It is important to mention that the findings from studies on emotion discrimination discussed below could be the result of various emotion recognition mechanisms. The designs of these studies lend themselves to adaptation in order to test emotional contagion and are therefore discussed at this point. However, it should be clear that also other mechanisms, such as cognitive empathy, could underlie these findings (see Section 3.1).

Simple experimental paradigms to test emotion recognition in primates have been used in several studies. In one of the first studies on emotion recognition in primates (Dittrich, 1990), longtailed macaques (*Macaca fascicularis*) were trained to discriminate a target facial expression ('slandering with grunt') from three simultaneously presented line drawings of other emotional expressions. The monkeys quickly learned to do so, regardless of colour, rotation, brightness and size. Interestingly, the dominant longtailed macaques performed better than the subdominant ones, implying that there might be individual differences in monkeys' emotion recognition capabilities.

Later designs focused on primates' discrimination of more than one emotional expression. A useful experimental procedure to test the discrimination of different emotional expressions is the matching-to-sample paradigm. In this task, the animal first sees a sample stimulus and then two stimuli: one with identical features to the sample and one distractor. The task is to select the correct match to the sample stimulus. When this task was used to study the recognition of facial expressions in four Japanese macaques, only one of the monkeys was able to match both monkey and human facial expressions correctly (Kanazawa, 1996),

again emphasising individual differences between members of the same species.

Using the same paradigm, rhesus macaques were found to be able to match facial expressions if the sample image was identical to the target image (Parr and Heintz, 2009). However, when the same expressions of different individuals had to be matched, performance was only above chance when the distractor was a neutral expression rather than an expression of another emotion. In contrast, Micheletta et al. (2015) conducted two experiments with crested macaques (*Macaca nigra*). Although their sample size was smaller (see Appendix), they found that these monkeys were able to categorise facial expressions regardless of the identity of the individual, suggesting differences between species. They were able to match a sample facial expression to an expression in a different subject and could also do so with dynamic video stimuli of facial expressions.

The matching-to-sample paradigm was also applied to chimpanzees, who appeared to be able to discriminate the bared-teeth display, hoot face, relaxed open mouth face and scream face, but not the relaxed-lip face from neutral faces (Parr et al., 1998). In a different study, chimpanzees learned to match computer-animated facial expressions of conspecifics correctly (Parr et al., 2008) and were shown to discriminate auditory expression stimuli as well (Parr, 2004).

Recently, a different paradigm has been used to test emotion recognition in capuchin monkeys (*Sapajus apella*), a New World monkey species (Calcutt et al., 2017). The authors used an oddity paradigm, in which the monkeys were presented with four different expressions and had to choose 'the odd one out'. The monkeys performed above chance in discriminating emotional expressions from neutral expressions, even when the neutral stimuli had different degrees of mouth opening, which was expected to complicate the discrimination of agonistic expressions.

The putative link between emotion recognition and emotional contagion has not been tested directly yet. Combining paradigms such as the matching-to-sample task and the oddity paradigm with manipulations to block mimicry and comparing performance between conditions with and without manipulation may provide insight into whether emotional contagion is at play. However, on a critical note, these paradigms may have a higher cognitive load than the automatic recognition of emotions in natural circumstances. An inevitable requirement for computer experiments with primates is that the animals are trained to interact with a screen. Also, these tasks require an active choice between several (images of) emotions. In the matching-to-sample task, subjects even need to remember an emotional stimulus during a short interval, rather than immediately acting upon a seen emotion, a problem that is absent in the oddity paradigm. The complexity of these tasks may be reflected in the above discussed differences in performance in the primates tested. Ideally, emotion recognition tasks used to determine underlying mechanisms should require as little cognitive effort as possible.

2.6. Discussion and recommendations for future research

2.6.1. The evolution of emotional contagion

Because emotional processes do not leave fossil records, different primate species need to be compared to study the evolutionary history of emotional contagion. Emotional contagion is considered an evolutionary early mechanism (de Waal, 2008; Preston and de Waal, 2002). Basic contagious processes appear to be present in both apes and Old World monkeys, as rapid facial mimicry and contagious scratching have been demonstrated in different catarrhine species. To our knowledge, no research has been conducted in New World monkeys and strepsirrhine species with respect to mimicry and contagious scratching. This gap in the literature raises the question whether these contagious processes emerged in the common forefathers of apes and Old World monkeys, or whether these mechanisms were already present before New World monkeys and strepsirrhines split off.

The picture for contagious yawning is even more inconsistent. Some ape species and some Old World monkey species show this behavioural

phenomenon, whereas other apes (gorillas) and strepsirrhine species (lemurs) do not. These results in combination with results for other mammals and birds led [Massen and Gallup \(2017\)](#) to suggest that contagious yawning might have evolved independently in different lineages, that is, by analogous evolution.

To be able to draw conclusions on the evolution of emotional contagion, and the question whether analogous evolution may possibly underlie this mechanism, there is a need for more comparative research and replications of studies on contagious behaviours. More research is needed in all primate species, but especially in New World monkeys, strepsirrhines and apes other than chimpanzees.

2.6.2. Differences within taxonomic groups

Even though it is highly relevant to study general social and emotional differences between different primate lineages, there may also be interesting variation within species in these taxa. For example, there are many different macaque species, some of which differ in their social characteristics. [Scopa and Palagi \(2016\)](#) noted that Japanese macaques and Tonkean macaques largely differ with respect to their social tolerance. Their finding that Tonkean macaques rapidly mimic each other's facial expressions whereas Japanese macaques do not, indicates that social and cognitive differences between closely related species should not be ignored in primate emotion research.

In line with this finding, we saw that monkeys of the socially tolerant Barbary macaque species do not appear to scratch contagiously ([Whitehouse et al., 2016](#)) whereas the more despotic rhesus and Japanese macaques do ([Feneran et al., 2013](#); [Nakayama, 2004](#)). The explanation for this difference is still unclear, as it could be due to interspecific differences in emotion processing or to methodological considerations. Before we can draw any conclusions on this matter, more research on interspecific differences between closely related but socially different species is needed.

Also in apes we may expect differences between species. The majority of research has been conducted with chimpanzees. However, orangutans, for example, have different living environments and do not live in large groups, as chimpanzees do. Also gorillas are known to have less social affiliations than chimpanzees and bonobos and live in a very different group structure (harem) ([Palagi et al., 2019](#)). Therefore, we might expect differences in their socio-emotional behaviour. For example, there is no evidence so far of contagious yawning in gorillas (thus far the only study investigating this reported an absence of contagious yawning in this species; [Amici et al., 2014](#)). Interestingly, orangutans do appear to show contagious yawning, contagious scratching and facial mimicry. To further study the influence of social differences between ape species on contagious expressions of emotion, studies comparing different ape species, such as the [Amici et al. \(2014\)](#) study, are worthwhile and highly recommended.

2.6.3. How 'low-level' is emotional contagion?

An important conclusion that can be drawn from studies on emotional expression in primates is that its contagion can be influenced by various psychological and social factors. Synchrony of expressions may depend on age, social relations and sex. This is in accordance with the description of emotional contagion by [Hatfield et al. \(1994\)](#) as a multi-faceted process, combining many different factors, rather than an uncontrollable, automatic mechanism.

For example, contagious yawning was found in adult gelada baboons, but not in infant or subadult baboons ([Palagi et al., 2009](#)). Also infant chimpanzees were not observed to show contagious yawning ([Anderson et al., 2004](#); [Madsen et al., 2013](#)) but juveniles (five–eight years old) did yawn contagiously ([Madsen et al., 2013](#)). A possible explanation for the lack of yawn contagion in infant primates, which is also reported for human infants under five years old ([Anderson and Meno, 2003](#)), is that their social and cognitive skills are immature ([Palagi et al., 2009](#)). This hypothesis implicates that contagious yawning requires social or cognitive resources that are not present from birth and

also that the different developmental trajectories of different primate species should be taken into account when comparing them. The presence of a social component in contagious yawning is also underlined by observations that yawn contagion may be more likely between socially close individuals ([Campbell and de Waal, 2011](#); [Demuru and Palagi, 2012](#); [Norscia and Palagi, 2011](#); [Palagi et al., 2009](#); [Preston and de Waal, 2002](#)) or dependent on the sex (and possibly the position in the dominance hierarchy) of the yawning individual ([Demuru and Palagi, 2012](#); [Massen et al., 2012](#)).

When comparing contagious yawning to facial mimicry and contagious scratching, there appear to be both similarities and differences with respect to the social complexity of the phenomena. [Mancini et al. \(2013a, 2013b\)](#) found that rapid facial mimicry does occur in immature gelada baboons. The same study found an association between mimicry and social closeness. Also [Davila-Ross et al. \(2008\)](#) proposed that familiarity promotes mimicry among orangutans. In contrast, the only study on contagious scratching that addressed social closeness ([Laméris et al., 2020](#)) found the opposite result: increased contagious scratching with low-quality bonding.

Together, these studies show that emotional contagion may be influenced by context. Possibly, the apparent social constraints on contagious yawning and facial mimicry are a result of cognitive inhibition on automatic processes. This could indicate that emotional contagion is not as low-level, uncontrollable and automatic as sometimes assumed. On the other hand, contextual differences in synchronous behaviour could be explained by interfering emotional states, associated with the social context. For example, primates may be more relaxed around close affiliates, resulting in increased mimicry. In the same vein, an increase in contagious scratching may be explained by higher rates of distress around unrelated individuals. To what extent emotional contagion can be subject to cognitive inhibition remains an interesting topic for future research.

2.6.4. Toward studying emotional contagion as a mechanism of emotion recognition

Eventually, we are interested in emotional contagion as a mechanism underlying emotion recognition. We conclude that research on this matter should take into account several factors. First, emotional contagion appears to be a multilevel mechanism. It does not automatically result from mimicry and it is influenced by different social factors. Therefore, studies should combine tests of different types of mimicry with physiological measures to study whether an emotion is indeed internalised by the observer of an expression. For example, studies could examine whether species that yawn contagiously in certain situations also show other signs of contagious emotions (i.e. scratching, mimicry) in those situations and to what extent they have physiological responses that match the emotion of the observed animal.

Second, a causal relation between emotion recognition and emotional contagion needs to be established by combining tests of emotion recognition with experimental manipulations of emotional contagion. Studies so far have only addressed different types of mimicry on the one hand or tests of emotion recognition on the other hand. Only when these are combined we are able to draw conclusions about emotional contagion as an emotion recognition system in primates.

2.6.5. Methodological considerations

Finally, we point out some methodological considerations that follow from the present literature on emotional contagion. First, many studies have demonstrated that contagion of emotional expressions can also occur in response to video stimuli of real or animated conspecifics (e.g. [Campbell and de Waal, 2011](#); [2014](#); [Feneran et al., 2013](#); [Reddy et al., 2016](#)). Compared to natural observations, the use of video presentation offers an efficient way to test contagious behaviours in various conditions, while for example controlling the amount, frequency and nature (e.g. visibility, type of individual) of the observed expression.

Second, the experimental or observational setting is important. In a

study on yawn contagion in lemurs (Reddy et al., 2016), a first experiment tested contagious yawning in individuals in response to video stimuli. In a second experiment, the videos were presented to the entire group, because the authors postulated that social context might be important for contagious yawning to occur. No contagious yawning was found in this study, but other studies also used a group setting to demonstrate contagious yawning in stump-tailed macaques (Paukner and Anderson, 2006), chimpanzees (Massen et al., 2012) and orangutans (van Berlo et al., 2020). A benefit from observing the group as a whole is the preservation of a natural social context. Also, this method is often-times less stressful for the animal. This could be advantageous in research on other contagious behaviours. On the other hand, individual testing has the advantage that the emotional responses can only be evoked by the video stimulus itself and not by the other group members. Therefore, we recommend to carefully consider which setup to select, and if possible, to include both individual and group conditions.

Also related to the social context, it is important that studies control for visual attention. Attention may have a confounding effect in studies of the influence of social factors on emotional contagion, because when an expression of a certain individual is copied more often, this may simply result from increased attention to that individual (Yoon and Tennie, 2010). This variable was already taken into account in some experimental and observational studies of contagious behaviour (Campbell and de Waal, 2011; Laméris et al., 2020; Nakayama, 2004; Stevens et al., 2017; Whitehouse et al., 2016). A promising experimental method to address this aspect is eye tracking, because of its detailed analysis on where in the visual field the attention of the subject is directed. For observational studies, a measure of looking times toward other individuals as assessed via an ethogram could be used as a control.

Another important consideration is the way that a contagious behaviour is defined. Time windows used for contagious behaviours may vary from 20 s (Baenninger, 1987) to 360 s (Feneran et al., 2013). Also, control conditions differ between studies. Control behaviour to which yawn behaviour is compared may differ from neutral or resting behaviour (Campbell and de Waal, 2011; Campbell and de Waal, 2011, 2014; Massen et al., 2012; Palagi et al., 2009; Reddy et al., 2016; Stevens et al., 2017; Whitehouse et al., 2016) to different facial displays (Anderson et al., 2004; Campbell et al., 2009; Madsen et al., 2013; Paukner and Anderson, 2006) and some studies use a baseline period in which subjects observe no behaviour at all (Amici et al., 2014; Demuru and Palagi, 2012). There is probably no ‘correct’ specification of a contagious yawn or scratch, but researchers should be aware of the different methodological possibilities and explain their decisions with respect to their experimental design.

Furthermore, several findings raise the question whether emotional contagion can occur non-visually. Gelada baboons were found to yawn contagiously in presence of only auditory stimuli (Palagi et al., 2009) and the nasal temperature of chimpanzees dropped in response to aversive calls (Dezecache et al., 2017). Emotional contagion through the vocal modality has also been proposed for other mammals and for birds (Briefer, 2018). Most research on emotional contagion in primates focuses on visual input, but experimental paradigms for testing primates’ ability to differentiate between different vocal and multimodal expressions are ready for use, as shown by Parr (2004), who used a multimodal version of the matching-to-sample paradigm in chimpanzees. More studies combining different sensory modalities could provide answers to the issue whether emotionally contagious processes also work via other sensory systems.

Another consideration is the type of emotion that is investigated. In mimicry research in primates, mostly positive facial expressions related to play have been studied (Davila-Ross et al., 2008; Mancini et al., 2013a, 2013b; Scopa and Palagi 2016). In contrast, in most thermo-imaging research, only physiological responses of fear and distress were measured (e.g. Nakayama et al., 2005; Kano et al., 2013). Because emotional contagion can occur with both positive and negative emotions, it is important to broaden our knowledge on contagious

emotions with research on emotions of different valence. Studies on mimicry of different negative emotions and physiological responses of positive emotions are needed to assess the mechanisms of emotional contagion as a whole.

Lastly, we should be aware of a possible null-bias in research on contagion and mimicry. As Massen and Gallup (2017) also note, the absence of certain behaviours in a species are often not reported, which may complicate conclusions regarding the evolution of emotional contagion in primate species. A related issue is of a more conceptual nature: if a behaviour has been observed in only one or a few individuals (as for contagious yawning in orangutans), we may conclude that their biology is fit to enable this behaviour. On the other hand, in psychology, conclusions are usually drawn based on occurrence in larger samples. This raises the question when we should conclude that a type of behaviour is ‘present’ in a species.

We encourage researchers to be aware of these methodological issues and to study emotion recognition through emotional contagion in different primate species using carefully designed experiments with behavioural as well as physiological measures. In this way, we can come closer to a better understanding of emotional contagion and emotion recognition in primates.

3. Cognitive empathy: understanding the meaning of others’ emotions

A route to emotion recognition that requires more complex cognitive abilities than emotional contagion is cognitive empathy. This mechanism is characterised by the maintenance of a distinction between others’ and own emotions and an understanding of the meaning of the emotion (Preston and de Waal, 2002). It is defined as a form of empathy in which the context is appraised and the cause of the other’s mental state is understood (de Waal, 2008). In other words, an observed emotion is not necessarily copied – as is the case with emotional contagion – but understood. Cognitive empathy can be seen as a cognitive evolutionary extension to emotional contagion (Preston and de Waal, 2002), but is not necessarily reliant on this more automatic mechanism: perceived emotions may be understood independently of whether they are mutually experienced.

A central question in the literature on emotion processing in primates is whether there is a division between apes and monkeys with respect to their understanding of others’ emotions (Clay et al., 2018). Based on observations of third party post-conflict affiliation (or ‘consolation’), observed in apes but not in monkeys, de Waal and Aureli (1996) argued that monkeys are not capable of cognitive empathy. Anecdotes of pro-social behaviour in apes, such as a chimpanzee rescuing an unrelated infant chimpanzee from the water (Goodall, 1986) and a gorilla rescuing a 3-year-old boy who had fallen into her zoo enclosure (de Waal, 1997) served as additional support for this proposal. However, third party post-conflict affiliation has since then also been observed in monkeys (Call et al., 2002; Palagi et al., 2014a) and there may be more similarities on a cognitive level between apes and monkeys than previously thought (Clay et al., 2018). Moreover, the capacity for cognitive empathy in apes has even been questioned (Koski and Sterck, 2010).

In this section, we discuss how experimental studies on emotion recognition in different primate species have contributed to a well-founded view on the evolution of cognitive empathy. We focus on evidence showing that different primates can infer meaning from both visual and vocal emotional expressions and discuss how emotion recognition in cases of contrasting emotions between sender and perceiver may prove to be informative of cognitive empathy as an emotion recognition mechanism.

3.1. Meaningful use of others’ emotional expressions

As discussed in Section 2.5, experimental studies show that different primate species are able to discriminate the different emotions of their

conspecifics. Research with different emotion discrimination tasks has found evidence for the ability to discriminate different facial emotional expressions in chimpanzees (Parr et al., 1998, 2008), longtailed macaques (Dittrich, 1990), Japanese macaques (Kanazawa, 1996), crested macaques (Micheletta et al., 2015), rhesus macaques (Parr and Heintz, 2009) and capuchin monkeys (Calcutt et al., 2017). However, studies showing that primates are able to recognise different emotions do not necessarily provide evidence that they also understand the meaning of these emotions, that is, that they have cognitive empathy.

Besides the discrimination of different facial expressions, another possible indicator for recognition of the emotion is the increase of attention toward emotional expressions. One study used a dot-probe paradigm to investigate whether bonobos have an attentional bias for emotional scenes (Kret et al., 2016). Bonobos responded faster to a dot appearing on a location on the screen at which an emotional scene had just been displayed, than to a dot appearing at the location of a neutral scene. Interestingly, this bias was most obvious for scenes depicting protective and affiliative behaviours, such as sexual behaviours and grooming, rather than stressful scenes. The same paradigm was used in a study in chimpanzees (Kret et al., 2018), but surprisingly, no attentional bias for emotional stimuli was found in this species. Possibly, chimpanzees would show an attentional bias for emotional scenes with more diverse and naturalistic stimuli, but further research is required to examine this.

Even though the dot-probe paradigm provides a simple and non-invasive measure to investigate the salience of different emotional stimuli to primates, it is not fully informative of the extent to which the meaning of the observed emotion is understood. From studies in humans it is known that attention and emotion recognition are tightly linked (e.g. Calvo and Beltrán, 2013) and from this we can assume that, for instance, the bonobos who showed an attentional bias toward emotional scenes in Kret et al. (2016) study also recognised the emotions depicted in the scenes. However, this is important to verify, for example by combining the dot probe paradigm with the matching to sample task, assessing this association.

Interesting cases that possibly indicate an understanding of the meaning of emotional expressions are experimental studies in which primates use the emotions of others for their own goals. When an individual does not only recognise an emotion, but also uses the valence of this emotion as a base for his or her own decisions, this may imply that the underlying meaning of the emotion has been understood. In addition, it is possible that relating an internal state of another individual to potential benefits for oneself entails a certain differentiation between own and other, in other words: the maintenance of a self-other distinction. Although the question to what extent sensible responding to others' emotions reflects true cognitive empathy is open for debate, the findings discussed in the remainder of this section provide relevant evidence for possible building blocks for emotion understanding in apes and monkeys.

Initial evidence for an understanding of emotional meaning in chimpanzees was provided in a study showing chimpanzees' ability to relate facial expressions to emotional meaning in a computer task (Parr, 2001). The chimpanzees were tested in a paradigm similar to the matching-to-sample tasks described in the previous section, but in this case the subjects matched videos with emotional content to emotional facial expressions. Without any training, they were able to match the videos to the correct facial expressions, indicating that they understood the emotional meaning of the facial expressions.

Another study addressed the use of others' emotions in four great ape species (Buttelmann et al., 2009). The authors investigated whether chimpanzees, bonobos, gorillas and Bornean orangutans are able to use human emotional expressions to decide between two food containers. The animals were shown two containers with hidden content, to which an experimenter reacted with different emotional expressions. All four species preferred the container to which the experimenter had reacted positively (which turned out to contain food) to the negative container

(containing wood shavings). To test whether these results were not caused by simple aversion of the negative stimulus, a second experiment was designed in which the correct choice was to select the container associated with the negative expression. In this experiment, both containers contained food. The experimenter first reacted positively to one and negatively to the other container and then the subjects saw him eating something. The ape was to select the negative container, because it was the only container that still contained food. The apes also performed above chance in this counter-intuitive task, indicating that their recognition of the emotional expressions was not based on emotional contagion, but involved an understanding of the meaning of the experimenter's expressions. Also remarkable is the fact that this study provides evidence of cross-species emotion recognition in apes.

With respect to monkeys, two early studies (Miller et al., 1962, 1963) already showed that rhesus macaques are able to use their conspecifics' emotions to respond correctly in a cooperative conditioning paradigm. One monkey perceived a light stimulus associated with an electric shock. A second monkey could observe the first monkey but not the light stimulus. The observing monkeys successfully used the emotional response of the demonstrator monkeys to press a lever and thereby prevent the other monkey from receiving a shock. The monkeys could do this based on audio-visual input, vocal expressions alone (Miller et al., 1962) and visual expressions alone (Miller et al., 1963). Although these early studies provide interesting evidence of goal-directed actions in monkeys based on emotional expressions of conspecifics, we emphasise here that we highly discourage the use of invasive methods in primate research. As we have shown, the central research questions in these studies could also have been investigated in non-invasive experiments.

A third study (Miller et al., 1966) tested rhesus macaques' responsiveness to positive affect. This time, the light stimulus was associated with a food reward. If the monkeys detected a positive emotional expression in their conspecific, they could press a lever to deliver a reward to both the demonstrator monkey and themselves. Only half of the six monkeys pressed the lever in response to positive expressions. The other monkeys showed no response to the observed positive affect. However, we should note that the monkeys were seated in restraint chairs and lightly anesthetised, which may have had considerable effects on their emotional responding.

Even though this research suggests the presence of the ability to recognise the meaning of emotions in a monkey species, the possibility that only emotional contagion is at the base of these responses cannot be ruled out. This hypothesis is supported by an increase in heart rate found when the monkeys watched positive expressions in another monkey (Miller et al., 1966). It is possible that the emotional expressions of the observed monkeys evoked matched emotions in the subject monkeys, which made them press the lever. This could happen without any distinction between self and other.

In more recent studies focusing on the interpretation of others' emotions in monkeys, the emotional expressions used as stimuli were often not directly targeted at the observing monkey, but at other individuals or objects instead. For example, one study found initial evidence that crested macaques use facial expressions of interacting conspecifics to predict the outcome of social interactions (Waller et al., 2016). A crested macaque was presented with videos of social encounters. The facial expressions of the approaching individuals in the last frame were manipulated. Then, the monkey had to select one of two possible social outcomes: grooming (positive) or injury (negative). It was found that both positive and negative expressions were associated with more friendly outcomes, whereas negative outcomes were selected for scenes with neutral expressions. Although not in line with the prediction that a negative outcome would be selected for negative expressions, these results show that monkeys can make different predictions based on the facial expressions of their conspecifics. This reflects an understanding of the implications of facial expressions for future situations.

Additional evidence for the understanding of the meaning of

emotional expressions has been found in longtailed macaques (Goossens et al., 2008). Longtailed macaques appear to be able to use information from human facial expressions to find relevant stimuli in their environment. The monkeys followed the experimenter's gaze more often when the experimenter had an emotional facial expression than when the experimenter had a neutral or meaningless facial expression. This suggests that even in a cross-species paradigm, monkeys consider emotional expressions as a relevant indicator for environmental stimuli. Also, they appear to understand that the other has an emotion directed to an object that they are not yet aware of themselves.

Morimoto and Fujita (2011, 2012) tested whether capuchin monkeys could use the meaning of others' emotional expressions correctly. Experiments similar to those conducted with chimpanzees (Buttelmann et al., 2009) were applied to capuchin monkeys, but with another monkey rather than a human as demonstrator. The monkeys reached more toward a container that was reacted to with positive emotional expressions (i.e. forehead raise displays) than with negative expressions (i.e. bared-teeth displays) (Morimoto and Fujita, 2011). These results suggest that capuchin monkeys can use the meaning of others' emotional expressions to guide their own behaviour. Results from a follow-up study (Morimoto and Fujita, 2012) indicated even more clearly that monkeys connected the emotional valence of their conspecifics' expressions to an external object. In this study, subjects were to choose between two containers, one of which was opened toward a demonstrator monkey to react to. This container could contain positive, negative or neutral content. Subjects avoided the container that was negatively reacted to and preferred the container associated with positive or neutral expressions of the demonstrator monkey. Interestingly, the frequency of agonistic vocalisations had the largest influence on the subjects' choices. This possibly demonstrates the relevance of vocal emotional expressions in this species. It may also indicate that aggressive emotional expressions are specifically salient, which is in line with the suggestion that different emotions may have different levels of salience in a certain species (Kret et al., 2016).

These two studies suggest that capuchin monkeys are capable of understanding the meaning of emotional expressions of others. Even though the possibility that the monkeys still relied on emotional contagion for this task (by associating their own emotional experience with the containers) is not completely ruled out, there are indications that this is an unlikely explanation. Firstly, there was no observable increase in emotional expressions such as forehead raise or vocalisations in the observing monkeys, which would have been expected if they contagiously experienced the emotions of the demonstrator. Secondly, relating the valence of others' emotional expressions to objects and using this information to select the appropriate object appears more complex than mere emotional contagion, as the direction of the emotion was understood and this information could even be applied in goal-directed behaviour.

Finally, also common marmosets appear to be able to use their conspecifics' emotional expressions to select appropriate behaviour. A study recorded the time that marmosets spent near a food bowl located in front of a video that displayed cage mates with fearful expressions or positive expressions (Kemp and Kaplan, 2013). The marmosets were found to spend less time near the food bowl when a fearful facial stimulus was shown than when a positive expression was displayed. Apparently, the marmosets used the valence of the facial expression to determine whether the food was attractive or not. This adds evidence to the findings that also monkeys are able to infer meaning from emotional expressions that can be used for personal goals.

All in all, several studies show that monkeys are able to extract meaning from their conspecifics' expressions, and sometimes even from humans' facial displays. The studies described above have in common that inferences from emotional expressions are made about external objects (e.g. food containers) or situations in the future (e.g. outcomes of social scenes). These are both novel concepts that the individuals are not yet attending to, and about which they gain more knowledge by

interpreting others' emotions. Apes (Buttelmann et al., 2009; Parr, 2001), Old World monkeys (Goossens et al., 2008; Waller et al., 2016) and New World monkeys (Kemp and Kaplan, 2013; Morimoto and Fujita, 2011; 2012) have been shown to have this kind of understanding, suggesting that already early in primate evolution, understanding of others' emotions emerged.

It is however important to note that not in all studies the possible role of emotional contagion was explicitly addressed, as was done in the hidden object task with capuchin monkeys (Morimoto and Fujita, 2011, 2012). In order to really examine whether the building blocks for cognitive empathy are present in monkeys, studies should complement their tests for understanding of emotional meaning with measures for emotional contagion.

3.2. Evidence from the vocal domain

In some of the studies discussed above, we saw that vocal expressions can be meaningful indicators of emotion. For example, rhesus macaques can use fearful vocalisations of a conspecific to anticipate an electric shock (Miller et al., 1962) and emotional vocalisations of a demonstrator monkey influenced an observing capuchin monkeys' choice of one of two containers with hidden content (Morimoto and Fujita, 2012). The majority of studies in primate emotion research focuses on facial expressions, but especially for species that live in environments with rich vegetation, it is more likely that part of the emotional communication occurs through the vocal modality as well (Fröhlich and van Schaik, 2018; for a review on great apes and humans, see Kret et al., 2020). Vocal expressions are also often related to the communicative domain (for a review on primate vocal communication see Fischer and Price, 2017) and many vocalisations are thought to contain both referential and emotional information (Liebal and Oña, 2018). While acknowledging that it may sometimes be difficult to distinguish emotional from referential functions, we argue that the vocal domain is an important modality for emotion recognition to occur, regardless of the (presence of) intentionality in the sender. In this section, we therefore review studies examining whether primates can infer emotional meaning from vocal expressions.

A famous study showed that vervet monkeys, an Old World monkey species, have different behavioural responses to different alarm calls of conspecifics (Seyfarth et al., 1980). When presented with playback alarm calls from a hidden speaker, the monkeys responded with appropriate responses for the type of danger associated with the call. Similar results were found in a study on blue monkeys (*Cercopithecus mitis*), also belonging to the Old World monkeys (Papworth et al., 2008). These studies illustrate that different vocalisations are associated with different kinds of danger and with an urge to warn the other group members. One could suggest that the expressions are simply 'copied' in the way emotionally contagious behaviours are copied. However, the monkeys were observed to produced more calls when group members were close to the speaker than when they were far away, suggesting an understanding of the goal of their behaviour.

Also in chimpanzees, interesting results have been found using playback paradigms. In a study examining these apes' ability to distinguish between different types of agonistic screams, they were presented with playback screams that were given in response to severe and to mild aggression (Slocombe et al., 2009). The chimpanzees looked longer toward the severe victim screams than toward the mild victim screams. They also looked longer toward severe victim screams than toward control tantrum screams that are acoustically similar to severe victim screams, indicating that the cause of this looking behaviour was not acoustical, but content-related.

In a follow-up study chimpanzees were presented with sequences of screams that were either consistent or inconsistent with the social hierarchy (Slocombe et al., 2010). An example of an inconsistent stimulus would be an aggressor scream of a lower-rank individual followed by a victim scream of a higher-rank individual. Chimpanzees looked longer

at the inconsistent than at the consistent stimuli, even though the latter were more acoustically salient. This difference in looking times indicates that chimpanzees form an interpretation based on a sequence of emotional vocalisations, suggesting that they attribute complex knowledge to vocal expressions of conspecifics.

In line with these results, another study showed that chimpanzees can distinguish between vocalisations of their conspecifics and use these to infer information about the mental state of the ape (Crockford et al., 2017). When chimpanzees first heard the vocalisations of a resting chimpanzee from a hidden speaker and then discovered a model snake, they emitted more vocal and visual signals than when they first heard alarm calls from the hidden speaker and then saw the model snake. This shows that the chimpanzees used the vocal signals of their supposed conspecifics to infer whether they were aware of the snake or not.

Another study examined whether chimpanzees have a preference for one modality over another when they categorise emotional signals (Parr, 2004). Chimpanzees were presented with visual facial expression stimuli, vocal expression stimuli and incongruent multimodal stimuli, in which the auditory and the facial expression did not match. They had to match these stimuli to one of two target facial expressions in a matching-to-sample task. The apes were able to select the correct emotional expression in both the auditory and visual conditions, but in the incongruent audio-visual condition, they relied on a single modality, depending on the expression category. The auditory modality was dominant in the discrimination of pant-hoods and play faces, while the visual modality was used for screams. No preference was found for bared-teeth displays. It would be highly interesting to compare these results with behaviour in other primate species. Possibly, preferences for modality differ depending on living environment and social structure (Hobaiter et al., 2017). Future research should study modality preferences in other primate species to find which factors are involved in the communication of emotions.

The studies discussed here indicate that various primate species are not only able to distinguish between vocal emotional expressions, but that they also infer meaningful content from these vocalisations. Even though there is a large base of literature on primate vocalisations, communication and the referentiality of vocal expressions (Fischer and Price, 2017), not many studies have focused on the recognition and understanding of emotional content from vocalisations. Also, the recognition of vocal expressions has not been related to cognitive empathy before. Future research should address the perception and understanding of emotions of others through vocal cues. Also, research is needed in more different ape and monkey species, as most studies discussed here focused on chimpanzees and Old World monkeys.

3.3. Contrasting emotions in sender and perceiver

An important aspect of cognitive empathy is the ability to make a clear distinction between one's own emotion and the emotions of others (Preston and de Waal, 2002). This could be assessed by measuring physiological arousal and external signs of emotion in the perceiver to investigate to what extent their states are matched. However, situations in which a self-other distinction is most evident are cases where the observer's emotion is completely different from the sender's. Studying cases in which the meaning of emotions is recognised despite contrasting emotions in observing and observed apes and monkeys could provide more information on the presence of cognitive empathy in different primate species.

In their study on emotion perception in capuchin monkeys, Morimoto and Fujita (2011) noted that when a container placed between two monkeys contained positive content, the monkey that could see the content displayed more open-mouth bared-teeth expressions, associated with negative emotion. Nonetheless, the observing monkeys reached for this container more than for containers with negative content. Apparently, the monkeys were able to use their conspecifics' negative emotional expressions (possibly caused by the will to protect the food) to

attribute positive valence to the container. This does not necessarily tell us that the observing monkey experienced a positive emotion and that therefore there were contrasting emotions in both monkeys. However, this result suggests that the monkeys could associate a positive meaning for themselves with a negative expression in others. Although the ability to desire something that another monkey is responding to with negative expressions to protect it may seem trivial, it is highly interesting that capuchin monkeys are able to understand positive meaning in this way.

Other research discussed above showed that the four great ape species are able to make similar positive inferences from negative emotional expressions (Buttelmann et al., 2009). When a human experimenter reacted negatively to a food container and then ate something, the apes selected the negative container, because it still contained food. Besides their ability to understand the meaning of emotions, they apparently also attribute positive valence to an object associated with negative emotion. Compared to the results found for capuchin monkeys (Morimoto and Fujita, 2011) this is an interesting finding, as in this case the negative expression was not even meant to keep the food away from the observing ape, but simply to connect a negative emotion to the object.

Intriguing evidence for a difference in emotional state between sender and perceiver was also found in chimpanzees. A study on laugh-elicited laughter showed that chimpanzees are able to respond to others' laughter with laughter, but that these vocal responses differ from spontaneous laughter in frequency and duration (Davila-Ross et al., 2011). Also, these laughs appeared with age and seemed to promote social play. Apparently, laugh-elicited laughs in chimpanzees are not simply contagious 'copies' of the emotion of the sender, but an emotionally intelligent response to the emotions of others that has a distinct underlying emotion.

We argue that it is worthwhile to study more cases of emotion recognition in which emotions in the perceiver differ from the emotion that is perceived. In that way, the maintenance of a self-other distinction, a prerequisite for cognitive empathy, can be investigated. A possible way to create this situation in future research is to test emotion recognition of different expressions in individuals experiencing different emotions themselves. Inducing emotions in primates may prove to be challenging and might even be undesirable in the case of negative emotions. However, a comparison between emotion recognition in neutral state and in positive state may be interesting to study, for example using the matching-to-sample paradigm discussed earlier. To come back to our methodological considerations in Section 2.5, this could also shed light on the distinction between emotional contagion and cognitive empathy: to what extent does the congruence or incongruence of one's own emotions with others' emotional expressions influence emotion recognition? If congruence promotes recognition, emotional contagion might be at play, but if the subject's emotional state does not influence emotion recognition, even though it is incongruent, the emotion may be recognised in a more cognitive way.

3.4. Discussion and recommendations for future research

In Section 3 we reviewed studies that tested the capacity of different primate species to attribute meaning to expressions of emotion and to use this knowledge to reach personal objectives. Also, we argued that cases in which the emotions of the sender and the perceiver did not match are interesting situations when it comes to cognitive empathy. From the limited evidence discussed in this section it is hard to draw firm conclusions, but important questions and directions for future research arose from the results found in both apes and monkeys.

3.4.1. The evolution of cognitive empathy

To gain a better understanding of the evolution of cognitive empathy as an emotion recognition mechanism, we discussed studies on emotion understanding in both apes and monkeys. Surprisingly little studies focused on emotion understanding in great ape species. Besides interesting findings on the interpretations of emotional expressions in

chimpanzees, bonobos, gorillas and orangutans (Buttelmann et al., 2009) and the demonstration that chimpanzees can attribute meaning to facial expressions of emotion (Parr, 2001), we are not aware of any other experimental studies that focused on the use of emotional expressions to gain knowledge about food or social consequences. Until now, researchers have often drawn their conclusions on cognitive empathy in great apes based on a) consolation behaviour (e.g. Preston and de Waal, 1996), which is a very specific and isolated type of behaviour, b) anecdotal evidence of targeted helping (e.g. Preston and de Waal, 2002; de Waal, 2008) and c) studies on other cognitive abilities, such as theory of mind. Theory of mind is the cognitive capacity of knowing that others may have knowledge that differs from your own knowledge (for a review on theory of mind in animals see Krupenye and Call, 2019). Even though theory of mind is similar to cognitive empathy with respect to understanding of the states of others and maintaining the distinction with oneself, the two concepts are different with regard to the non-emotional nature of theory of mind (Koski and Sterck, 2010). Therefore, we call for more experimental research on emotion recognition and mental state attribution in great apes.

If we look at monkeys, experimental studies provide some evidence that complex socio-emotional mechanisms exist in these primates. Old World monkey species appear to use facial expressions to predict the outcomes of social interactions (Waller et al., 2016) and to find relevant objects in their environment (Goossens et al., 2008) and New World monkey species have been shown to make inferences about the attractiveness of food (Kemp and Kaplan, 2013) or hidden objects (Morimoto and Fujita, 2011, 2012) based on facial expressions of conspecifics. Also, these inferences can still be made when the emotions differ between sender and perceiver (Morimoto and Fujita, 2011). These findings all point toward the presence of different building blocks for cognitive empathy in monkey species, although it should be noted that the possible contribution of emotional contagion has not been addressed in any of these studies.

The scarce evidence for emotion understanding in monkeys is not enough to conclude that monkeys have cognitive empathy, but certain cognitive aspects of their emotion recognition capacities seem to go beyond simple emotional contagion. If monkeys already show an understanding of others' emotions, this aspect of cognitive empathy evolved before ape and monkey lineages split. Alternatively, it is possible that aspects of cognitive empathy evolved analogously in different species, because of the adaptiveness of understanding others' emotional expressions. More research in different monkey species could resolve this issue.

3.4.2. The importance of research in the vocal domain

Possible clarifications in the debate on cognitive empathy in apes and monkeys can be provided if we include research in the vocal domain, which is often neglected in the present hypotheses (de Waal and Aureli, 1996; Gruber and Clay, 2016; de Waal and Preston, 2017; Koski and Sterck, 2010; Kret et al., 2020). Primates often convey their emotional state using different calls, which has the advantage of reaching others over larger distances and in forested habitats. We argue that the ability of primates to understand different emotional vocalisations is informative of a possible capacity of cognitive empathy.

We discussed results from playback paradigms in both apes and monkeys. These studies showed that Old World monkeys are able to extract meaningful content from others' alarm calls about the presence of predators and that chimpanzees cannot only distinguish different types of screams, but also understand the emotion of the producer of the call (Crockford et al., 2017; Slocombe et al., 2009) and to what extent sequences of calls correspond with expectations (Slocombe et al., 2010).

From these studies it appears that chimpanzees are able to attribute mental states to others based on their vocalisations. However, to what extent the same can be concluded for monkeys is questionable. When a monkey hears an alarm call and responds with avoidance behaviour (Seyfarth et al., 1980), this may point toward an association between the

signal and a fearful stimulus, rather than an understanding of the distressed state of the producer of the call. Further experimental research could explore this issue. Experiments presenting vocalisations that are not necessarily alarm calls but rather expressions of intrinsic emotions could test for conspecifics' understanding of the emotional state, in designs comparable to those in studies in chimpanzees discussed above.

3.4.3. Other methodological considerations

It is clear that more research on cognitive empathic abilities in both ape and monkey species is needed. The container selection method has been found to be a useful paradigm to study the understanding of emotional expressions. This method was first applied in chimpanzees (Buttelmann et al., 2009) in a design adapted from human child research (Repacholi, 1998) and also used with capuchin monkeys by Morimoto and Fujita (2011, 2012). The latter studies even showed that the primates themselves can be used as demonstrator, which creates a naturalistic controlled situation in which the expressions and responses of the observer can be closely monitored.

Interesting modifications could be added to the design, to gain a better understanding of the processes at play. First, physiological and behavioural measurements of emotion, such as thermo-imaging and scoring of self-directed behaviours could be added to address to what extent the observed and the observing individual experience similar emotions. In this way, the additional effects of contagious emotions can be assessed. Also, the effects of vocal expressions and visual expressions can be addressed separately, by using sound-proof cages or hiding the observed individual from sight. Possibly, also other designs from human child research could be adapted to test cognitive empathy in primates.

Studying the effects of vocal and visual input separately is recommended in other designs as well. Chimpanzees have been shown to have preferences for different modalities depending on the specific expression (Parr, 2004). Similar studies testing modality preferences in other primate species would provide valuable knowledge for research on the perception of emotional expressions. Possibly, some species are more likely to recognise the meaning of vocal expressions while other species attribute more knowledge to facial expressions, also depending on the environment in which the species evolved (Fröhlich and van Schaik, 2018).

With respect to understanding of vocal emotional expressions, playback studies have been most commonly used so far. A great advantage of playback studies is the ability to manipulate which expressions are perceived, while preserving the natural environment and setting. In fact, together with one thermo-imaging study (Dezecache et al., 2017), playback studies are the only studies discussed in this review focusing on wild animals, whereas experimental research is usually restricted to captive animals. However, we do suggest that laboratory research with playback calls could be a valuable addition, because responses of individuals can be monitored more closely and the calls can be combined with specific tasks or stimuli. Possibly, more experimental research could provide more clarity on the debate to what extent the meanings of emotional vocalisations are understood.

Finally, we emphasise that interesting cases are situations in which the internal states of sender and perceiver differ, but the emotions are still understood. A fascinating example is the finding that chimpanzees produce laugh-elicited laughter that differs from spontaneous laughter (Davila-Ross et al., 2011), indicating two different emotional states. However, these emotional states are still both positive and closely related. Experimental studies creating situations in which the emotions of sender and perceiver do not match could provide answers to the question to what extent emotions of others can still be understood if they do not match one's own emotion. Eventually such designs can also help to distinguish emotional contagion from cognitive empathy.

4. Conclusion

The aims of the present review were to gain insight into the evolution

of emotion recognition in primates and to evaluate how experimental research can help us understand the underlying mechanisms. We addressed two routes to emotion recognition in primates: emotional contagion and cognitive empathy. Specifically, we discussed aspects of these mechanisms in both primate species that are evolutionary close to humans and evolutionary more distant species. In this way, we aimed to find indications for the evolutionary history of aspects of emotional contagion and cognitive empathy.

The results of experimental studies in the last decades addressing emotion perception in primates allowed us to provide an overview of ways in which primates may recognise each other's emotions. Of course, research leads to questions, and questions open up possibilities for future research. We end this review by providing a brief summary of the main conclusions regarding the evolution of emotion recognition, the main questions that arose from the literature discussed, and the most important directions for future research.

4.1. The evolution of emotion recognition

Both apes and monkeys appear to be able to form basic internal representations of their conspecifics' emotions based on emotional expressions. Primates from both lineages are able to distinguish their conspecifics' facial and vocal expressions, but it is subject to debate whether the mechanisms underlying recognition differ between species (Clay et al., 2018).

We saw that different ape and Old World monkey species mimic each other's facial expressions and yawn and scratch contagiously, but that these aspects of emotional contagion appear to be absent in other closely related primate species. Interestingly, the absence of these contagious behaviours is not restricted to one lineage, but there seem to be differences between species within taxa. Aside from the fact that the evidence for most species exists of only one or a few studies, it is possible that analogous, rather than homologous evolution underlies the contagion of different emotional expressions. We argued that to further investigate emotional contagion as a possible evolutionary early mechanism for emotion recognition, experimental research should combine non-invasive physiological measures, observations of contagious behaviours and different stimulus conditions.

Analogous evolution is also a possible explanation for the findings that many different primate species, including a species of strepsirrhines, are able to attribute emotional meaning to facial and vocal expressions of their conspecifics. We discussed evidence of apes, Old World monkeys and New World monkeys being able to relate the meaning of their conspecifics' expressions to external concepts such as food and future events. The literature shows that the prerequisites for cognitive empathy are present in different monkey species, in contrast to previous beliefs (de Waal and Aureli, 1996). Possibly, the ability to attribute meaning to others' emotional expressions provides such strong adaptive benefits that this capacity evolved independently in different species. It is however possible that even more cognitively advanced and empathic levels of emotion recognition than the ones discussed in this review, such as perspective taking – the third level of 'Russian doll model' proposed by de Waal (2008) – developed later in primate evolution in a homologous way and appears only in apes and humans.

More informed conclusions regarding the evolution of emotional contagion and cognitive empathy as emotion recognition mechanisms can only be drawn when more research is conducted in different primate species. For apes, there is a large bias in the literature toward chimpanzees. Also, especially New World monkeys are rarely studied and almost no studies at all address primate species more distant from humans than New World monkeys. A comparison with for example strepsirrhines could be very informative of the evolutionary nature of emotion recognition in primates. In addition, research in evolutionary distant species such as other mammals and birds may provide interesting information on whether different aspects of cognitive empathy and emotional contagion have evolved independently, that is, via analogous

evolution (de Waal and Preston, 2017; Massen and Gallup, 2017).

4.2. Remaining questions

We concluded that the literature does not clearly point toward a moment in primate evolution where cognitive empathy emerged as a possible emotion recognition mechanism. Also, different aspects of emotional contagion were found in different species within the same taxon. Possibly, environmental factors determined the ways in which emotions are best recognised in a certain species. We know that emotional expressions are subject to ecological and social constraints (Hobaiter et al., 2017; Snowden, 2003) and we speculated that for example orangutans, living in dense forest habitats, may rely more on vocal expressions of emotion than primates living in less dense forests. However, not much is known about how different habitats, predators and other environmental factors may have influenced the evolution of emotion recognition (Fröhlich and van Schaik, 2018). It would be highly interesting to study how ecological constraints influenced ways of emotional transfer in different primate species.

Focusing on the underlying mechanisms of emotion recognition, in the first half of this review we saw that emotional contagion is a multilevel phenomenon in which emotional expressions bring about a representation of the same emotion in an observing individual. However, the causal relation between emotional contagion and emotion recognition remains to be studied. An important question is to what extent emotion recognition is altered when emotional contagion is impaired. Carefully designed experiments combining tests of emotion recognition while preventing the copying of expressions could reveal the extent to which emotional contagion is a requirement for emotion recognition in certain species.

In the second part of this review, we discussed cognitive empathy as a cognitive extension to the more automatic emotional contagion. Because emotional contagion and cognitive empathy are not mutually exclusive, the question arose to what extent emotional contagion still plays a role when cognitive empathy is at play. Studies in different primate species showed an understanding of the cause, meaning and direction of the emotional expressions that were perceived, sometimes even if own emotions did not match observed emotions. However, few studies addressed the transference of the emotion to the observing individual, using for example physiological or behavioural indicators of emotion such as skin temperature or visible emotional expressions. This is an important suggestion for future research when identifying and distinguishing the underlying mechanisms of emotion recognition.

4.3. Recommendations for future research

Even though observational research is important in investigating whether a type of behaviour is present in a certain species, we argued that experimental research is necessary to reveal the underlying mechanisms. Throughout this review we proposed methodological considerations for future research and we conclude here by highlighting the main recommendations.

With respect to experiments addressing responses to emotional expressions, most research so far focused on facial expressions. However, in primates' natural environments emotions are also perceived through vocal expressions and bodily expressions, such as scratching. Moreover, in this review we have not yet addressed touch (Schirmer and Adolphs, 2017) and olfaction (Laska and Salazar, 2015) as possible modalities of emotional communication. As highlighted above, species may differ in the types of emotional expressions that are most salient, depending on ecological constraints. Therefore, research in domains other than facial expressions is necessary. Also, multimodal stimuli may be included as an even more natural approach to emotional expressions.

Furthermore, different types of studies appeared to be exclusively focused on certain types of emotions. For example, facial mimicry was usually tested for positive play faces, whereas vocal research often

focused on alarm calls. The most complete picture of emotion recognition and its underlying mechanisms can be achieved through comparison between positive as well as negative expressions of emotion.

We would like to conclude by emphasising that the huge advantage of experimental studies is the ability to manipulate conditions and to create controlled situations that would not often appear in natural environments. Different facial expressions can be compared by showing them on a screen, vocalisations can be played back via speakers, food content can be selectively hidden from one individual and emotional responding can be monitored closely and even measured physiologically. We encourage researchers to apply the paradigms described in this review on more different species and to extend these with different measures of emotion, in order to get a better understanding of emotional contagion and cognitive empathy as possible mechanisms underlying emotion recognition.

Declaration of Competing Interest

All authors declare that they have no conflict of interest.

Acknowledgements

We thank two anonymous reviewers for their useful comments on our manuscript. This research was supported by the European Research Council (Starting grant # 804582) and the Templeton World Charity Foundation (the Diverse Intelligences Possibilities Fund # TWCF0267) to Mariska E. Kret.

Appendix

Table A1

Table A1

Overview of key studies on emotion recognition in nonhuman primates.

Reference	Purpose	Sample	Procedure	Measures	Results
Amici et al. (2014)	This study tested whether great ape species yawn contagiously in response to humans and conspecifics.	14 chimpanzees (<i>Pan troglodytes</i>), 4 bonobos (<i>Pan paniscus</i>), 5 Western gorillas (<i>Gorilla gorilla</i>), 4 Sumatran orangutans (<i>Pongo abelii</i>) (all captive)	In the human condition, the apes saw a live human demonstrator involved in yawning, nose-wiping, scratching, hand closing or wrist shaking and in the conspecific condition they saw a video of a conspecific yawning, nose wiping or scratching. Behaviour of the subjects was scored.	Human demonstrator, video presentation	Only chimpanzees yawned contagiously in response to the videos, but not to the human demonstrator. For the other behaviours and the other species, no significant differences were found.
Anderson et al. (2004)	This study investigated whether chimpanzees show contagious yawning in response to videos of yawning conspecifics.	6 captive chimpanzees (<i>Pan troglodytes</i>)	Chimpanzees were shown both videos of conspecifics that were naturally yawning and videos of conspecifics with an open mouth. The reactions of the chimpanzees were recorded.	Video presentation	Two of the six chimpanzees showed significantly more yawning in response to the yawning videos than to the open mouth videos and no chimpanzees showed the reverse effect.
Baenninger (1987)	This study examined yawning frequency and yawn contagion in mandrills, Siamese fighting fish, lions and humans.	4 mandrills (<i>Papio sphinx</i>), 15 Siamese fighting fish (<i>Betta splendens</i>), 5 lions (<i>Panthera leo</i>) (all captive), unknown number of humans (<i>Homo sapiens</i>)	Groups of the four species were observed and yawn frequency, yawn type and yawn contagion within 20 s was scored. The Siamese fighting fish were observed both in pairs, in an individual setting and with a mirror present. In addition, contagious yawning in 40 humans was examined in an experiment with a demonstrator yawning once.	Behavioural sampling, human demonstrator	Yawning was found in all species studied. In Siamese fighting fish, yawning increased when a conspecific was present and even more during combat. Contagious yawning was not found in mandrills nor in lions. In the human experiment, only three yawns were elicited in total.
Buttelmann et al. (2009)	This study tested whether apes can understand humans' emotional expressions and whether they can use these expressions to make inferences about desires.	17 chimpanzees (<i>Pan troglodytes</i>), 5 bonobos (<i>Pan paniscus</i>), 5 Western gorillas (<i>Gorilla gorilla</i>), 5 Bornean orangutans (<i>Pongo pygmaeus</i>) (all captive)	In experiment I, the apes chose between two containers with hidden content (one of which contained food) to which a human experimenter had reacted either happily or with disgust. In experiment II, the same procedure applied, but both containers contained food and the apes saw the experimenter eating something after their emotional reactions. In this experiment, the correct choice was the container to which the experimenter had responded negatively, because this container still contained food.	Hidden object task	In experiment I, the apes performed correctly in choosing the container associated with the positive emotion. In experiment II, they performed above chance in selecting the 'negative' container, which was correct because it still contained food.
Calcutt et al. (2017)	This study tested the ability of capuchin monkeys to differentiate between different facial expressions and whether these expressions are processed configurally or feature-based.	9 captive tufted capuchin monkeys (<i>Sapajus apella</i>)	Subjects were presented with four images on a touch screen and had to select the odd one out. In experiment I, affiliative and agonistic facial expressions had to be selected over three other neutral expressions. Experiment	Odd-item visual search task	The monkeys performed above chance in discriminating emotional expressions from neutral expressions, even when the neutral expressions had different degrees of mouth opening. They also showed an

(continued on next page)

Table A1 (continued)

Reference	Purpose	Sample	Procedure	Measures	Results
			II was similar, except that the target was always agonistic and the neutral expressions had different degrees of mouth opening. Experiment III contained trials with inverted images, where a scalp lift had to be distinguished from neutral images.		inversion effect: performance was less for inverted trials compared with upright trials.
Campbell and de Waal (2011)	This study tested in-group biases for contagious yawning in chimpanzees.	23 captive chimpanzees (<i>Pan troglodytes</i>)	Chimpanzees from two groups were presented with videos of spontaneous yawns and control videos of resting behaviour of both in-group and out-group members. The number of yawns was counted per condition.	Video presentation	There was a higher frequency of yawning for in-group yawn videos than for in-group control videos and out-group yawn videos. Looking times were higher for out-group videos than for in-group videos, which rules out attention levels as an explanation.
Campbell and de Waal (2014)	This study examined yawn contagion in chimpanzees in response to familiar and unfamiliar humans and gelada baboons.	19 captive chimpanzees (<i>Pan troglodytes</i>)	Chimpanzees were presented videos of familiar humans, unfamiliar humans and gelada baboons, yawning and in rest. Yawning rate was scored.	Video presentation	With respect to the videos of familiar and unfamiliar humans, the chimpanzees yawned more in response to the yawn videos than to the control videos. Yawning did not differ significantly between the two types of videos of gelada baboons. Combined with the results of Campbell and de Waal (2011), no significant difference was found between human and in-group chimpanzee videos, but a significant difference was found between humans and in-group chimpanzees on the one hand, and gelada baboons and out-group chimpanzees on the other hand.
Campbell et al. (2009)	This study tried to answer the question whether chimpanzees show contagious yawning in response to computer animations of yawning subjects.	24 captive chimpanzees (<i>Pan troglodytes</i>)	Subjects were presented with computer animations of chimpanzees that either yawned or made control mouth movements. The amount of yawning in the subjects was measured.	Video presentation	Chimpanzees yawned significantly more in response to the yawning animations than to the control animations.
Crockford et al. (2017)	This study tested whether chimpanzees are able to adapt their signalling according to their understanding of the receiver's mental state, based on vocalisations of these receivers.	32 wild chimpanzees (<i>Pan troglodytes</i>)	In experiment I, a snake model was placed on the path of a chimpanzee group and the responses of the chimpanzees to the snake model were recorded. In experiment II, subjects first heard a playback rest hoo call or an alert hoo call from a hidden speaker. Then they encountered a snake model. The signalling of the subjects was recorded.	Playback sound presentation	In experiment I, the chimpanzees' marking of the location of the snake model was influenced by the awareness of their group members, and the group members used others' marking to locate the snake model. In experiment II, the subjects emitted more vocal calls and non-vocal signals when the playback stimulus had been a resting stimulus than when it had been an alert stimulus.
Davila-Ross et al. (2008)	This study examined laugh-elicited laughter in chimpanzees and compared this to spontaneous laughter.	59 captive chimpanzees (<i>Pan troglodytes</i>)	Rapid laugh replications, delayed laugh replications and spontaneous laughter during dyadic play bouts were analysed acoustically and with respect to their occurrence in four colonies: two colonies that were grouped together more than 14 years ago (old colonies) and two colonies that were grouped together less than five years ago (new colonies).	Behavioural sampling	The amount of calls per laugh differed between laugh replications and spontaneous laughter. Also, chimpanzees in new colonies showed more laugh-elicited laughter than chimpanzees in old colonies. No differences in acoustics and occurrence were found between rapid and delayed laughs. Laugh-elicited laughter also had a positive influence on the duration of the play bouts.
Davila-Ross et al. (2011)	This study investigated rapid facial mimicry for open mouth faces in Bornean orangutans.	25 captive Bornean orangutans (<i>Pongo pygmaeus</i>)	Dyadic play bouts of the Bornean orangutans were video recorded and observers scored the	Behavioural sampling	16 of the Bornean orangutans mimicked the open mouth displays of their play mates,

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Table A1 (continued)

Reference	Purpose	Sample	Procedure	Measures	Results
			presence of open mouth faces that occurred within one second since the display of the other individual.		but nine did not show congruent facial displays.
Demuru and Palagi (2012)	This study investigated contagious yawning in bonobos and studied the effects of relationship quality, rank and sex.	12 captive bonobos (<i>Pan paniscus</i>)	A group of bonobos was observed and responses to yawns were collected. Responses to yawns by an individual that perceived the yawns were compared to behaviour of those who did not perceive these yawns.	Behavioural sampling	Bonobos yawned contagiously to yawns of conspecifics, compared to baseline. Individuals yawned more in response to socially bonded individuals, and female yawns were more contagious than male yawns.
Dittrich (1990)	This study investigated temperature changes in nose and ear in wild chimpanzees in response to vocalisations of conspecifics.	14 wild chimpanzees (<i>Pan troglodytes</i>)	The faces of chimpanzees were photographed with a thermal imager up to 30 s after the occurrence of different vocalisations of other chimpanzees.	Infrared thermography	After hearing aversive calls, the nose temperature of the chimpanzees dropped and the ear temperature remained the same. Neutral vocalisations were associated with an increase in temperature of the ear region, but no difference for the nose temperature.
Dittrich (1990)	This study tested the ability of longtailed macaques to learn to discriminate different facial emotional expressions. It was also investigated whether recognition is influenced by colour, brightness, size and orientation and which facial components are important for recognition. Lastly, this study investigated whether faces are processed as a gestalt.	4 captive longtailed macaques (<i>Macaca fascicularis</i>)	In each trial, the subjects were presented with four drawings of different facial expressions, one of which was the target expression: slandering with grunt. In the first session, the four drawings were shown in a regular way. In the second session, variations of colour, brightness, size and orientation were applied. In the third session, only specific features of the face were shown.	Visual search task	The monkeys learned to select the target expression quickly. Colour, brightness, size and rotation did not influence performance. Outline, eye region and mouth were important features for face recognition. The relation between different facial features was found to be important for recognition. The dominant monkeys learned the task better than the subdominant ones.
Feneran et al. (2013)	This study investigated contagious itch, as observed from scratching behaviour, in rhesus macaques.	26 captive rhesus macaques (<i>Macaca mulatta</i>)	In experiment I, rhesus macaques were observed in pairs. Their scratching behaviour was scored and the time between scratches of the two individuals was measured. In experiment II, rhesus macaques were presented with videos of the scratching monkeys from experiment I and videos of their neutral behaviour. Scratching behaviour was recorded.	Behavioural sampling, video presentation	In experiment I, 14 of the 16 monkeys scratched contagiously within 360 s and there was an increasing trend of scratching within the first minute after an observed scratch. In experiment II, scratching videos evoked significantly more scratches than neutral videos.
Goossens et al. (2008)	This study investigated the effect of social facial expressions on gaze following in longtailed macaques.	13 captive longtailed macaques (<i>Macaca fascicularis</i>)	In experiment I, subjects watched an experimenter either shifting the gaze or looking straight. In experiment II, the experimenter shifted her gaze while displaying a neutral facial expression or a bare teeth display, lip smack or open mouth. Experiment III was the same as experiment II, except that a fourth meaningless facial expression was added. The behaviour of the macaque was videotaped in all experiments.	Human demonstrator	Trials where a gaze shift was accompanied by a facial expression elicited more gaze following than trials where the expression was neutral. Meaningless facial expressions did not elicit more gaze following than neutral expressions.
Kanazawa (1996)	This study examined facial expression discrimination in Japanese macaques and also analysed which facial cues were important for recognition. This was compared to recognition of facial expression in humans.	4 captive Japanese macaques (<i>Macaca fuscata</i>), 2 humans	Subjects saw an image of a facial expression of a monkey and had to match this stimulus to one of two subsequently presented images. The distracting image contained a different facial expression. Only the monkey that succeeded did the same task with human faces. Human subjects did the same. A multidimensional scaling procedure was performed to analyse which features were important for recognition.	Matching-to-sample task	Only one monkey performed above chance in matching the monkey facial expressions, and did so too for human facial expressions. Important features for recognising monkey facial expressions were thrusting the mouth and raising the eyebrows. The monkey recognised human happy faces but did not distinguish sad from angry faces.
Kano et al. (2016)	This study assessed the usability of thermo-imaging as a measure of emotion in	12 captive chimpanzees (<i>Pan troglodytes</i>)	In experiment I, chimpanzees were presented with playback sounds of fighting conspecifics	Video presentation, playback sound presentation, infrared	In both experiments, nasal temperature dropped in the experimental but not in the

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Table A1 (continued)

Reference	Purpose	Sample	Procedure	Measures	Results
	chimpanzees. The measure was combined with other measures of emotion.		and allospecific display calls as control sounds. In experiment II, videos of conspecifics fighting were presented, with resting chimpanzees as control videos. In both experiments, behaviour, heart rate variability, salivary cortisol and thermo-imaging were used as measures of emotional responding.	thermography, heart rate variability, salivary cortisol measurement	control conditions. These changes were related to behaviour and heart rate variability, but not to salivary cortisol levels.
Kemp and Kaplan (2013)	This study investigated whether marmosets are able to use conspecifics' facial expressions as social signals.	12 captive common marmosets (<i>Callithrix jacchus</i>)	In experiment I, facial expressions of marmosets were studied and recorded by presenting them with different olfactory and auditory stimuli. In experiment II, videos of these positive and negative expressions were presented to their conspecifics and the time spent near the food bowl was measured.	Video presentation	The marmosets displayed a variety of facial expressions in response to odours and sounds. They spend more time near a food bowl when a positive facial expression of a conspecific was shown, than when a negative facial expression was shown.
Kret et al. (2014)	This study investigated whether bonobos have an attentional bias for emotional scenes, and which emotions attract their attention most.	4 captive bonobos (<i>Pan paniscus</i>)	Bonobos were presented with a neutral and an emotional image. Then, the images disappeared and a dot appeared at the location of either the neutral or the emotional scene. Reaction times until the dot was pressed were measured.	Dot-probe task	Bonobos showed an attentional bias to emotional scenes compared to neutral scenes, as reflected by longer reaction times for these stimuli. Their attention was drawn to images of other bonobos yawning, grooming and mating, but not to scenes depicting distress, panthood, play or food.
Kret et al. (2016)	This study examined attentional biases for emotional expressions in humans and chimpanzees.	8 captive chimpanzees (<i>Pan troglodytes</i>), 711 humans (<i>homo sapiens</i>)	In experiment I, chimpanzees were presented with two images with different emotional expressions of conspecifics: fear, anger or neutral. The images were presented 33 milliseconds or 300 milliseconds and masked with a neutral body image. Then, a dot appeared at the location of one of the images and reaction times until the dot press were measured. Experiment II was similar to experiment I but with human stimuli and one participant less. Experiment III was similar to experiment I and II but tested human participants with images of both chimpanzees and humans.	Dot-probe task	Chimpanzees did not show any attentional bias toward emotional stimuli of conspecifics nor humans, as indicated by a nonsignificant difference between the response times in the different categories. Humans did show an attentional bias for stimuli of both species.
Kret et al. (2020)	This study investigated whether chimpanzees mimic the pupil-size of conspecifics and humans.	8 captive chimpanzees (<i>Pan troglodytes</i>), 18 humans (<i>Homo sapiens</i>)	Chimpanzees and humans watched videos of both species with dilating or constricting pupils. Pupil dilation was measured using an eye tracker.	Pupillometry	Both species showed more pupil dilation when they observed a member of their own species with dilating pupils than when they observed a conspecific with constricting pupils. In both species, mothers showed the strongest pupil mimicry.
Kuraoka and Nakamura (2011)	This study examined changes in nasal skin temperature in rhesus macaques in response to the emotional behaviour and expressions of conspecifics.	6 captive rhesus macaques (<i>Macaca mulatta</i>)	In experiment I, subjects were presented with a video clip of an unknown raging conspecific. In experiment II, subjects watched video clips of monkeys showing different emotional expressions (aggressive threat, scream and coo). In experiment III, audio-visual, visual and auditory recordings of aggressive threat were presented.	Video presentation, infrared thermography	Nasal skin temperature decreased in response to threatening stimuli. Threat displays had a larger effect than screams and coos. Audio-visual perception of threat led to a larger decrease in nasal skin temperature than visual and auditory threat alone.
Laméris et al. (2020)	This study investigated contagious yawning and contagious scratching in Bornean orangutans and also studied the effect of social and contextual factors.	9 captive Bornean orangutans (<i>Pongo pygmaeus</i>)	Scratching and yawning behaviour was recorded and these behaviours were also recorded from bystanders within a period of three minutes after the initial behaviour.	Behavioural sampling	No contagious yawning was found, but scratching increased the occurrence of scratching behaviour in surrounding orangutans within the first 120 s. Contagious

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Table A1 (continued)

Reference	Purpose	Sample	Procedure	Measures	Results
Madsen et al. (2013)	This study asked whether chimpanzees show cross-species yawning, studied the ontogeny of yawning in chimpanzees and tested whether emotional closeness affected contagious yawning.	33 captive chimpanzees (<i>Pan troglodytes</i>)	Infant and juvenile chimpanzees saw a human model either yawn, gape or nose-wipe and these behaviours were also scored for the chimpanzees.	Human demonstrator	scratching occurred more often when the initial behaviour was seen than when it was not perceived. Also, contagious scratching was stronger between low-quality bonded orangutans. Juvenile chimpanzees yawned significantly more in the yawn conditions than in the other conditions, but infant chimpanzees did not show contagious yawning. Emotional closeness did not affect contagious yawning. Gelada baboons were reported to show both delayed facial mimicry (within five seconds) and rapid facial mimicry (within one second). Play bouts with a high occurrence of rapid facial mimicry lasted longer than play bouts characterised by delayed facial mimicry. Also, mother-infant play sessions had the highest frequency and the fastest responses of rapid facial mimicry.
Mancini et al. (2013a, 2013b)	This study examined rapid facial mimicry of the play-face in gelada baboons and also asked whether rapid facial mimicry had an influence on the duration of play sessions.	38 captive gelada baboons (<i>Theropithecus gelada</i>)	Dyadic play bouts of the gelada baboons were recorded and play face and full play face responses to displays of play mates were scored on two variables: rapidness and congruency with the observed display. Only the data of individuals showing all four combinations of these variables was analysed. The duration of the play sessions was also recorded.	Behavioural sampling	Yawning and stretching behaviour rarely occurred, scratching and tongue protrusion occurred in more sessions than yawning and stretching and increased with age. Only gnawing and scent-marking, which often co-occurred, were temporally clustered, indication contagion.
Massen et al. (2012)	This study focused on behavioural contagion in common marmosets and asked whether they show contagious yawning, stretching, scratching, tongue protrusion, gnawing and scent-marking.	14 captive common marmosets (<i>Callithrix jacchus</i>)	The marmosets voluntarily entered an experimental compartment and were videotaped in groups of four. Their behaviour was scored and contagion was assessed by analysing whether the behaviours were temporally clumped.	Behavioural sampling	Chimpanzees yawned more in response to yawn videos than to control videos and male yawns were more contagious than female yawns. No effect was found for relationship quality.
Massen et al. (2016)	This study investigated the function of contagious yawning in chimpanzees by assessing the effects of relationship quality and sex of the yawning individual.	15 captive chimpanzees (<i>Pan troglodytes</i>)	Videos of different yawning and resting individuals were shown to the whole group and their yawning behaviour was scored.	Video presentation	The ability of crested macaques to match facial expressions to those of different individuals was above chance for both the images and the video stimuli.
Micheletta et al. (2015)	This study tested whether crested macaques are able to distinguish different emotional facial expressions.	3 captive crested macaques (<i>Macaca nigra</i>)	In experiment I, subjects were to match a target facial expression to the same facial expression in a different subject, presented subsequently, together with a distractor stimulus. This task included four facial expressions and one neutral expression. Experiment II was identical, except that a video recording of a facial expression had to be matched to an image of the same facial expression.	Matching-to-sample task	In half of the pairings, the rhesus macaques responded by pressing the lever upon perceiving positive affect in the stimulus subjects. In these monkeys, this response was also accompanied with an increased heart rate.
Miller et al. (1962)	This study investigated whether rhesus macaques can use the positive emotional expressions of conspecifics to initiate an appropriate response.	6 captive rhesus macaques (<i>Macaca mulatta</i>)	A rhesus macaque could observe a conspecific via a television screen. The observed monkey perceived a light that was associated with the expectation of a food reward. The other monkey could not see this light, but could press a lever in response to positive emotional expressions of the observed monkey. Upon pressing, both animals received a food reward. Heart rate was also measured for the responder animal.	Cooperative conditioning task	The monkeys avoided the shock more often than
Miller et al. (1962) ^a	This study investigated whether rhesus macaques can	3 captive rhesus macaques (<i>Macaca mulatta</i>)	Two rhesus macaques were placed opposite each other. One	Cooperative conditioning task	(continued on next page)

Table A1 (continued)

Reference	Purpose	Sample	Procedure	Measures	Results
	detect negative emotional expressions in a conspecific and use this information to initiate an avoidance response.		of them perceived a light stimulus that was associated with the expectation of an electric shock. The other monkey did not perceive the light but had to use its conspecific's emotional expression to avoid it from getting a shock by pressing a lever at the right moment.		expected from chance, indicating that they used their conspecifics' emotional expressions to press the lever at the correct moment. When visual information was eliminated by placing a screen between the individuals, the animals still performed above chance levels, indicating that also vocal expressions played a role.
Miller et al. (1963)a	This study examined whether rhesus macaques can detect negative visual emotional expressions in a conspecific and use this information to initiate an avoidance response.	6 captive rhesus macaques (<i>Macaca mulatta</i>)	A rhesus macaque could observe a conspecific via a television screen without sound output. The observed monkey perceived light stimulus that was associated with the expectation of an electric shock. The other monkey did not perceive the light but had to use its conspecific's emotional expression to avoid it from getting a shock by pressing a lever at the right moment.	Cooperative conditioning task	The avoidance responses were more frequent than spontaneous lever presses, indicating that the monkeys correctly avoided the shock based on visual information from their conspecific.
Morimoto and Fujita (2011)	This study examined whether capuchin monkeys use conspecifics' emotional expressions to modify their reaching behaviour toward an object container.	7 captive tufted capuchin monkeys (<i>Sapajus apella</i>)	A demonstrator monkey reacted toward a positive, negative or neutral object in a container. The subject could not see the object, but only the demonstrator's reaction. The reactions of the subjects (i.e. reaching toward the container) were analysed.	Hidden object task	Subjects reached for the object more often in the positive condition than in the negative and the neutral condition. With respect to the effect of specific expressions, the monkeys appeared to reach longer in response to forehead raises and less in response to open-mouth bared-teeth displays.
Morimoto and Fujita (2012)	This study investigated whether capuchin monkeys use conspecifics' emotional expressions to modify their reaching behaviour toward two different object containers.	7 captive tufted capuchin monkeys (<i>Sapajus apella</i>)	Subjects watched a demonstrator monkey's reaction to one of two containers containing different objects hidden from the subject. The subject was required to choose one of the two containers.	Hidden object task	The subjects reached less toward the container that evoked a negative emotional response than to the container that evoked positive or neutral responses in the observer monkey. Vocalisations from the demonstrator monkey were particularly influential for the subjects' reaching behaviour.
Nakayama (2004)	This study investigated contagious scratching in Japanese macaques.	5 captive Japanese macaques (<i>Macaca fuscata</i>)	The monkeys were distributed over three adjacent cages in a row. The middle cage contained the 'target' monkey, which could observe a 'stranger' monkey (not familiar with the others) through a peephole in one cage and was observed through a glass wall by 'observing' monkeys in the remaining cage. In the stranger condition, the stranger was present, in the no stranger condition it was absent and in the obstructed view condition, the stranger was present and the glass wall between the observers and the target was replaced by a stainless steel panel. Visual scanning behaviour and scratching behaviour in the target monkey and the observing monkeys was scored.	Stranger / no-stranger observational setup	In the stranger condition, the target monkey looked through the peephole more and scratched more than in the no stranger condition. The observing monkeys scratched more when the target monkey scratched, even though their scanning behaviour did not differ between conditions, indicating contagious scratching regardless of visual attention. In the obstructed view condition, the observing monkeys scratched less frequently than in the stranger condition, ruling out the effect of vocalisations.
Nakayama et al. (2005)	This study explored the reliability of facial skin temperature as measured with infrared thermography as an indicator for emotional responding in rhesus macaques.	4 captive rhesus macaques (<i>Macaca mulatta</i>)	The macaques were presented with a threatening person: a human demonstrator in a veterinary coat with a catching net, making threatening movements. Facial skin temperature was compared to a baseline period before the demonstrator entered.	Human demonstrator, infrared thermography	Nasal temperature of the rhesus macaques dropped in response to the threatening stimulus. Also, the monkeys displayed silent bared-teeth faces, staring open-mouth faces and lip-smacking, indicating negative arousal.

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Table A1 (continued)

Reference	Purpose	Sample	Procedure	Measures	Results
Palagi et al. (2020)	This study examined whether gorillas show contagious yawning.	17 captive Western gorillas (<i>Gorilla gorilla</i>)	Yawning was recorded in two groups of gorillas in a naturalistic setting. Yawner identity, time of the yawn, and individuals able and unable to see the yawn were scored. In addition, gorillas were shown videos of both unfamiliar real and virtual gorillas in an experimental setting. The videos contained yawns and control mouth movements. Yawning and self-directed behaviours were scored and attention was checked.	Behavioural sampling, video presentation	In the naturalistic setting, gorillas did not yawn more in response to an observation of a yawn than in absence of a perceived yawn. Also the yawn videos did not elicit more yawns than the control videos. Yawns in the experimental setting were accompanied by increased self-directed behaviours.
Palagi et al. (2014b)	This study investigated whether contagious yawning occurs in gelada baboons and which factors influence this response.	21 captive gelada baboons (<i>Theropithecus gelada</i>)	Yawning behaviour was observed in a group of gelada baboons. Type of yawn, identity of the yawning individual and other behaviours including grooming behaviour were also scored.	Behavioural sampling	Gelada baboons yawned more in response to yawns than in response to other behaviours of conspecifics. Emotional proximity was correlated with yawn contagion, also after correction for spatial proximity. Females also copied the type of yawn (i.e. degree of mouth opening) they observed.
Palagi et al. (2008)	This study compared contagious yawning between bonobos and humans.	16 captive bonobos (<i>Pan paniscus</i>), 33 humans (<i>Homo sapiens</i>)	Yawning behaviour of a group of humans was observed when there were at least five humans present. Yawning behaviour in a group of bonobos was also observed.	Behavioural sampling	Humans and bonobos appeared equally susceptible to yawn contagion. Also, in both humans and bonobos, strong relationships had a positive effect on contagious yawning.
Parr (2001)	This study investigated the responses of blue monkeys to alarm calls of conspecifics.	34 groups of wild blue monkeys (<i>Cercopithecus mitis stuhlmanni</i>), group size unknown	Groups of blue monkeys were presented with different predator vocalisations (eagles shrieks and leopard growls) and conspecific vocalisations (hacks, specific for eagles, and pyows, used for leopards and other disturbances) from a hidden speaker. Vocalisation responses of the monkeys and contextual information (e.g. distances between the producer and the speaker or other individuals) was recorded.	Playback sound presentation	In response to the predator calls, blue monkeys produced pyows for leopard growls and hacks in response to eagle shrieks. When pyows and hacks were played back, the monkeys responded with hacks in response to hacks and pyows in response to pyows. If group members were close to a speaker playing hacks, more hacks were produced by observing monkeys than when the others were far away from the speaker. No difference in amount of calls was found between different distances if the speaker played the more generally applicable pyows.
Parr and Heintz (2009)	This study examined discrimination of facial expressions in rhesus macaques and addressed holistic vs. feature-based processing.	7 captive rhesus macaques (<i>Macaca mulatta</i>)	Rhesus macaques had to match a target facial expression to one of two subsequently presented stimuli. In experiment I, four different facial expressions were included. In experiment II, neutral portraits were included and subjects matched facial expressions to those of different individuals. A multidimensional scaling analysis was performed to analyse which features were important for discrimination.	Matching-to-sample task	In experiment I, performance was above chance with no difference between expression types. In experiment II, monkeys discriminated the expressions across individuals, but only when the distractor was a neutral face. The features important for recognition were mouth shape and lip retraction/opening.
Parr (2001)	This study examined chimpanzees' responses to emotional stimuli, to study emotional awareness in these animals.	3 captive chimpanzees (<i>Pan troglodytes</i>)	In the first task, skin temperature was measured when chimpanzees watched emotional videos of chimpanzees displaying agonism in response to veterinarians with a dart gun, chimpanzees being injected with the dart gun and videos of the dart gun itself. In the second task, the chimpanzees were required to match negative and positive emotional scenes to facial expressions of conspecifics.	Video presentation, skin temperature measurement, matching-to-meaning task	In the first task, decreases in skin temperature were lower for videos of chimpanzees being injected and videos of the dart gun, than for videos where chimpanzees displayed agonistic behaviour. In the second task, chimpanzees were able to use facial expressions to categorise emotional scenes.

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Table A1 (continued)

Reference	Purpose	Sample	Procedure	Measures	Results
Parr (2004)	This study investigated whether chimpanzees have perceptual preferences for different sensory modalities when categorising affective signals.	3 captive chimpanzees (<i>Pan troglodytes</i>)	A matching-to-sample procedure was used. Chimpanzees matched facial expression videos to a sample stimulus. Some stimuli only contained auditory cues, some only visual cues and some incongruent auditory-visual combinations.	Matching-to-sample task	Chimpanzees could discriminate different emotional expressions, but in case of the incongruent visual-auditory stimuli, they relied more on one modality than another, depending on the expression category: pant-hoods and play faces were discriminated using the auditory modality and screams using the visual modality. No modality preference was found for bared-teeth displays.
Parr et al. (2008)	This study tested chimpanzees' ability to discriminate five species-typical expressions and investigated the influence of shared features between different facial expressions.	Unknown number of captive chimpanzees (<i>Pan troglodytes</i>)	Chimpanzees had to distinguish an emotional expression from a neutral face by matching a target stimulus to one of two subsequently presented stimuli. In experiment II, stimuli with shared features were used instead of a neutral stimulus as distractors.	Matching-to-sample task	Chimpanzees could discriminate the bared-teeth display, hoot face, relaxed open mouth face and scream face from neutral faces but not the relaxed-lip face. When expressions shared similar features, performance was impaired, indicating that feature distinction might be a strategy to distinguish facial expressions.
Paukner and Anderson, (2006)	This study examined the processing of different artificially created facial expression stimuli in chimpanzees, specifically addressing the inversion effect and holistic vs. feature-based processing.	6 captive chimpanzees (<i>Pan troglodytes</i>)	Subjects saw a target animated facial expression stimulus that had to be matched to one of two subsequently presented expressions. In experiment I, the salience of the animated stimuli was tested by having subjects discriminate seven prototypical poster stimuli with different expressions. In experiment II, upside down stimuli were included. In experiment III, multidimensional scaling was used to determine relevant facial features for discrimination. In experiment IV, individual facial features were adapted.	Matching-to-sample task	Chimpanzees learned to discriminate the facial expression stimuli above chance levels, with some (e.g. screams) being easier to learn than others (e.g. pant hood). Processing of facial expressions was impaired for inversed faces. Mouth closure and lip-puckering/retraction were found to have the highest influence on discrimination. It was found that each expression had one feature that was more salient than the other features.
Paukner and Anderson (2006)	This study explored contagious yawning in stumptailed macaques.	22 captive stumptailed macaques (<i>Macaca arctoides</i>)	Stumptailed macaques were presented with videos of conspecifics yawning and videos with control facial movements. The behaviour of the monkeys was scored.	Video presentation	Overall, yawning videos induced more yawning than control videos. Also, there was more self-directed scratching in the yawn condition than in the control condition.
Reddy et al. (2016)	This study investigated whether lemurs show contagious yawning.	14 ruffed lemurs (<i>Varecia rubra</i>), 19 ring-tailed lemurs (<i>Lemur catta</i>) (all captive)	In experiment I, the lemurs' responsiveness to video content was assessed by presenting videos of either a predator or a human caretaker to the whole group and scoring their responses. In experiment II, lemurs were shown videos of conspecifics either yawning or resting, in individual setting (session 1) and in group setting (session 2).	Video presentation	In experiment I, the lemurs moved to a higher location and produced more vocalisations in the predator condition than in the caretaker condition, indicating responsiveness to the videos. In experiment II, the lemurs rarely yawned: one yawn was observed in session 1 and two yawns in session 2.
Scopa and Palagi (2016)	This study examined differences in play sessions and rapid facial mimicry between the tolerant macaque species of Tonkean macaques and the less tolerant Japanese macaques.	17 Tonkean macaques (<i>Macaca tonkeana</i>) and 17 Japanese macaques (<i>Macaca fuscata</i>) (all captive)	Dyadic play bouts of the two macaque species were recorded and the occurrence of facial expressions and the duration of the interactions was scored.	Behavioural sampling	No difference in the facial display repertoire was found between the two species, but bared teeth displays and lip smacking was more frequent in the more tolerant Tonkean macaques. Rapid facial mimicry was only found in Tonkean, but not in Japanese macaques.
Seyfarth et al. (1980)	This study tested vervet monkeys' responses to different alarm calls of conspecifics.	3 groups of wild vervet monkeys (<i>Cercopithecus aethiops</i>), each group containing 16–34 individuals	Three different types of alarm calls were played back from a hidden speaker to groups of vervet monkeys: leopard alarms, eagle alarms and snake alarms.	Playback sound presentation	The monkeys showed different responses to different alarm calls: they ran into trees for leopard calls, looked up for

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Table A1 (continued)

Reference	Purpose	Sample	Procedure	Measures	Results
Slocombe et al. (2009)	This study tested whether chimpanzees can extract information from screams about the social roles of fighting chimpanzees, even when they cannot see them.	10 captive chimpanzees (<i>Pan troglodytes</i>)	Responses of the monkeys were recorded. Chimpanzees were presented with sequences of screams that were congruent or incongruent with the social hierarchy. For example, a congruent stimulus would be an aggressor scream of a lower-rank individual followed by a victim scream of a higher-rank individual. Looking durations were measured.	Playback sound presentation	eagle calls and looked down for snake calls. Subjects looked longer toward incongruent scream sequences than toward congruent scream sequences.
Slocombe et al. (2010)	This study asked whether chimpanzees can distinguish between different scream types.	6 wild chimpanzees (<i>Pan troglodytes</i>)	The chimpanzees were presented with playbacks of severe, mild victim screams and tantrum screams and their responses were recorded. All stimuli were also analysed acoustically.	Playback sound presentation	Chimpanzees looked longer at severe victim screams than at mild victim screams and tantrum screams, even though tantrum screams are acoustically similar to severe victim screams.
Stevens et al. (2017)	This study tested yawn contagion in bonobos in response to videos of in-group and out-group conspecifics.	8 captive bonobos (<i>Pan paniscus</i>)	The bonobos were presented with videos of in-group and out-group conspecifics. Yawning in response to the videos was compared to yawning in response to control videos of neutral expressions taken from the same video recordings as the yawns. Visual attention was measured as well.	Video presentation	There were no significant differences in yawning between yawn and control videos. Also, no significant difference was found in yawning between in-group and out-group videos. Attention did not differ significantly between conditions.
Tan et al. (2017)	This study examined to what extent bonobos help and yawn contagiously in response to unfamiliar, non-group members.	40 captive bonobos (<i>Pan paniscus</i>)	Experiment I tested whether bonobos would release a pin to provide an unfamiliar conspecific with food. In experiment II, bonobos were presented with videos of yawning group mates and strangers, as well as videos of neutral faces from the same individuals. The amount of yawns was counted for each video type. Experiment III was a control experiment to test whether bonobos were able to discriminate the videos of strangers from the videos of group members.	Food provision task, video presentation	Bonobos helped unfamiliar non-group members to gain access to food without any selfish benefits, even if the other subject did not signal for help. They also yawned significantly more in response to yawn videos than to neutral videos. Contagious yawning did not differ between videos of strangers and videos of group mates, even though the bonobos could discriminate videos of strangers from videos of group mates, as shown by longer looking times for the stranger videos, at least on the first day of presenting.
Waller et al. (2016)	This study tested whether crested macaques can use conspecifics' facial expressions to predict the outcome of a social scene.	3 captive crested macaques (<i>Macaca nigra</i>) (2 training only)	The subject was presented with a video of two monkeys approaching each other. The facial expression at the end was manipulated to be neutral, or to display a scream, open-mouth threat or bared-teeth display. Then, the monkey chose between the outcomes grooming and injury.	Video presentation, 2-alternative forced choice task	More peaceful outcomes were chosen after a positive expression and more negative outcomes when a neutral expression was displayed. In the negative expression conditions, the subject did not choose more negative outcomes. Overall, the presence of facial expressions was associated with more friendly outcomes.
Whitehouse et al. (2016)	This study asked whether Barbary macaques have increased attendance to scratching behaviour, whether they show contagious scratching and whether there were effects of familiarity.	6 captive Barbary macaques (<i>Macaca sylvanus</i>)	Barbary macaques were shown videos of familiar and unfamiliar conspecifics engaged in scratching or in neutral behaviour. Their scratching behaviour and attention toward the video was scored.	Video presentation	No contagious scratching was reported, but the Barbary macaques attended more to the scratching videos than to the neutral videos. Also, they attended more to familiar individuals than to unfamiliar individuals. The monkeys attended most to familiar, weakly bonded individuals.

^a Although these studies provided valuable insights into rhesus macaques' responding to emotional expressions, we highly discourage the use of electric shocks in present and future primate research.

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