



Social contagion in primates: Moderating factors and significance for individuals and the group

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ABSTRACT

Social contagion, which involves behavioural and emotional state matching, is a crucial process for healthy social functioning. In humans as well as other species, it underpins key elements of social interaction, including empathy and social learning, thereby allowing individuals to effectively engage with others and their environment. Given their highly social nature and complex societies, studying social contagion in primates sheds light on the evolution of these processes and their significance in individuals' daily lives. Here, we review this research, and identify factors that are thought to moderate the presence of social contagion; namely age, sex, dominance rank and social closeness. Although there are few direct comparisons in the literature, patterns of contagion and the factors influencing them vary across species and behaviour, appearing to differ especially between emotional contexts. We therefore seek to categorise contagious behaviour along an affective dimension, highlighting when there are ambiguities, and then considering the distinct evolutionary benefits of positive and negative social contagion. We further consider the significance of social contagion within social learning, using this as a unifying framework to understand contagion.

1. Introduction

As social animals, the lives of human and non-human primates are constructed and shaped by their relations with others, from fleeting interactions to life-long relationships. The scientific literature is increasingly emphasising the importance of affective mechanisms that underly social behaviours, with some proposing that we are now in a new scientific era of 'affectivism' (Dukes et al., 2021). Basic state matching processes can be divided into three core behavioural and affective components – *mimicry*, *behavioural contagion*, and *emotional contagion*. Together, these mechanisms underly social contagion, a broad term for the spread of behaviours or affect from one individual to another (Levy and Nail, 1993). Studying these three components, and the pattern of factors that influence their expression across different contexts, can reveal the nature of these contagious processes and their underlying mechanisms. This in turn can elucidate the importance of these processes, both for wider social functioning and for more specific processes including empathy and social learning.

Although behavioural and affective state matching have been extensively studied within the Primate order, a comprehensive review is lacking. Comparing findings from different primate species and contexts

offers an invaluable route to understanding the nature and significance of social contagion, including in humans. In this review, we start by defining the relevant concepts and the key models and processes. We then highlight the factors that affect contagious processes, structuring the review around the three components of social contagion. Secondly, we consider the importance of contagion for the social lives of primates, using multiple lenses to assess the significant contributions.

1.1. Components of social contagion

Mimicry, behavioural contagion, and emotional contagion are core building blocks of empathy (Adriaense et al., 2020; Brooker et al., 2021), whereby empathy is broadly defined as the sharing and understanding of others' emotional states (Cuff et al., 2016; Preston and de Waal, 2002). Empathy is proposed to include affective elements, relating to experiencing the relevant emotions, and also cognitive elements, including perspective taking and theory of mind (Cuff et al., 2016). The structure of this highly important ability has received much research attention. The central mechanism by which we are influenced by the emotions of others around us was theorised in the influential *Perception-Action Model* (PAM; Preston, 2007; Preston and de Waal, 2002). The

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PAM holds that when an individual perceives the affective state of another, this spontaneously activates their own personal neural representations for the target and their state and situation, thus leading to a complementary experience and understanding of the emotion. In other words, behavioural and emotional mimicry that are thought to underpin empathy. De Waal developed the Russian Doll Model, (De Waal, 2007) which holds this mechanism as being the heart of empathy, around which further layers are organised, such as perspective taking, consolation, and targeted helping. These increasingly complex cognitive and affective layers are all dependent on the core self-other matching mechanisms.

Although the Russian Doll model has been so far very impactful, some have challenged its underlying linear structure which may not accurately reflect the relation between empathy's underlying elements. An alternate model proposed is the 'combination model' (Yamamoto, 2017), which describes three key components: emotional contagion, understanding of others, and prosociality. These components are independent but can combine to underpin empathic behaviours (such as consolation, arising from a combination of all three). Importantly, the Combination model does not treat emotional contagion as the basis which all other empathic components depend on, which contrasts to the Russian Doll model. Nevertheless, the Combination model still considers emotional contagion a bedrock necessary for much empathic functioning, including cognitive contagion, collaboration, and consolation.

The state matching processes at the heart of empathy can be distinguished into three key processes, which can all be considered forms of social contagion. Firstly, **mimicry** is defined as the involuntary, automatic and fast copying of another's physical appearance (Chartrand and Bargh, 1999; Zentall, 2001). This can also be referred to as motor mimicry or behavioural mimicry, and has been largely studied through the mimicry of facial expressions. Secondly, **behavioural contagion** is when an individual demonstrates a species-typical behaviour after perceiving another demonstrate a similar behaviour (Zentall, 2001). This is also referred to as motor contagion, and is different to mimicry in that it encompasses entire self-directed or social behaviours and actions, rather than basic single-component expressions and postures. Examples include contagious scratching and grooming. It is important to note that the theoretical distinction between mimicry and behavioural contagion can become blurred, as some behaviours lie in the middle of the spectrum. For example, yawn contagion involves the automatic copying of a facial expression, so could be considered mimicry, but also involves additional components (i.e. associated bodily and auditory elements), and so is generally classified as behavioural contagion. In most observational studies, there is also no way to verify whether copying is happening automatically, or under voluntary control, and so this distinction is largely theoretical.

The third component is **emotional contagion**, also known as emotional mimicry, emotional transfer or affective empathy. This is the emotional state matching of one individual with another (De Waal, 2007). Behaviour can induce specific emotions, and emotions can induce specific behaviours, thus behavioural and emotional contagion are intimately linked. However, while behavioural contagion does not necessitate a particular emotional profile, and can be identified purely through behavioural observations, emotional contagion must be measured through means that assess the underlying affective state.

1.2. Social contagion and emotion

Emotion is understood and defined very differently by separate research groups and disciplines. Here, we follow Anderson and Adolphs (2014) definition of emotion that is inclusive of many species: an emotional state is a core neural state, triggered by particular internal or external stimuli, which in turn controls a range of somatic, cognitive and behavioural changes – changes which are persistent, scalable, generalisable, and have valence. Emotions are often characterised along two dimensions; arousal and valence. Arousal refers to the general level of

activation, and valence refers to the positive or negative 'charge' attached to the state, which is generally understood in terms of pleasure vs displeasure (Russell, 1980). As specific emotions can be associated with specific behaviours, behavioural states can also be considered in relation to these affective dimensions. Emotional contagion research has traditionally focussed on negatively valenced emotions, as they are clearer to induce and to observe (Pérez-Manrique and Gomila, 2022). This research focus on negative valence may have biased our understanding as to how and when contagion occurs, and future studies are needed to address this by considering a broader range of emotional contexts. Here, we emphasise the distinction between negative and positive behavioural and emotional contagion, highlighting areas of missing research. Categorising the research according to valence can reveal distinct patterns of influence reflecting different underpinning mechanisms, and this division also highlights separate evolutionary benefits that positive and negative social contagion bring to the individual and the social group.

1.3. Social living

As has been found across a wide range of taxa, including primates (Alexander, 1974), living in a social group bestows an animal with numerous survival benefits, notably: reduced predation risk and increased resource access. Further advantages are obtained by animals within the group who develop strong dyadic relationships with others: the quantity and quality of these relationships, in humans and other primates, are a crucial predictor for lifespan, reproduction, and offspring survival (Archie et al., 2014; Silk et al., 2003; Snyder-Mackler et al., 2020).

In the second half of this review, we consider the significance of social contagion for the individual and the group, drawing on how contagion is shaped by and increases the benefits of group living. We consider these implications in terms of how social contagion can strengthen and increase an individual's dyadic relationships, and also how social contagion multiplies the broader benefits of being in a group. Contagion enables higher level empathic processes which facilitate rich and successful social living, and additionally, contagion allows knowledge and information to be effectively transferred from one individual to another. It is intrinsically linked to social learning, which is defined as the learning of the value of stimuli in the environment from observing others (Olsson et al., 2020). Whilst categorising contagion according to valence may help make sense of the patterns of influences, considering contagion in the broader context of social learning offers a unified view for the importance of all forms of social contagion.

2. Social contagion in primates

State matching can occur across neurophysiological, cognitive and behavioural dimensions, and the three levels of social contagion - mimicry, behavioural contagion and emotional contagion - are studied using different methodologies. Mimicry and behavioural contagion have been studied through recording motor movements in observational and experimental set-ups, whilst emotional contagion has been studied using behavioural correlates of emotion and physiological measures of the underlying emotional state.

2.1. Mimicry

Mimicry is broadly defined as the involuntary copying of another's movements, posture, facial expressions or vocalisations (Chartrand and Bargh, 1999; Zentall, 2001). An intimately linked concept is imitation, which is broadly defined as when an observer copies a feature of the body movement of a model (Heyes, 2001). Some definitions of imitation require that the observer understands the intentions of the behaviour and its consequences, emphasising imitation as a cognitive process (Tomasello, 1990). Moreover, a distinction is often made between forms

of true imitation and the more basic, species-typical processes of mimicry and contagion (Zentall, 2006). Whilst mimicry refers to an automatic, involuntary process, imitation refers to voluntary, deliberate behaviour.

Much of mimicry research explores under which conditions mimicry is most likely to occur, which is key to understanding the cognitive underpinnings of mimicry and the top-down cognitive mechanisms at play. It appears that mimicry develops at some stage in infancy, and can be affected by the sex, rank and social closeness of involved individuals, according to species-specific patterns. Thus far, research is dominated by a focus on facial mimicry, although there is also evidence for bodily mimicry within the social learning literature.

2.1.1. Facial mimicry

Facial mimicry has been established across numerous primate taxa within the context of play. Palagi et al. (2019) found evidence for facial mimicry in chimpanzees (*Pan troglodytes*) and western gorillas (*Gorilla gorilla*) during play, across individuals of all sexes, ages and ranks, although they did not compare rates across these demographic factors. In both apes, there was evidence for Rapid Facial Mimicry (RFM), defined as mimicry that occurs within 1 second of perception, which indicates an automatic and involuntary process. Delayed Facial Mimicry – mimicry that happens between 1 and 5 seconds after perception – was found amongst the chimpanzees but not gorillas. It is likely that this response involves more indirect neural pathways, and top-down control mechanisms. Bresciani et al. (2022) replicated the finding of RFM in gorillas, and analysed the influence of sex, age, or social closeness on RFM occurrence and latency. They found that players of the same sex mimicked each other faster than in opposite sex pairs, which they interpret as evidence that similarity between individuals facilitates faster RFM. However, this was not the case in terms of similar age, as age had no influence on RFM. Counter to their prediction, pairs with closer social bonds, as measured by grooming and contact sitting, mimicked each other less often, although the authors warn that the measure of social closeness used may not be valid.

Facial mimicry in play is present from early in development in bonobos; both RFM and DFM were found in bonobo infants, with no sex difference (Bertini et al., 2022). RFM has also been established in orangutans (*Pongo pygmaeus*) (Davila Ross et al., 2008), who found different patterns of mimicry according to age. Whilst RFM did also occur in infants, the effect was more pronounced in juveniles and in adolescents, as well as in partners whose ages differed by more than 2 years. Play with individuals of a different age involves more of an imbalance and so synchrony with one another is even more important than usual. They also found that RFM was non-universal (9 out of 25 orangutans didn't mimic facial expressions at all), which emphasises that this automatic process can be influenced by individual and socio-emotional factors, and may be most pronounced in specific contexts.

Evidence for facial mimicry in play is also found in select monkey species. Mancini et al. (2013) studied geladas (*Theropithecus gelada*), and found that play happened faster and more often between mother-infant pairs than other pairs, emphasising the effect of social closeness from early in development. RFM has also been found in wild geladas, where rates were highest in play sessions that were balanced, and where individuals lip-smacked (a context-independent affiliative expression) (Gallo et al., 2022). Patterns of RFM in two macaque species differed: Tonkean macaques (*Macaca tonkeana*) – a more socially egalitarian species – rapidly mimicked facial expressions, and the closely related but more despotic Japanese macaques (*Macaca fuscata*) did not (Scopa and Palagi, 2016). The authors suggest that this may be because Tonkean macaque society is less hierarchically rigid and play is used to test and negotiate social relationships, and therefore mimicry and coordination in play is key. However, RFM was subsequently found in another despotic macaque species – the rhesus macaque (*Macaca mulatta*) (Facondini et al., 2024). Here, RFM was most commonly directed to

dominant individuals, and most frequent in play-bouts involving two sub-adults, suggesting a role played in uncertain or competitive interactions. One study has identified RFM in Platyrrhini ('new world primates'); three species of spider monkey demonstrated RFM in play, with no significant effects of sex, age, relationship quality, or the species (Cordoni et al., 2024). Whilst these nonvoluntary mimicry mechanisms must therefore be deep rooted in our primate evolutionary history, it is clear that even small social differences make an impact on how and when mimicry is employed.

Overall, facial expressions in play are mimicked by individuals across rank and sex, even from early in development. RFM appears to occur especially in contexts when play could be more unpredictable and therefore must be carefully coordinated: when age gaps are larger, and in species and at development stages where play is used to test social relationships. This could perhaps also explain why RFM is more common among gorillas who are less socially close, and whose interactions may therefore be more unpredictable. The influence of social closeness has not been extensively studied however, and the faster and more frequent RFM in mother-infant gelada pairs is at odds with the gorilla finding.

Facial mimicry outside of the context of play has received little research attention. The only other context in which RFM in primates has been explored is during sexual contact in bonobos (*Pan paniscus*), by examining the silent bared teeth display. This study revealed that social closeness did not predict occurrence of RFM, although it was more common in sex between females (the dominant sex) than in heterosexual contacts (Palagi et al., 2020). Bonobos use sex to regulate social tension and strengthen alliances (Clay and de Waal, 2015; de Waal, 1989), which is especially important in females, and so – similar to play that tests social boundaries – this may drive the heightened mimicry between females.

Whilst play is traditionally considered a positive interaction, there is however no established correlation between play and positive affect across animal species (Adriaense et al., 2020; Ahloy-Dallaire et al., 2018). It is a varied and nuanced behaviour that can involve shifting between positive, cooperative states and negative, competitive states (Cordoni and Norscia, 2024). This variance of play could explain the apparently opposing effects found in the literature. RFM may occur most where individuals are motivated to pay attention to and synchronise with their interacting partners, but influential factors may vary widely between the context and type of play. During play that is an affiliative reinforcement of social bonds, individuals may preferentially mimic those they are socially close with. During play that serves to test social boundaries, factors such as rank may drive the effects more. Future RFM research in play could restrict analyses to play that occurs within a particular context (e.g. in times of social tension), or include measures of overall emotional arousal, to explicitly test these hypotheses.

Mimicry in the context of play has also been studied in terms of vocalisations. Chimpanzees replicated their playmates' laughter during play bouts, with evidence for both rapid mimicry (within 1 second) and delayed mimicry (between 1 and 5 sec), although there was limited evidence for laugh replications in infants (Davila-Ross et al., 2011). Whilst laugh mimicry has not yet been studied in other species, this would be an important parallel line of study, as vocal mimicry may play a complementary role in coordinating interactions.

Facial mimicry in primates has not been studied in any purely negatively valenced contexts: it is unknown if other animals mimic 'negative' facial expressions such as fear or disgust. In humans, there is limited evidence for the mimicry of negative expressions, with effects either not present (Fischer et al., 2012), or only distinguishable in highly empathic people (Rymarczyk et al., 2016). Testing when and whether negative facial mimicry occurs in other primates is an important next step. It would allow us to tell whether mimicry mechanisms are widespread and inclusive of any emotional display, or are only selected for when they serve a particular social function, as in play.

2.1.2. Bodily mimicry

Facial mimicry has an important role in primate face-to-face interactions, but interactions are also shaped by synchrony in bodily posture and motor actions. Although bodily motor mimicry is infrequently referred to as such in the contagion literature, the wider literature on social learning in primates offers some evidence for motor mimicry beyond facial expressions.

There is evidence across many different species that individuals replicate the motor actions of others (reviewed by Whiten and van de Waal, 2018). For example, tufted capuchins (*Cebus apella*) copied the motor actions of their group members when foraging for food in a novel piece of equipment (Dindo et al., 2009). Marmosets (*Callithrix jacchus*) copied the way a model used their mouth rather than hands to open a food canister (Voelkl and Huber, 2000), and this was also replicated in vervets (*Chlorocebus pygerythrus*) (Waal and Whiten, 2012). Another study with found that infant vervets copied the specific way their mothers processed a novel food item (sandy grapes), highlighting copying even in young individuals (van de Waal et al., 2014). Similarly, infant marmosets, when watching older individuals forage, acted synchronously, by moving to manipulate the same object or feed on the same source (Schiel and Huber, 2006).

An experimental study of how chimpanzees learn to crack nuts revealed evidence for motor mimicry (Marshall-Pescini and Whiten, 2008), and an analysis of the synchrony between chimpanzee model and observer revealed that the observer does indeed unidirectionally mimic the model, giving rise to behavioural synchrony (Fuhrmann et al., 2014).

The nature of this apparent replication remains a matter of debate: Tennie et al. (2009), (2020) propose the 'zone of latent solutions' hypothesis, arguing that instead of copying the behavioural form, individuals are simply cued by others to re-innovate the same behaviours, and therefore motor mimicry is not involved. Support for this theory comes from findings that there are very few instances of behaviours that are truly unique to only one population (Motes-Rodrigo and Tennie, 2021), and that specific behaviours, including nut cracking in chimpanzees, appear to have been re-innovated in multiple separate populations (Tennie et al., 2020) – although field experiments have not found any evidence for nut cracking re-innovation (Koops et al., 2022). Whilst simpler behavioural forms, e.g. leaf swallowing (Menzel et al., 2013), may be explained by this account, it remains controversial as an explanation for more complex, multi-step behaviours that are more challenging to re-invent, e.g. termite fishing (Lonsdorf, 2006); although these behaviours also must involve processes beyond basic motor mimicry. Some instances of motor mimicry could also be explained by other motivational mechanisms (Zentall, 2012). Social facilitation, wherein a behaviour is increased by the presence of another individual (Zajonc, 1965), could account for apparent mimicry of foraging techniques; for example, other individuals foraging nearby an observer may lead to increased arousal and subsequent increased exploration of their environment. Controlling for the social surroundings, as well as studying the detail of the form matching in motor mimicry, is important for distinguishing mimicry from other social processes. Further evidence for exact temporal synchrony, as in the nut-cracking research (Fuhrmann et al., 2014), would also strengthen the case for motor mimicry.

Beyond the copying of motor actions independent to an instrumental goal, specific motor actions without any clear goal can also spread through populations; a group of capuchins were observed to develop the habit of pushing fingers into specific facial areas of close companions (Perry et al., 2003), and Japanese macaques developed specific forms of handling stones (Leca et al., 2007). Although it is also possible that such behaviours could be explained as a result of emulation, whereby individuals copy the outcome of the action, the replication of apparently non-functional motor patterns could also indicate the presence of motor mimicry rather than a mimicry of a goal-directed action irrespective of form. Further evidence comes from a study of rhesus macaques, which found several correlating types of motor mimicry, including the rapid

mimicry of bodily posture (Anderson and Kinnally, 2021).

Whilst all of these behaviours are not rapid mimicry as such, they suggest a propensity to copy particular motor actions, which may well be underlain by rapid mimicry mechanisms. The behaviours are varied in context and form, and found in individuals across ages, sexes and ranks. It therefore follows that primates should rapidly mimic body posture and motor actions during emotional exchanges and social interactions too. Bodily gestures are particularly important in play, to communicate playful intention (e.g., Hobaiter and Byrne, 2014), and so primates may mimic each other's actions in play as well as facial expressions. Rapid mimicry of body movements during play has already been found to occur in dogs (Palagi et al., 2015). Future research could also test whether bodily motor mimicry is used in other affiliative contexts, e.g. grooming or sex, or negative social interactions, e.g., bluff displays. Comparative research could then reveal in which species and contexts facial or bodily synchrony is most important, which would have interesting implications for the evolution of communication.

2.2. Behavioural contagion

Behavioural contagion refers to the contagion of species-typical behaviours. This includes self-directed behaviours (e.g. scratching and yawning) that are sometimes considered mimicry. However, here we class these as behavioural contagion, as they take place over a longer time-frame, and have multiple motor and auditory components and forms (Brooker et al., 2021). Behavioural contagion also includes social behaviours (e.g., grooming), which must be considered over a longer time-frame than other forms of motor mimicry, and may be influenced by more top-down control processes. As with mimicry, behavioural contagion studies have emphasised the role of sex, rank and social closeness as key factors that influence behaviour.

2.2.1. Yawn Contagion

The majority of behavioural contagion studies in primates (and other animals) focus on yawning. The function of yawning itself is debated: as reviewed by Massen and Gallup (Massen and Gallup, 2017), it is thought to serve the physiological purpose of altering blood supply and thereby cooling the brain, and has also been linked to promoting a change of state (between wake/sleep, or high/low cortical activity). Whilst some yawns are triggered spontaneously, yawns are also triggered by perceiving others yawn (or even just imagining it), and this contagious yawning effect has been found across numerous primate species.

Contagious yawning in chimpanzees has been shown across many different populations, using a range of methods. Initial evidence came from a smaller scale experimental study showing adult chimpanzees yawned in response to video stimuli, although infants accompanying their mothers did not (Anderson et al., 2004). Campbell and de Waal (2011) showed that the yawn contagion effect was more pronounced in response to videos of known individuals than out-group members, and the effect was robust across adult males and adult females. A separate study found that among different known individuals, yawn contagion did not increase with improved relationship quality, and that male yawns were more effective triggers than female yawns (Massen et al., 2012). Furthermore, adult chimpanzees yawned in response to videos of the yawns of conspecifics, but not of humans (Amici et al., 2014). An observational study confirmed that the yawn contagion effect is found across different contexts in the daily lives of chimpanzees, and although males spontaneously yawned more often, they were not more likely to either trigger a yawn or catch a yawn (Campbell and Cox, 2019). This study also found that infants yawned after perceiving others yawn, although numbers were too low to draw firm conclusions.

In bonobos, yawn contagion was shown in response to video stimuli, irrespective of whether the video was of a familiar or unknown individual (Tan et al., 2017). This has been interpreted to reflect their xenophilic nature. Nevertheless, a familiarity effect was demonstrated in an observational study, re yawns were more effective triggers (Demuru

and Palagi, 2012). Another observational study found no familiarity effect – possibly due to high levels of social closeness throughout the group – but did find that females with sexual swellings were more powerful triggers of contagion (Norscia et al., 2022). Finally, a study using both experimental and observational techniques found opposite trends according to the methods used (De Vittoris et al., 2024). When bonobos were shown videos of yawns, younger and familiar individuals were the most powerful triggers, whereas in the observational data, older and less socially close individuals were more powerful triggers. This is an important reminder that the exact experimental methods – e. g., whether yawns are presented without context, what time frame is used – greatly influence the results found. Yawn contagion has also been reported in adult orangutans, where video avatars of both known and unknown individuals induced yawns to a similar degree (van Berlo et al., 2020). In gorillas however, across age, rank, and sex, video stimuli did not elicit yawns (Palagi, Norscia, and Cordoni, 2019).

Research has also been carried out with monkey and lemur species, with patterns of findings inconsistent across studies. In captive geladas, yawn contagion was higher between individuals who groomed each other more (Palagi et al., 2009), although in wild geladas, yawn contagion was higher between individuals from different sub-groups (Gallo et al., 2021). Palagi et al. (2009) also reported no occurrence of contagious yawning in juveniles and infants, and a greater degree of contagion in females, whilst Gallo et al. (2021) report that male and female yawns were similarly effective as triggers, and males caught yawns more. Stump-tailed macaques (*Macaca arctoides*) yawned more in response to yawn vs control videos, but also self-scratched more, indicating unusual anxiety behaviours at the stimuli (Paukner and Anderson, 2006). Red-capped mangabeys (*Cercocebus torquatus*) also yawned more in response to yawn vs control videos, of conspecifics, baboons, and humans, and demonstrated a familiarity effect for conspecifics and humans (Pedrucci et al., 2022). Beyond Cercopithecidae (Old world monkeys), an observational study identified yawn contagion in wild Geoffrey's spider monkeys (*Ateles geoffroyi*) (Valdivieso-Cortadella et al., 2023). The effect did not vary according to sex, kinship or social closeness. An initial experimental study found that two species of lemur – ring-tailed lemurs (*Lemur catta*) and ruffed lemurs (*Varecia variegata*) – did not respond differently to yawn and control stimuli (Reddy et al., 2016). However, an observational study with wild indri lemurs (*Indri indri*) did find evidence for contagious yawning; the effect was not influenced by age or sex, but contagious yawning was more common between pairs that groomed more (Valente et al., 2022). Additionally, another recent observational study found that yawns were contagious in ruffed lemurs, and that the contagion effect was consistent across different levels of social integration (Lemes and Amici, 2024).

On the whole, whilst contagious yawning occurs in numerous primates, there is no clear trend in factors that universally moderate it. The effect of familiarity is variable across and between species, seemingly depending on slight methodological changes. The varying influence of males vs females as triggers reflects differences in social structure across species, with female yawns being more contagious in bonobos, and male yawns being more contagious in chimpanzees. This could reflect variation in the salience of different individuals' behaviour, with more socially important individuals being more closely attended to. Variation in attention makes it challenging to interpret the literature in general, as attention is biased by familiarity (Whitehouse et al., 2016), which could drive the familiarity preferences. Even when attention is measured through considering gaze, it is unclear what aspect of the yawn is being attended: certain features may be more salient in certain contexts (for example exposed teeth may draw less attention in affiliative contexts).

To add further nuance, recent literature indicates that there are different types of yawn, which may have different social meanings. The emotional profile of yawning is unclear: yawns are associated with relaxation, occurring more often in times of rest than in times of social conflict (e.g., Demuru and Palagi, 2012; Leone et al., 2014; Zannella et al., 2015), and yet are also associated with anxiety, as indicated by

increased scratching (Leone et al., 2014; Vick and Paukner, 2010). Distinguishing yawns based on their duration, and whether or not teeth are covered, reveals that different yawn types are associated with different contexts (Leone et al., 2014; Zannella et al., 2015). Overall then, seemingly contradictory patterns could be explained firstly by differences in the underlying emotional and attentive state of the observer, which may bias them to attend to particular individuals or features of the yawn, and secondly by differences in the yawn that they are exposed to, which could signal multiple different emotional states. Future research is needed to carefully control for the context that yawns are observed in, and distinguish between differences in length and openness of the yawn. Uncertainty as to what emotions are associated with yawns could be addressed by complementing behavioural observations with physiological measures of arousal (as discussed in Section 2.3). This would allow for meaningful comparisons of the contagion of corresponding yawn types across species, and comparisons with the contagion of other more emotional behaviours.

2.2.2. Negative behavioural contagion

Scratching is a self-directed behaviour that primates perform to alleviate itching, but also during times of psychological and physiological stress. For instance, scratching is elevated during aggressive interactions and predation attempts (Palagi and Norscia, 2011) and reduced during affiliation and after play (Aureli and Yates, 2010; Norscia and Palagi, 2011). For this reason, scratching is considered to be associated with negative emotional states. Scratching has been found to be contagious in multiple species of monkey and ape. Japanese macaques scratched after observing a familiar conspecific scratch (Nakayama, 2004), and rhesus macaques scratched when their cage-mates scratched, and when viewing videos of unfamiliar conspecifics (Feneran et al., 2013). Interestingly, Barbary macaques (*Macaca sylvanus*), when shown videos of both familiar and unfamiliar conspecifics scratching, attended to the stimuli, but did not start scratching themselves (Whitehouse et al., 2016). The authors suggest this species difference could be explained by differences in the presentation of video stimuli, or by the fact barbary macaques are more socially tolerant, meaning they may have a different strategy for noticing and responding to negative emotions. In line with this idea, the more despotic Tibetan macaques (*Macaca thibetana*) also demonstrated scratch contagion, and there was a social closeness effect (Zhang et al., 2022). Scratch contagion has also been recently reported in lemurs and spider monkeys, with no evidence for a social closeness effect (Lemes and Amici, 2024; Valdivieso-Cortadella et al., 2023). Contagious scratching is also present in Bornean orangutans, who increased self-scratching when observing conspecifics scratching, and (to a lesser extent) when perceiving only the sound of scratching (Lam  ris et al., 2020). Surprisingly, in tense social situations, individuals caught scratching from their close social partners much less than from individuals they were not socially close with.

Scratch contagion is evidently not a universally automatic process, and is controlled by higher level processes that reflect social function. The reverse familiarity effect in orangutans is contrary to much of the yawn contagion and facial mimicry literature, but can be understood in the negative context of scratching, as interactions between weakly bonded individuals are more likely to be tense and unpredictable, and monitoring of each other's negative arousal is key. Likewise, this may be of more importance to rhesus, Japanese and Tibetan macaques, as species that are less tolerant, and have higher levels of inter-individual tension, than in Barbary macaques. One problem with this interpretation is that it has been suggested scratching could indicate general arousal rather than specifically negative arousal - it is elevated in play during marmosets (Neal and Caine, 2016). This could be further tested in different species, for example by using cognitive bias tests to assess emotional valence (Adriaense et al., 2019) and is especially important in species such as orangutans where the associations with scratching have not been tested, but just generalised from other primates.

Tense social situations are also associated with other behaviours,

beyond self-scratching. Japanese macaques exhibit vigilance behaviour, raising their heads in a state of alertness, in response to potential ingroup threats. This vigilance behaviour is contagious, especially to lower ranked individuals, and to mothers observing their infants rather than vice-versa (Iki and Kutsukake, 2021). Lower ranked individuals are more prone to ingroup aggression and must therefore be more wary of threats, and mothers must be ready to protect their offspring, so within the context of this specific behaviour, these trends are easy to understand. Other behaviours that are anecdotally reported as temporally clustered may be contagious too. Massen et al. (2016) studied gnawing and scent-marking in marmosets, a fixed-action pattern thought to be used as a territorial defence. Marmosets gnawed and scent-marked significantly more after perceiving others engage in the behaviour.

Some studies have documented an increase in aggression after witnessing it in wild vervet monkeys (*Chlorocebus pygerythrus*) and captive Japanese macaques, kin of a victim of an initial aggression were more likely to subsequently initiate aggression towards the kin of the original aggressor (Aureli et al., 1992; Cheney and Seyfarth, 1986). It is possible this behaviour reflects a contagion process although this would not fully explain its socially-targeted nature. In mandrills (*Mandrillus sphinx*) and Barbary macaques, bystanders showed increased rates of aggression, and this was not just directed towards the kin of the aggressor (Blood and Semple, 2023; Schino and Sciarretta, 2015). These studies did not analyse which factors predict the occurrence of the spread of aggression, and it would be interesting to directly compare whether patterns of the contagion of aggression and anxiety behaviours follow similar trends within and across species, or if social influences differ even for behaviours of similar valence.

2.2.3. Positive behavioural contagion

The contagion of affiliative social behaviours is comparatively under-studied; a more comprehensive approach, that considers contagion in all settings, is needed to fully understand the evolution of contagion and its significance for social functioning. There are no obvious self-directed behaviours associated with positive emotion, but the contagion of allogrooming and social play has been studied.

Grooming in primates is considered to be an affiliative, relaxing behaviour that reinforces bonds and social structures (Russell and Phelps, 2013). Primates engage in self-grooming and allo-grooming, and although no research yet has addressed self-grooming contagion, several studies have looked at the contagion of allo-grooming (hereafter: grooming). The first evidence that grooming was contagious came from an experimental study with marmosets, where individuals initiated grooming more often after watching video playbacks of familiar conspecifics grooming than after watching control videos (Watson, 2011). However, prolonged exposure to the videos resulted in an increase in scratching, indicating the video stimuli were stressful, and the increase in grooming may have been a coping strategy. Alternatively, the scratching could just indicate high emotional arousal. Two studies of macaques have found a grooming contagion effect in non-experimental conditions however. Berthier and Semple (2018) found that in female Barbary macaques, observing grooming led to a decrease in self-directed behaviour, and that observers were faster to groom others, and more likely to initiate the grooming and take an active role. Ostner et al. (2021) replicated the grooming contagion finding in the less socially tolerant rhesus macaques. After observing grooming, adult females engaged in grooming behaviour faster, and were more likely to take an active role. The effect was more pronounced for higher ranked individuals, presumably because their high status means that they are less confined by social restrictions and more able to interact freely. There was no effect of relationship quality however, with individuals being equally influenced by others, regardless of social closeness. The authors suggest this could be due to a ceiling effect, or alternatively because this study, unlike others, controlled for the attention levels stimuli received, and it is possible that attention levels drive social closeness effects.

Grooming contagion has also been reported in chimpanzees (Sandars

et al., 2024). Here, there was an increased contagion effect between socially close individuals, in line with the yawn contagion literature, which could be due to an attention bias. Additionally, social play was also contagious in chimpanzees, with increased rates of contagion in younger individuals, perhaps because play is a key mode of socialisation for juveniles and therefore more salient to them (Sandars et al., 2024). No effects of rank or sex were observed.

Overall, it appears that social closeness and rank are important factors influencing the presence of behavioural contagion across different behaviours and contexts, and in some negative situations there may be an inverse effect of the social closeness bias. The effects of age and sex are yet unclear, and the patterns found may depend on the specific methodology used, as well as the specific context.

2.3. Emotional contagion

When an individual perceives an emotion and then automatically experiences a matched emotion, this involves changes on neurophysiological, cognitive, behavioural and experiential dimensions, and the process can therefore be studied on these multiple levels. Analysing behavioural indicators of emotion, such as scratching behaviour, does not definitively indicate the underlying neurophysiological changes however, and so to truly establish emotional contagion, studies should also address the physiological basis of emotion itself. So far, a variety of physiological measures have been used to demonstrate emotional transfer, and behavioural observations prove vital to supplement these. An ongoing challenge in emotional contagion research in non-human animals is how we can study the subjective experience of emotion; the cognitive bias paradigm has been recently applied to shed light on this. Overall, there is still a notable lack of research on positive emotional contagion, and research into which factors influence emotional contagion.

2.3.1. Physiological research

Early research involved exposing primates to negatively valenced emotional stimuli and recording changes in skin temperature due to arousal driven shifts in blood flow. Baker et al. (1976) tested pigtailed macaques (*Macaca nemestrina*), establishing a drop in temperature when negative audio and visual stimuli were presented. Parr and Hopkins (2000) measured chimpanzees' eardrum temperature, whilst showing them videos of an unfamiliar individual displaying positive/negative emotions, and found a lateralised temperature shift effect, in addition to behavioural indicators of negative arousal (piloerection, pant-hooting and bluff displays) in the negative condition. Similar temperature changes were also recorded in response to general non-social negative stimuli (e.g., displays of needles) (Parr, 2001). This highlights the importance of considering which particular aspects of stimuli are eliciting emotions in the subject. It is challenging to distinguish between a subject 'catching' a negative emotion from a social stimulus, and a more generalised fear response to aversive stimuli. These initial studies involved the animals being constrained in a highly artificial environment, creating an unnatural and probably stressful situation. The development of infrared thermography, a non-invasive way to monitor changes in skin temperature, holds exciting potential for studying emotional arousal in a more ethologically valid way. Nakayama et al. (2004) used this technique to record a drop in the nasal temperature of rhesus macaques when observing threatening stimuli. When presented with audio-video stimuli of conspecifics expressing neutral and negative emotions (coos and screams), nasal skin temperature dropped in response to the negative expressions. Similarly, Kano et al. (2016) used this method to record decreases in the nasal temperature of captive chimpanzees exposed to audio-visual stimuli of other chimpanzees fighting. This effect was then replicated in wild chimpanzees (Dezecache et al., 2017), where aversive vocalisations elicited a drop in nasal temperature, with highly emotional stimuli such as aggressive barks causing the largest drop. A drop in nasal temperature has been repeatedly

verified as an indicator of emotional arousal: in a large cross-species comparison, [Chotard et al. \(2018\)](#) documented a consistent nasal temperature effect across three monkey and two ape species. The thermography literature is therefore clear evidence of a socially precipitated emotional reaction. However, as with the older literature, it is still unclear whether it marks emotional transfer from contagious processes, or a more general fear response to the risk and danger posed by the scenes and stimuli.

In addition to skin temperature changes, arousal-based physiological changes have also been studied through monitoring heart rate and, more recently, pupil dilation. [Miller et al. \(1959\)](#), (1963) ran a series of experiments with rhesus macaques, involving one individual observing another receiving electric shocks. The macaques exhibited clear behavioural signs of distress and chose to avoid the experience if possible (although not when a puppet or rat was substituted in place of the other individual). Their heart rate response whilst perceiving distress in others matched the response when experiencing noxious stimuli themselves, indicating negative emotional contagion, although as before, the negative arousal could also be explained as being a fear response.

One way to circumvent the problem of intrusive stimuli is to study the small nonvoluntary changes in emotional arousal in response to more implicit stimuli. A method used to monitor subtle changes in physiological arousal is through measuring pupil dilation - an involuntary automatic response indicative of increased attention and emotional arousal, linked to activity in social brain areas ([Prochazkova et al., 2018](#)). [Kret et al. \(2014\)](#) presented humans and chimpanzees with videos of unfamiliar conspecifics where the eyes dilated or constricted, and found that subjects from both species synchronised pupil dilation with conspecifics, indicating a matching of arousal. The effect was strongest in human and chimpanzee mothers, which the authors suggest could be due to greater levels of experience prioritising stable relationships. Future studies exploring the conditions under which this automatic and non-conscious state matching is enhanced could elucidate the most fundamental processes that influence emotional contagion.

In summary, changes in skin temperature and heart rate are key methods used to demonstrate the transfer of emotional arousal, although it is a challenge to determine how much arousal is generated just from fear of stimuli and unfamiliar experimental set-ups. Continuing to use non-invasive research techniques such as thermography and pupillometry, and testing primates in a way that causes them minimal possible stress - for example through allowing them to voluntarily approach testing equipment - would minimise the emotional interference from these experimental set-ups. Additionally, these paradigms have much less severe ethical implications, offering captive primates enjoyable enrichment rather than subjecting them to invasive procedures. The existing research has used stimuli of a variety of ages, sexes and familiar/unfamiliar conspecifics, and so contagion can clearly happen across demographic factors, but the varying effects have yet to be explicitly tested. Furthermore, the emotional contagion of positive arousal has yet to be established and must be further researched. Going beyond neurophysiological indicators of arousal, and using behavioural indicators to verify the valence of arousal, will be crucial for correctly interpreting findings.

2.3.2. Behavioural indicators

Emotional contagion has also been studied on a behavioural level. Although the visual contagion of behaviours discussed in the previous section could be explained by motor matching mechanisms that do not necessitate particular emotional states, behavioural observation is still a highly valuable tool for deducing underlying affective states. Behaviours that are firmly linked to a particular emotion are key here. One recent study involved exposing marmosets to negatively aroused cage-mates, whose state of negative arousal was demonstrated through piloerection of their tail ([de Oliveira Terceiro et al., 2021](#)). Upon perceiving

the distressed cage-mates, the marmosets would become aroused (as demonstrated by piloerection) and initiate consolatory behaviours. As piloerection is a non-voluntary behaviour that directly indicates arousal, this behavioural observation forms convincing evidence of emotional transfer too.

Some studies have addressed whether emotion can be vocally transmitted, exposing individuals to vocal expressions of emotion, and inferring changes in affective state from their behaviour. This form of social contagion cannot only involve motor mimicry, as the subjects do not visually perceive the behaviour, and so it must involve responses to the affective content of vocalisations. [Baker and Aureli \(1996\)](#) found that when captive chimpanzees heard agonistic vocalisations from neighbouring groups, they increased aggressive displays and vocalisations themselves. [Videan et al. \(2005\)](#) replicated this finding, and also showed that when chimpanzees heard grooming vocalisations from neighbouring groups, they increased rates of grooming. Individual differences were not studied, but in both studies the effect was found across male and female adults, subadults and juveniles. [Watson and Caldwell \(2010\)](#) carried out a similar study in captive marmosets, finding that when there were high levels of agonistic neighbour vocalisations, the subjects increased agonistic behaviours themselves (e.g. bristling fur). Conversely, when the subjects overheard high levels of affiliative vocalisations from their neighbours, they were more likely to engage in affiliative behaviours such as food sharing and grooming. These behavioural indicators of emotional valence are persuasive, but would be most revealing when used in combination with physiological measures of arousal - for example as in [Dezecache et al. \(2017\)](#)'s audio playback thermography study. Further experimental playback studies involving behavioural and physiological analyses would also be useful in confirming these results and understanding whether vocalisations from particular individuals are more effective in eliciting a response. One behavioural playback study showed that squirrel monkeys (*Saimiri sciureus*) responded more, orienting themselves for longer, to calls that were artificially manipulated to indicate high arousal ([Fichtel and Hammerschmidt, 2003](#)). Pairing artificial manipulation techniques with stimuli from familiar individuals would offer a way to unpick how features such as inherent salience of stimuli vs social and contextual cues affect the transmission of emotion.

Emotional contagion can also be studied on a behavioural level through use of the cognitive bias tests, of which the most commonly used paradigm is the Judgement Bias test. This involves first training animals to associate one cue with a positive outcome and one cue with a negative outcome. They are then presented with an ambiguous cue, and their interpretation of the cue as either positive or negative can reveal their underlying affective state in that moment ([Mendl et al., 2009](#)). The ability to identify the valence of emotional states has been crucial for research into animal welfare ([Clegg, 2018](#)). This test has been recently applied to study emotional contagion in animals, by first exposing the animals to others in negative or positive emotional states, and then presenting them with an ambiguous cue. Pioneering studies in rats found evidence for both positive and negative emotional contagion ([Saito et al., 2016](#)), whilst in ravens there was evidence for negative emotional contagion although no effect in the positive condition ([Adriaense et al., 2019](#)). So far only one study has used primates: [Adriaense et al. \(2021\)](#) socialised a subject marmoset with a peer who just had either a positive experience (their preferred food) or a negative experience (encountered a fake spider), and then tested the subject marmoset with a judgement bias test. They did not find evidence for emotional contagion in either the positive or negative condition, which may be due to challenges with the specific study design or time-frames of the emotions involved. The paradigm remains an exciting new route for studying the subjective experience of emotional contagion in primates, and further studies which use a range of cognitive tests and experimental set-ups will doubtless reveal further insights.

It is overall clear that emotional transfer of both positive and negative emotions does occur, nevertheless the literature does not yet clearly

address the factors that influence when emotional contagion is most pronounced. Future research could distinguish between responses to varied stimuli, to test whether the factors implicated in positive and negative behavioural contagion also drive the contagion of affective states. This link will prove key to understanding the relationship between behavioural and emotional contagion. More generally, future studies that directly compare contributing factors, as well how these shape types of social contagion among different species will enable us to more confidently identify the patterns of variance in how contagious processes are influenced by individual and group characteristics.

3. Significance of social contagion

In [Section 2](#), we reviewed how experimental and observational studies have repeatedly found that contagion effects are influenced by social factors including the sex, rank, and social closeness of the individuals involved. These patterns of influence are highly specific to the species and behaviour in question, and apparent contradictions can only be understood when considering the importance of contagion in the particular social and emotional context. It is therefore imperative to consider the evolutionary functions of contagion, and here we summarise the multiple benefits that automatic contagion processes can serve.

Self-other matching mechanisms and contagious processes enable many social skills fundamental to effective group living, including empathy. Dividing social contagion according to overall valence reveals a possible dichotomy between immediate survival benefits of negative contagion and longer term social advantages of positive contagion. However, it is challenging to classify all behaviours according to this division, and when behavioural and emotional transfer is viewed within the framework of social learning, it is clear that contagion of all valences and degrees has the holistic significance of facilitating knowledge transfer between members of a social group.

3.1. Significance through empathy

Emotional contagion is considered one of the key facets of empathy - as summarised previously, it is the affective process at the core of empathy, that gives rise to cognitive processes such as perspective taking and empathic concern ([De Waal, 2007](#); [Yamamoto, 2017](#)). The significance of empathy to social functioning cannot be understated: the ability to emotionally relate to others is crucial for effective group living and communication, enables prosocial and moralistic behaviours that serve benefits to the group, and ultimately, empathy enables meaningful social connections, which give value to our lives.

The human psychology literature has long emphasised the connection between empathy and communicative skill ([Hogan and Henley, 1970](#)). Understanding the emotional state and knowledge of others allows us to tailor what information to convey, and accurately respond to others' feedback within an interaction. Effective communication is an important skill for all primates, especially great apes, who communicate through a variety of modalities to navigate complex social environments ([Kret et al., 2020](#)). In turn, effective communication facilitates coordination and cooperation, enabling smooth group living.

Empathy is also consistently linked with prosocial behaviour, a link established in the human literature across hundreds of studies, and stable across cultures ([Ding and Lu, 2016](#)). As reviewed by [Decety et al. \(2016\)](#), the ability to relate to the emotional state of others motivates many prosocial behaviours, including helping and comforting individuals in distress. Prosociality is multifaceted, and not all forms are a consequence of empathy - for example, the occurrence of cooperation can simply follow a rule of cost-benefit analysis. Nonetheless, a range of prosocial behaviours found across primate species are underpinned by empathy (and therefore emotional contagion); behaviours that are advantageous to the group and ultimately the individual, aiding survival through inclusive fitness ([de Waal, 2008](#)).

Empathy can drive our evaluation of and responses to complex social

scenarios, and is thought to play a key role in moralistic behaviour. Although emotional contagion and empathic processes are influenced by factors such as familiarity, which can work against moral impartiality, morality is built on certain facets of empathy, especially the ability to take the perspective of others ([Decety and Cowell, 2014](#)). Although a developed morality system is not present in non-human primates, precursors such as targeted helping and an egocentric sense of 'fairness', are established ([De Waal, 2005](#)). Overall, empathy is considered crucial for effective social functioning in complex groups, and through underpinning this ability, behavioural and emotional contagion endow individuals with key skills to navigate their social world.

3.2. Significance of contagion through the lens of emotional valence

Social contagion may facilitate interactions in a wide range of contexts beyond empathy, and a possible separation emerges between additional benefits endowed to an animal experiencing negative or positive contagion. In this section, we use this valence dichotomy to describe how there are immediate survival benefits attributable to the rapid social contagion of negative emotions and behaviours, whilst positive contagion may generate longer positive interactions and social favour.

3.2.1. Negative social contagion

The ability to catch others' negative emotions holds immediate benefits for the observer, as negative emotions often relate to imminent danger. Scratching is a highly contagious behaviour, characterised as unpleasant ([Rothman, 1941](#)) and (as discussed in [Section 2.2.2](#)) is prevalent across many primate species, although is not consistently moderated by the relationship quality between individuals, or other demographic factors. Scratch contagion can have an instant physical benefit if the cause of the original scratching is something harmful to the skin, and an individual responds to another's signal by scratching and remove the harmful substance from themselves ([Sanders et al., 2019](#)). More generally though, scratching is an indicator of negative arousal, and these aroused individuals pose a threat to others in the group as they behave unpredictably ([Aureli et al., 1992](#)). Being emotionally in tune with these individuals, as facilitated by contagious scratching, would enable the group to navigate tense situations better and avoid conflicts ([Whitehouse et al., 2016](#)). One recent study found that macaques with central positions in the social network were more likely to trigger and to catch scratch contagion ([Zhang et al., 2022](#)), which highlights the association between effective social functioning and behavioural contagion.

Behavioural contagion of vigilance also has obvious evolutionary advantages, enabling the group to increase their awareness of danger and synchronise their responses. A collective wave of vigilance is much more effective in predator detection than uncoordinated individual behaviours ([Hare et al., 2014](#)), and mimicking neighbours' behaviour in risk of predation is widespread in preyed species beyond primates, being observed in birds, fish and insects ([Brown and Laland, 2003](#); [Miller et al., 2012](#); [Treherne and Foster, 1981](#)). This evolutionarily ancient behaviour is effective when complex anti predation behaviours are mimicked rapidly, and there is no advantage to selectively mimicking socially close individuals.

The rapid social contagion of negatively valenced emotions and behaviours therefore offers immediate evolutionary advantages, especially to more vulnerable individuals such as those at the bottom of the social hierarchy. As threats can come from anywhere, a bias towards mimicking socially close individuals would not be selected for, although biases to pay attention towards familiar and high ranked individuals may mean that these factors still influence the occurrence of negative contagion.

3.2.2. Positive social contagion

Although social contagion of positive behaviours and emotions may

have less obvious immediate survival benefits, it may nevertheless promote effective and smooth social interactions and aid social relationships, and thus generate longer term fitness advantages.

It appears that facial mimicry can serve to improve social encounters, helping individuals stay in sync and prolonging interactions. Although the emotional associations of play are debated, we here consider mimicry during play as fitting in the positive domain, as it is thought to promote social bonding. Multiple studies have established that play bouts characterised by rapid facial mimicry last longer than those with lower rates of rapid facial mimicry. This has been found in chimpanzees, gorillas, geladas, Tonkean macaques, rhesus macaques and spider monkeys (Cordoni et al., 2024; Facondini et al., 2024; Gallo et al., 2022; Mancini et al., 2013; Palagi, Norscia, Pressi, et al., 2019; Scopa and Palagi, 2016). Similarly, mimicry of laughter in chimpanzee play led to longer durations (Davila-Ross et al., 2011). Mimicry in play is thought to improve communicative exchanges and facilitate behavioural coordination – something especially important in the context of play, where action patterns are high energy and can be similar to aggressions. In bonobo sexual contacts, interactions with RFM lasted longer than those without (Palagi et al., 2020), which the authors attribute to a similar role played by RFM in coordinating motor actions and facilitating reciprocal involvement. In a hetero-sexual context, mimicry could facilitate a direct evolutionary advantage, as longer copulations are more likely to lead to pregnancy, but there are also indirect advantages from extended homosexual encounters, whereby prolonging the positive interaction enables individuals to strengthen social bonds. Likewise, prolonging play interactions builds social relationships and allows individuals to further test and practice action patterns that overall improve social competence. There may be a positive feedback cycle of empathic and social processes, that means close social partners more often interact, attending to and mimicking each other more, which leads to increased social bonding and mimicry.

Positive behavioural and emotional state matching presumably benefits individuals not just on the level of a single positive interaction, but in the longer term too. Research has begun to explore the specific benefits of the ability to catch social behaviours and emotions during interactions. When adult capuchins were exposed to humans who either imitated their motor actions, or performed contingent but non-imitative actions, they spent longer with the imitators, and subsequently chose to interact with them over others (Paukner et al., 2009). An observational study found that adolescent rhesus macaques who mimic conspecifics (including self-directed, object-directed, and postural mimicry) were not more prosocial but received more play solicitations from other individuals - indicating that those who were more in sync with their social surroundings were more socially favoured (Anderson and Kinnally, 2021). It is challenging to unpick the direction of influence here however, as social competence and opportunity for the development of social competence can influence each other in a positive cycle. One longitudinal study found that infant rhesus macaques who mimicked affiliative facial expressions in human carers then grew to be less anxious and more dominant a year later (Kaburu et al., 2016). Whether infants do truly mimic the facial expressions of others, or whether results are a statistical artefact driven by other processes, remains a contentious issue (Davis et al., 2021), but at the least, this study provides evidence that an early responsiveness to the emotional expressions of others does imbibe individuals with some social benefits. Whether the contagion of affiliative social behaviours such as grooming or play provide individuals with long term social benefits has not yet been studied. Further research that addresses which individuals (in terms of age, sex and rank) are more prone to join in social interactions, or longitudinal studies monitoring changes in social competence in these individuals, would provide evidence for the significance of positive behavioural contagion.

On the whole, a propensity to mimic the facial expressions and motor actions of others can benefit individuals through elongating and expanding social interactions, and in some situations generating social favour. This could lead to a feedback cycle that exacerbates effects for

socially close individuals. Effects of affiliative behavioural contagion could also be more pronounced in higher ranked individuals who are less socially constrained, which would also feed into a positive cycle of social favour.

3.3. Contagion and social learning

Separating the significance of social contagion by emotional valence offers a potential explanation for the differing patterns of influences found across different forms of negative and positive valence. However, not all forms of contagion fit neatly within this classification, with behaviours such as yawning and play-fighting having a variable emotional profile, and other forms of contagion such as bodily mimicry not having any obvious emotional associations. The unified role that all forms of social contagion play could be summarised as allowing an individual to respond in the correct way to the socioenvironmental context – whether by sharing a facial expression that facilitates a successful interaction, or by scratching to remove a harmful substance.

Across all contexts, sharing the emotional and behavioural state of others allows information and knowledge to spread through a group. Social contagion is therefore intrinsically linked to social learning - defined as the learning of the value of stimuli in the environment from the observation of others (Olsson et al., 2020). Social learning is pervasive across many domains from foraging to social behaviour, and is of crucial importance to animals who must adapt their behaviour to navigate changing environments. Contagious processes can underpin effective social learning, on both the level of behavioural contagion and emotional contagion.

As discussed in Section 2.1.2, there is a wide range of evidence for the mimicry of particular bodily actions, commonly observed in experimental set ups where animals forage for food. Efficiently learning the best ways to extract resources from the environment, through copying particular motions, would be highly adaptive, and preserved in evolution. Of course, much social learning involves longer periods of attending to other individuals, and cycles of individual learning, exploring and practicing the action, gradually fine-tuning it (Whiten, 2019). This behaviour may have its roots in spontaneous mimicry though; any form of imitation is associated with the fundamental neural mechanisms that allow individuals to relate an action that they observe to a matching action within their own body. It has been suggested that behavioural mimicry is not conscious, but rather that observing specific behaviours triggers individuals to spontaneously perform a familiar action or even re-invent the behaviour themselves (Tennie et al., 2009, 2020). Even with this understanding, individuals with an enhanced tendency to replicate observed behaviours would benefit from an increased transfer of knowledge. This stance does remain controversial, especially in accounting for the mimicry of non-goal oriented actions, and more complex behavioural forms. Overall, the ability and inclination to copy the movements and behaviours of others - instantaneously and non-consciously, or repeatedly over the course of development - is crucial for social learning.

Beyond motor contagion, the contagion of emotions is important for social learning, in particular learning that involves ascribing a value to objects, individuals or events. Clément and Dukes (2017) introduce ‘affective social learning’ as a framework to study this emotional social learning, and distinguish four levels based on the intentionality of the learner. Their first level, requiring no intentionality of social transmission, is emotional contagion itself. When an individual ‘catches’ an emotion from another, this will naturally be associated with the given situation; for example, a mother may scream with fear at a particular hazard, and her child will catch this fear and subsequently associate it with the hazard. More intentional forms of social learning are then built on this foundation: ‘affective observation’ refers to scenarios where the learner actively tries to seek the cause of the emotion, ‘social referencing’ is when, in an ambiguous situation, a learner seeks guidance which is communicated by the knower, and finally, ‘natural pedagogy’ is

when a knower sets out to transmit precise information to the learner.

Affective social learning that does not involve intentionality appears widespread across animals. Puścian et al. (2022) review social learning studies, largely carried out with rodents, and emphasise the role of both negative and positive emotions. The immediate spread of fear in response to aversive stimuli, or an appetitive response after watching others eat, is crucial for social learning about the environment. In primates, there appears to be evidence for all but the last level of affective social learning, as reviewed by Gruber and Sievers (2019). For example, the study of the ontogeny of specific alarm calls in vervet monkeys, whereby infants learn to produce specific calls only for specific dangerous stimuli (e.g., an Eagle alarm call, Seyfarth et al., 1980) could be explained by the reinforcement of a mother replicating a call, and causing emotional transfer, only in the proper dangerous scenario. An example of more intentional social referencing is how chimpanzees evaluate the danger of crossing a road, by pausing and checking the behaviour of others (Cibot et al., 2015; Hockings et al., 2006).

Considering the affective basis of social learning may be especially important when studying biases into when social learning is conducted, and from whom. Recent research has emphasised that in primates, as in humans, individuals bias their learning to those who are more knowledgeable, older, or dominant (reviewed by Whiten and van de Waal, 2018). For example, in an artificial foraging task, chimpanzees were biased to copy the actions of high ranking and expert individuals (Kendal et al., 2015). In humans, socially close individuals are preferentially copied (e.g., Buttelmann et al., 2013), and this may be the case in other primates too. In the wild, social learning is also enhanced between socially close individuals, although presumably this is due to increased time spent in proximity with each other (Price et al., 2017). Considerable overlap between social learning biases and emotional contagion trends has been noted in the rodent literature (Puścian et al., 2022) and for primates, there appears to be a trend of enhanced attention to dominant and socially close individuals in both social learning and contagion. However, the social learning literature largely ignores affective arousal, instead concentrating on cognitive data in humans, or behavioural data in animals (Gruber et al., 2022). This makes it challenging to unpick the extent to which social learning strategies are based on emotional contagion tendencies, or to what extent they involve overcoming conflicting biases of affective contagion. Uniting social learning research with an affective approach would reveal key insights here.

4. Conclusions

Mimicry, behavioural contagion and emotional contagion have been studied across primate species, using both experimental and observational, behavioural and physiological techniques. Some behaviours have received much research attention: yawn contagion, and the occurrence of facial mimicry in play, have been explored across many different taxa, and a range of moderating social factors have been addressed. However, the emotional profiles of even these well-studied behaviours remain ambiguous. Other areas have received little or no research attention. Facial mimicry in negative social contexts has not yet been studied in primates, and may be regulated by different processes to those in play. Mimicry on the level of bodily rather than facial movements is also under-studied. The factors influencing the prevalence of yawning and self-directed behaviours are relatively well researched, but due to restricted methodologies, it is as yet unclear what moderates the contagion of affiliative social behaviours. This form of behavioural contagion may be especially important for social bonding and affiliation, and so is an important area to research further. Finally, the contagion of affective states has been studied in the context of negative emotions, but little physiological research has addressed the spread of positive emotions. These emotional contagion studies have used a variety of stimuli and subjects, but have not directly compared which social lead to increased emotional contagion. Research addressing this question would

allow more direct comparisons to be made, elucidating how behavioural and emotional contagion relate to each other.

The three core contagion processes were conceptualised in regard to empathy, and it is well researched how, through empathy, they contribute to healthy social functioning. Beyond empathy, considering how positive and negative social contagion may have evolved to give distinct benefits allows us to make sense of differing patterns of factors that moderate social contagion. Negative social contagion offers immediate survival advantages, especially for lower ranked individuals and in despotic species where interactions are more unpredictable, and these factors may be linked to higher rates of contagion. Positive social contagion increases affiliative interactions and provides long term social benefits, and feedback cycles could result in increased contagion between socially close pairs, and in higher ranked individuals. Patterns of influence should not be generalised from one form of behaviour to another, or even from one species to another, as although contagion can be rapid and involuntary, its expression is intimately linked to the emotional state of the observer, and the surrounding context.

A wide array of emotional transfer is involved in situations where social learning takes place, and yet this spread of arousal is rarely considered in the primate literature. Even in terms of rapid mimicry and behavioural contagion, social learning studies rarely analyse the temporal matching between learner and knower, which could be driven in part by rapid mimicry processes. Analysing how these basic contagion mechanisms are integrated into social learning would contribute to topics of research such as social learning biases, and shed light on which processes underly different forms of social learning. An integrated view of social learning and social contagion also emphasises the important role that social contagion plays, in enabling individuals to respond adaptively to their social environment.

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Data Availability Statement

No (new) data were generated for this study.

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