ChimpanSee, ChimpanDo: A Review of the Significance of Social Contagion, and Exploration of Grooming and Play Contagion in Chimpanzees

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Georgia Sandars

GENERAL ABSTRACT

The ability to catch behaviours from others, and share their emotional states, is fundamental to numerous aspects of human social functioning. This state-matching capacity is of great evolutionary importance and is widespread in the primate lineage. Studying which forms of contagion are present in different primate species, and when contagion is most pronounced, can help reveal the fundamental underpinnings and the context-specific facets of these processes, allowing us to understand the nature and significance of social contagion. In chapter 1, I critically review research on mimicry, behavioural contagion and emotional contagion in primates, highlighting which factors are important moderators, and the benefits that contagious processes afford individuals and the group. Research reveals notable difference in trends in positive and negative valenced contexts, although research is limited with regards to positive emotional and behavioural contagion. I emphasise the wide-reaching adaptive benefits of both positive and negative social contagion, and consider social contagion as a basis for social learning, allowing for a unified view of its significance.

In chapter 2, I seek to advance the literature by addressing the research gap of positive social contagion. I conducted an observational study of 47 sanctuary living chimpanzees, to test whether chimpanzees catch grooming and play behaviours from each other, and what predicts this effect. Results reveal the first evidence for the contagion of affiliative behaviours in chimpanzees. The presence of grooming contagion was predicted by social closeness, and was more pronounced in females, whilst play contagion was more pronounced in younger individuals. It is evident that behavioural contagion is not confined to negative contexts, but is widespread and influenced by a multitude of factors, specific to species and behaviour.

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CHAPTER 1

A Review of Social Contagion in Primates: Moderating Factors and Significance for Individuals and the Group

ABSTRACT

Social contagion, which involves behavioural and emotional state matching, is a crucial process for healthy social functioning. It underpins key elements of social interaction, including empathy and social learning, thereby allowing animals to effectively engage with other individuals and their environment. Given their highly social nature, studying social contagion in primate species sheds light on the evolution of these processes and their significance in individuals' daily lives. Here, I review this research, and identify factors that are thought to moderate the presence of social contagion; namely age, sex, dominance rank and social closeness. Patterns of contagion vary across species and contexts, appearing to differ especially between contexts involving positive vs, negative emotional states. I therefore seek to categorise contagious behaviour along this affective dimension, highlighting when there are ambiguities, and then considering the distinct evolutionary benefits of positive and negative social contagion. I further consider the significance of social contagion within social learning, using this as a unifying framework to understand contagion.

INTRODUCTION

As social animals, the lives of human and non-human primates are constructed and shaped by their relations with other individuals, from fleeting interactions to life-long relationships. Scientific literature over recent decades has emphasised the importance of affective mechanisms that underly social behaviours. Basic state-matching processes can be divided into three core behavioural and affective components – *mimicry*, *behavioural contagion*, and *emotional contagion*. 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 further our understanding of the importance of these processes, both for wider social functioning and for more specific processes including empathy and social learning. Behavioural and affective state-matching have been extensively studied within the Primate order, and comparing findings from different contexts across our primate relatives offers an invaluable route to understanding the nature and significance of social contagion.

In this literature review, I outline the existing primate research on the three core components of social contagion: mimicry, behavioural contagion, and emotional contagion. Thus far, the three elements of contagion were first conceptualised as core components of empathy. However, research is increasingly revealing their importance for wider social functioning and survival, which includes for enabling effective social learning. The aim of this review is to highlight the factors that affect contagion, and consider the valence of underlying emotion-states involved (positive/negative), to reveal distinct patterns. I then consider the importance of contagion for the social lives of primates, emphasising the role of contagion not just for underlying empathy, but also for social learning.

THREE COMPONENTS OF SOCIAL CONTAGION

Mimicry, behavioural contagion, and emotional contagion are considered to be core building blocks of empathy (Adriaense et al., 2020; Brooker et al., 2021), whereby empathy is broadly defined as the sharing and understanding of other's emotional states (Cuff et al., 2016). 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 & de Waal 2002; Preston 2007). The 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, it is behavioural and emotional mimicry that are thought to underpin empathy. Accordingly, the Russian Doll Model (de Waal 2007) holds this mechanism as being the core heart of empathy, around which further increasingly complex cognitive and affective layers are organised, such as perspective taking, consolation, and targeted helping. 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)- a distinction which may be helpful to researchers investigating ecologically relevant behaviours in species without bias, and resolving ambiguous boundaries (Adriaense et al., 2020). Although the Combination model does not treat emotional contagion as the basis which all other empathic components depend on (as the Russian Doll model does) emotional contagion is still considered a bedrock necessary for much empathic functioning, including cognitive contagion, collaboration, and consolation.

The state-matching processes at the heart of empathy can be further broken down 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 & Bargh, 1999; Zentall, 2001). This can also be referred to as motor 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 specific self-directed or social behaviours and actions, rather than basic single-component expressions and postures. Examples include contagious scratching and grooming (Feneran et al 2017; Ostner et al 2021). Thirdly**, emotional contagion**, also known as emotional transfer or affective empathy, is the emotional state matching of one individual with another (de Waal, 2008). 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.

Research into the neural circuitry behind these processes overall supports the theory that automatic and behavioural mimicry underpin emotional contagion and further empathic processes (Palagi et al., 2020). The discovery of mirror neurons in the premotor area of rhesus macaques (*Macaca mulatta*) - neurons that fired when individuals executed specific actions and observed corresponding actions (Di Pellegrino et al., 1992) - sparked a wave of research into the neural basis of motor and emotional mimicry. Numerous human neuroimaging studies find that the same brain networks are active when an individual observes a facial expression or action as when they generate it, (Palagi et al., 2020), and despite large methodological variation, a meta-analysis found that activity in the mirror neuron systems is correlated with emotional and cognitive empathy (Bekkali et al., 2019). Evidence for the causal relationship between motor and emotional contagion comes from manipulation and neuromodulation studies. Disrupting motor mimicry through experimental constricts to reduce movement, or disrupting the associated brain networks, results in impairments in emotional and cognitive empathy (Keysers et al., 2018; Palagi et al., 2020). Prochazkova and Kret (2017) formed a Neurocognitive Model of Emotional Contagion (NMEC) specifying the neural pathways involved in emotional contagion. They emphasise the importance of two forms of automatic mimicry: 'autonomic mimicry' encompassing non-voluntary, physiological synchrony, and 'motor mimicry', which is partly implicit but can be consciously controlled. This automatic mimicry enables emotional contagion, which then underpins empathy and wider social cognition processes.

EMOTIONAL VALENCE

Emotion is intricately linked to empathy, yet separate research groups and disciplines have long used many different definitions of emotion itself. Anderson and Adophs (2014) formulate a definition of emotion 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 can be distinguished from feelings, which are the mental representations of the changes that occur during an emotion (Damasio, 2004).

Emotional states and their associated behaviours are often characterised by two dimensions; arousal and valence. Arousal refers to the general level of activation whereas valence refers to the positive or negative 'charge' attached to the state, which is generally understood in terms of pleasure vs displeasure (Russell, 1980). Whether this valence is intrinsic to specific whole emotions, or to specific individual conscious feeling states ('affects') is a perhaps unanswerable philosophical question (Charland, 2005). However, the presence of valenced emotions is well established in primates and many other animals, and can be measured on multiple levels corresponding to the behavioural, physiological, and cognitive changes that emotion brings about. For example, even in insects, a predator-like stimulus elicits persistent defensive behaviours, associated physiological changes (Gibson et al., 2015), and subsequent "pessimistic" cognitive biases (Bateson et al., 2011; Schlüns et al., 2015), whilst an unexpected sucrose reward elicits "optimistic" cognitive biases. Such findings are commonly interpreted through choosing the simplest possible cognitive mechanisms (i.e. this behaviour may be unconsciously controlled, with no subjective experience attached).

Whilst this may hold true, Kret et al (2022) warn that when studying close phylogenetic relatives, a rule of evolutionary parsimony as well as cognitive parsimony ought to be used: we must assume that similar behaviour in closely related species is paired with similar emotions and in some cases feelings.

Even without using this rule to interpret behaviour, there is ample evidence that primates experience a large range of emotional states. For example, chimpanzees (*Pan troglodytes)* exhibit the negatively valenced emotions of fear, disgust and anger, and positive affect during affiliation with others; these emotions are associated with particular facial expressions and behaviours, comparable to homologous human expressions (Kret et al., 2020). Emotional contagion research has however traditionally focussed more on negatively valenced emotions, as they are clearer to induce and to observe (Pérez-Manrique & Gomila, 2022). This focus on negative valence may have biased our understanding as to how and when contagion occurs. Future studies could address this by considering a broader range of positive emotional contexts, in order to better understand the underpinnings and significance of emotional contagion.

Here, I 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.

SOCIAL LIVING

Living in a social group bestows an animal with numerous survival benefits (notably, reduced predation risk and increased resource access), as has been found across a wide range of taxa, including all primates (Alexander, 1974). 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 (Silk et al., 2003, 2010; Archie et al., 2014, Snyder-Mackler et al., 2020).

In Chapter 2 of this review, I consider the significance of social contagion for the individual and the group, drawing on how contagion increases the benefits of group living. I consider these implications in terms of the relevance for individual dyadic relationships; how social contagion can strengthen and increase the number of these connections. I also consider 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 aid in our understanding of the patterns of influences, social learning offers a unified view for the importance of all forms of contagion.

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. Here, I will summarise the findings within each level of social contagion, for behaviours and emotions of positive and negative valence.

MIMICRY

Research into mimicry - the involuntary copying of another's movements, posture, facial expressions or vocalisations - is dominated by a focus on facial mimicry, but there is also evidence for mimicry of particular bodily movements. Many of the facial mimicry studies seek to establish 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 and social closeness of involved individuals, according to species specific patterns.

Facial Mimicry

Face-to-face interactions during play are important for high emotion situations, social bonding and relationship building, and 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 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 one 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 (2021) replicated the finding of RFM in gorillas, and sought to unpick whether sex, age, or social closeness influenced 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. This was however not also 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. 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. 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 socio-emotional factors, and may be most pronounced in specific contexts. Play with individuals of a different age involves more of an imbalance and so synchrony with one another is even more important than usual. 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, indicating mimicry mechanisms are present from a young age and are influenced by social closeness from early in development. RFM in two macaque species differed however: Tonkean macaques (*Macaca tonkeana*) - the more socially egalitarian species - rapidly mimicked facial expressions, and the closely related but more despotic Japanese macaques (*Macaca fuscata*) did not (Scopa & Palagi., 2016). The authors suggest that this may be because Tonkean macaque society is less fixed and play is used to test and negotiate social relationships, and therefore mimicry and coordination in play is key. This discrepancy highlights that whilst nonvoluntary mimicry mechanisms may be deep rooted in our primate evolutionary history, even small social differences make an impact on when and how mimicry is employed.

Overall, it is clear that 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 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.

Play is highly varied, in its behavioural makeup and the contexts it is carried out in, both within and between species. Even the fundamental valence of play is far from uniform. It is generally considered a positive interaction, assumed to promote feelings of joy, reduce aggression and increase social unity. However, this hypothesis has not been empirically confirmed across animal species. Play has been shown to improve social cohesion in dogs (*Canis familiaris*) (Sommerville et al., 2017), reduce social tension in chimpanzees (Yamanashi et al., 2018), and promote social bonding in macaques (Shimada & Sueur, 2018); but does not increase cohesion or reduce aggression in meerkats (*Suricata suricatta*) (Sharpe & Cherry 2003; Sharpe, 2005). A review revealed there is no established correlation between play and positive affective state across animal species (Ahloy-Dallaire et al., 2018), and as Adriaense et al. (2020) argue, a lack of research on animals' emotional state during play itself, and the variation between different species, means that we must not assume that play is always indicative of positive emotions. This variance of play between species 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 the factors that predict when this is the case 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.

Facial mimicry outside of the context of play has not received much research attention so far. The only other context in which RFM in primates has been explored is during sexual contact in bonobos (*Pan paniscus*), where social closeness did not predict occurrence of RFM, although it was more common in sex between females (the dominant sex) than in hetero-sexual contacts (Palagi et al., 2020). Bonobos use sexual contacts to regulate social tension and strengthen alliances (Clay & 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.

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 (Rymarczik 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.

Bodily Mimicry

Facial mimicry plays an important role in face-to-face interactions, but interactions are also shaped by synchrony in bodily posture and motor actions. Although bodily motor mimicry has received much less research attention, 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 & 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 cannister (Voelkl & Huber, 2000), and this was also replicated in vervets *(Chlorocebus pygerythrus)* (van de Waal and Whiten, 2012). An experimental study of how chimpanzees learn to crack nuts revealed evidence for motor mimicry (Marshall-Pescini & 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 reinnovate 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 & 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 recent field experiments have not found any evidence for nut cracking re-innovation (Koops et al., 2022). Whilst less complex 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, e.g. termite fishing (Lonsdorf et al., 2006) which are more challenging to re-invent. Further evidence for exact temporal synchrony, as in the nut-cracking research (Furhmann et al., 2014) would also strengthen the case for motor mimicry.

The zone of latent solutions hypothesis also does not easily account for the copying of motor actions independent to a goal. Specific motor actions without any clear goal are 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 (Gunst et al., 2007). The replication of these apparently non-functional motor patterns indicate the presence of motor mimicry rather than a mimicry of a goal-directed action irrespective of form.

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 wide ranging in context and form, and found in individuals across ages, sexes and ranks. It is therefore highly possible that primates 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 & Byrne, 2014), and so primates may mimic each other's actions in play as well as facial expressions. Rapid mimicry of body movements has already been found to occur in play 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 sexual contact, 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.

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 I class these as behavioural contagion due to their 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.

Yawn Contagion

The majority of behavioural contagion studies focus on yawning. The function of yawning is debated: as reviewed by Massen and Gallup (2017), it is currently 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 study groups, 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 & de Waal (2011) then 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 individuals known to the subject, 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 conspecifics yawning but not of humans yawning (Amici et al., 2014). Finally, 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 & 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). A familiarity effect was demonstrated in an observational study however, where bonobos yawned more in response to individuals they had a closer relationship with, and additionally, female vs male yawns were more effective triggers (Demuru & Palagi., 2012). Yawn contagion was also found in adult orangutans, where video avatars of known and unknown individuals both 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 et al., 2019).
Research has also been carried out with monkey species; two observational studies found a contagion effect in gelada baboons, although there is mixed evidence from other species. In captive geladas, yawning contagiousness was higher between individuals who groomed each other more, although in wild geladas, yawning contagiousness 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 & Anderson., 2006), whilst two species of lemur did not respond differently to yawn and control stimuli (Reddy et al., 2016).

On the whole, whilst contagious yawning is established within numerous apes and catarrhine monkeys, there is no clear trend in factors that universally moderate the effect. 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. 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 complication, recent literature indicates that there are different types of yawn, which may have different social meanings. The emotional profile of yawning is very unclear: yawns are associated with relaxation, occurring more often in times of rest than in times of social conflict (e.g. Demuru & Palagi, 2012; Zannella et al., 2015; Leone et al., 2014), and yet are also associated with anxiety, as indicated by increased scratching (Vick & Paukner, 2010; Leone et al., 2014). 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., 2021). 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 concentrate on 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 could carefully control for the context that yawns are observed or presented 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 the next section). This would allow for meaningful comparisons of the contagion of corresponding yawn types across species, and comparisons to the contagion of other more emotional behaviours.

Negative Behavioural Contagion

Scratching is a self-directed behaviour that primates perform to alleviate itching, but also during times of psychological and physiological stress. In primates, scratching is elevated during aggressive interactions and predation attempts (Palagi & Norscia, 2011) and reduced during affiliation and after play (Norscia & Palagi, 2011; Aureli & Yates, 2010), and so is associated with a negative emotional state. Scratching has been found to be contagious in multiple species of monkey and ape. Japanese macaques started scratching themselves upon observing a familiar conspecific scratch (Nakayama, 2004), and rhesus macaques started scratching when their cage-mates scratched, and when viewing videos of unfamililar 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 difference between rhesus, Japanese and Barbary macaques could be explained by slight differences in the presentation of video stimuli, or perhaps by the fact barbary macaques are more socially tolerant, meaning they may have a different strategy for noticing and responding to negative emotions. Contagious scratching is also present in Bornean orangutans, who increased self-scratching when observing conspecifics scratching, and (to a lesser extent) also when perceiving only the sound of scratching (Laméris et al., 2020). Surprisingly, in tense social situations, individuals “caught” scratching from their close social partners to a much lesser degree 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 and Japanese 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 & 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 associated with other behaviours, beyond self-scratching, which have started to receive more research attention. Japanese macaques exhibit vigilance behaviour, raising their heads in a state of alertness, in response to potential within-group threats. This vigilance behaviour is contagious, especially to lower ranked individuals, and to mothers observing their infants rather than vice-versa (Iki & 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. Although the effects of relationship strength, rank and sex were not studied, it is likely that, as this behaviour has social implications, the degree of contagion would be influenced by social factors too. It would be interesting to directly compare whether patterns of scratch contagion and the contagion of other behaviours associated with tension follow similar trends within and across species, or if social influences differ even for behaviours of similar valence.

Positive Behavioural Contagion

With the majority of literature focussing on yawning and scratching, the contagion of positive behaviours is under-studied. With large variance between contexts and species, let alone the distinction of emotional valence, it is inaccurate to consider observations of negative behavioural contagion as representative of contagion on the whole: positive behaviours may be ‘caught’ in different ways and to different degrees. 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 (referred to as grooming from here) has recently been studied, and appears to be influenced by social factors in different ways to other behaviours.

Grooming in primates is considered to be affiliative, relaxing behaviour that reinforces bonds and social structures (Russell & Phelps, 2013). 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 rather than a spread of positive behaviour. Alternatively, the scratching could again actually just indicate high emotional arousal, and further research is needed to clarify the valence of this arousal. Two recent 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 able to interact more 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 relationship quality could influence behaviour due to individuals paying more attention to those they are socially close with.

From this initial evidence, it appears that for social vs self-directed behaviours, high rank is more important in determining whether individuals can enact a behaviour they have ‘caught’. The effect of age and sex have not been addressed, and the importance of social closeness is as yet unclear. These are important questions to address next: just as the factors underpinning scratch and yawn contagion differ, a separate range of factors influence positive behavioural contagion.

EMOTIONAL CONTAGION

When an individual perceives an emotion and then automatically experiences a matched emotion, this involves changes on neurophysiological, cognitive and behavioural 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 must 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. However, there is a notable lack of research on positive emotional contagion, and addressing what factors influence emotional contagion in general.

Physiological Research

Early research involved exposing primates to negatively valenced emotional stimuli and recording changes in skin temperature due to arousal driven shifts in cutaneous 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' tympanic membrane (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, and so the recent 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 (2005) 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, 1967) 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. Heart-rate changes to emotional social stimuli have also been studied in infant chimpanzees, who wore surface electrodes and were exposed to auditory stimuli in a testing chamber (Berntson et al., 1989). Perceiving conspecific scream vocalisations led to a decelerated heart-rate, but in a laughter vocalisation condition, the chimpanzee infants' heart rates increased, and they made vocalisations similar to adult threat-barks - a response indicative of a defensive reaction. As the only study to explore the contagion of emotional arousal in infants, these results are puzzling to interpret, but they do emphasise that although infants' responses may be influenced in a different way to adults' responses, infants are also highly affected by others' emotional expressions. It is probable they too are just fearful of the stimuli, rather than experiencing emotional transfer.

One possible 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 recently developed 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. The emotional contagion of positive arousal therefore has yet to be established and must be further researched: the majority of studies only used negatively valenced stimuli, and the Berntson et al. (1989) infant chimpanzee study found an unexpected response to laughter. As indicated by this experiment, when distinguishing between positive and negative arousal, it is useful to go beyond neurophysiological indicators of arousal, and use behavioural indicators to verify that the arousal is negative or positive.

Behavioural Indicators

Emotional contagion has also been studied on a purely 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 the underlying affective states. Behaviours that are firmly linked to a particular emotion are particularly 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 inducing changes in affective state from their behaviour. This form of social contagion cannot only involve motor mimicry, as the subjects do not visually perceive any motor behaviour, and must involve responses to the affective emotional 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 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 & 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.

It is overall clear that emotional transfer of both positive and negative emotions does occur, but the literature here does not 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 especially key to understanding the relationship between behavioural and emotional contagion.

SIGNIFICANCE OF SOCIAL CONTAGION

In the previous section, I have 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 I 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. Dividing social contagion according to overall valence then 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 fitted 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.

CONTAGION AS A BUILDING BLOCK OF 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 et al., 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 (e.g. Hogan & 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. This is true for all primates, and especially great apes, who communicate through a variety of modalities, expressing both positive and negative emotions (Kret et al., 2020). In turn, effective empathic 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 & 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, unrelated to empathy. 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 and responses to complex social scenarios, and is thought to play a key role in moralistic behaviour. Although emotional contagion and further empathic processes are heavily 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 & 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, positive and negative behavioural and emotional contagion alike endow individuals with key skills to navigate their social world.

SIGNIFICANCE OF CONTAGION THROUGH THE LENS OF EMOTIONAL VALENCE

As noted earlier, social contagion may facilitate interactions in a wide range of contexts beyond empathy. The apparent separation between contagious processes relating to negatively and positively valenced scenarios mirrors the separation in additional benefits endowed to an animal experiencing negative or positive contagion. In this section, I use the 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.

Negative Social Contagion

The ability to catch the negatively valenced emotions of others 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 previously discussed, is prevalent across many primate species, although does not appear to be 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 can respond 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 high 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).

Behavioural contagion of vigilance behaviours 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 predated species beyond primates, being observed in birds, fish and insects (Miller et al., 2012; Brown & Laland, 2003; Treherne & Foster, 1981). This evolutionarily ancient behaviour is effective when the 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.

Positive Social Contagion

The social contagion of positive behaviours and emotions have less obvious immediate benefits for survival, but may contribute more to effective and smooth social interactions, and generate longer term social 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, I 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 facial mimicry. This has been found in chimpanzees and gorillas (Palagi et al., 2019) and in geladas and Tonkean macaques (Mancini et al., 2013; Scopa & 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, 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 therefore benefits individuals not just on the level of a single positive interaction, but in the longer term too. Recent research has begun to explore the specific benefits associated with the ability to catch social behaviours and emotions when engaging in 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 responsive to their social surroundings were more socially favoured (Anderson & Kinnally, 2020). It is challenging to unpick the direction of influence here however, as social competence and opportunity for the development of social competence are theorised to 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 benefits individuals through elongating 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 in turn also feed into a positive cycle of social favour.

CONTAGION AND SOCIAL LEARNING

Separating the significance of social contagion by emotional valence offers an explanation for the differing patterns of influences found across different forms of negative and positive valences. 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 are understood to underpin effective social learning, on both the level of behavioural contagion and emotional contagion.

As previously discussed, there is a wide range of evidence for the mimicry of particular bodily actions, commonly observed in experimental set ups where animals can forage for food. Efficiently learning the best ways to extract resources from the environment, through mimicking 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 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 an individual to relate an action that they observe to a matching Action within their own body. As discussed previously, it has been suggested that behavioural mimicry does not involve conscious replication, but rather that observing specific behaviours triggers an individual to spontaneously perform 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 absolutely crucial for social learning.

Beyond the contagion of motor actions, 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 their 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 (2021) 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 the 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 & 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, 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 an 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., 2021), 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 mainly just on cognitive data in humans, or behavioural data in animals (Gruber et al., 2021).

This makes it challenging to unpick to what extent social learning strategies are based on emotional contagion tendencies, or alternatively, are overcoming conflicting biases of affective contagion. Uniting social learning research with an affective approach would reveal key insights here.

CONCLUSIONS

Mimicry, behavioural contagion and emotional contagion have been studied across multiple monkey and ape species, using both experimental and observational, behavioural and physiological techniques. Some behaviours have received much research attention: as discussed, 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, even within these domains, ambiguity remains as to their emotional profiles. Other areas have received little or no research attention. Facial mimicry in negative social contexts has not yet been studied in primates, and yet may be regulated by different processes to those in play. Mimicry on the level of bodily rather than facial movements has also not been studied, and could have different communicative value. The factors influencing the prevalence of yawning and self-directed behaviours are relatively well researched, but due to restricted methodologies and studies, it is as yet unclear what moderates the contagion of affiliative social behaviours. This positive behavioural contagion is theorised to 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 extensively 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 none so far have directly compared which social characteristics of stimuli and observers lead to increased emotional contagion. Research addressing this question would allow more direct comparisons to be made, to elucidate how behavioural and emotional contagion relate to each other.

The three core contagion processes were originally conceptualised in regard to empathy, and it is well researched how within empathy they contribute to multiple facets of healthy social functioning. However, this review has demonstrated that social contagion should be studied within the context of other social processes too. In particular, the social learning literature often draws on situations that invoke the spread of emotion (e.g. the production of alarm calls), and yet the spread of affective arousal is rarely considered. 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. Furthermore, they could shed light on the hotly debated topic of which processes underly different forms of social learning.

Studying the mimicry and behavioural contagion literature in terms of the valence of the associated emotions and contexts reveals differing patterns in what moderates social contagion. Considering how positive and negative social contagion may have evolved to give distinct benefits then allows us to make sense of these differences. Negative social contagion can offer immediate survival advantages, especially towards lower ranked individuals, and in less tolerant species where interactions are more unpredictable, and these factors may predict 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.

CHAPTER 2

Positive Behavioural Contagion in Chimpanzees: An Empirical Study

ABSTRACT

Behavioural contagion - the onset of a species-typical behaviour soon after witnessing it in a conspecific - forms the foundation of behavioural synchrony and cohesive group living in social animals. Although past research has mostly focused on negative emotions or neutral contexts, the sharing of positive emotions in particular may be key for social affiliation. To address this research gap, I investigated the contagion of two positive interactive behaviours, grooming and play, in chimpanzees. I collected naturalistic observations of 47 sanctuary-living chimpanzees at Chimfunshi Wildlife Orphanage, taking 5-min focal follows of chimpanzees after they had observed grooming and play, and pairing these with matched controls. I explored whether contagion is moderated by age, sex and social closeness, and how individual differences in contagion predict social integration. My results reveal the first evidence for grooming and play contagion in chimpanzees. In my sample, grooming contagion appeared to be influenced by a social closeness bias, whilst play contagion was more pronounced in younger individuals. These findings emphasise that contagion is not restricted to negative or self-directed behaviours, and that considering the behavioural context is crucial when determining predictors of contagious behaviour. Studying what influences this foundational social process, and its significance for social integration, deepens our understanding of the underpinnings of affective state matching, social bonding and group dynamics.

INTRODUCTION

CONTEXT AND SIGNIFICANCE

Our social environments are shaped by our ability to understand and respond to the states and behaviours of those around us. Behavioural contagion – the onset of a species-typical behaviour soon after witnessing it in a conspecific (Zentall, 2001) - is a fundamental form of sensitivity to others' behaviour, and is intimately linked to emotional contagion, and other socio-cognitive processes such as empathy and social learning. 'Negative' behavioural contagion includes the contagion of self-directed or non-social behaviours such as scratching and vigilance, that are associated with displeasure, and that can hold immediate survival benefits (Iki & Kutsukake, 2021). 'Positive' behavioural contagion includes the contagion of affiliative social behaviours, that are associated with pleasure and that allow animals to develop and strengthen cooperative social bonds (Berthier & Semple, 2018). Despite positive behavioural contagion forming the basis of many crucial social processes, this phenomenon is very understudied.

Within primates, grooming and play are consistently cited as important social behaviours for maintaining and developing social bonds. Grooming is a low-cost cooperative behaviour, involving combing through the fur of a partner to remove dirt, foreign objects or parasites (Videan et al., 2005). In addition to providing physiological benefits such as fur cleaning and parasite removal (Zamma, 2002), grooming is associated with pleasurable emotions and there are numerous social benefits endowed to grooming partners (Russell & Phelps, 2013). Grooming is used to form and maintain social bonds and is thought to establish alliances and facilitate coalitionary support, which in turn increases rank and therefore overall fitness (Seyfarth 1977; Henzi & Barrett, 1999). Dyads that groom more are also more likely to mate, share food, and protect one another's infants (Newton-Fisher & Kaburu, 2017). Models of primate grooming behaviour suggest that grooming patterns arise from each individual trying to maximise their benefit from grooming, with some individuals gaining priority to groom others due to higher dominance rank (Tiddi et al., 2012). It is therefore well understood that grooming drives the formation of cooperative social relationships, across primate species.

Primate social play is a complex, multifunctional behaviour, frequently performed by infants and juveniles, but also adults (Goodall, 1986; Palagi, 2018). Definitions vary, with play broadly understood to consist of all activity which can be reminiscent of serious functional contexts (e.g. anti-predatory and mating behaviour), or of simply playful actions, but which have no immediate function or benefit (Miller, 2017). Burghardt (2005, 2011) proposed 5 criteria which playful behaviours must fulfil: they must be non-functional, voluntary, structurally or temporally modified, performed repeatedly, and instigated in a relaxed environment. Play can be identified by typical action patterns, and is frequently associated with a ‘play face’ which can be used to signal playful intentions (Palagi et al., 2019). Play can be carried out alone, but social play (henceforth just ‘play’) involves these playful behaviours being carried out in proximity to or whilst interacting with another individual. This is widespread across mammals, and numerous benefits have been cited. Play is used to establish and maintain social relationships, integrating an individual into a wider social group (Shimada & Sueur, 2018). Play also enables animals to learn about other individual’s specific behavioural tendencies, enabling effective interactions with them in the future, and allows animals to practise particular skills and motor patterns useful for future interactions (Spinka et al., 2001; Heintz et al., 2017; Palagi, 2018).

The benefits of engaging in grooming and play have so far just been considered in broad terms, but it is possible that there are distinct benefits associated with a propensity to ‘catch’ these behaviours from others, rather than spontaneously initiating them. Firstly, when others are already engaging in the behaviour, this could represent a general willingness to play/groom, meaning that there is a greater chance of relative reciprocation. This avoids the cost of wasting energy and time with a failed initiation of behaviour. It is also possible that, if it is initiated at an appropriate time, the instigated bout will last longer and thus lead to greater affiliation.

Moreover, it is possible that ‘catching’ grooming and play behaviour, rather than initiating it, could broaden an individual’s range of social contacts. A primate’s choice of play and grooming partner is thought to be influenced by a variety of factors, notably rank, social closeness and similarity (Mielke et al., 2018; Lutz et al., 2019). However, a broader propensity to join in play and grooming whenever it is observed, even if the individuals involved are not favoured partners, would mean individuals would create the foundations for a wider social network. This effect would be tempered by the fact that individuals are more likely to spend time with their favoured social partners, and thus are more likely to observe grooming and play involving them. Nonetheless, a sensitivity to the behaviour of surrounding individuals, and a motivation to join affiliative behaviours when observing them, may increase an individual’s social bonds and social integration.

Recent research has started to address whether this propensity to catch behaviours exists in our primate family (Adriaense et al., 2020). Chimpanzees in particular are an excellent candidate when conducting research on this phenomenon. As one of our closest relatives, chimpanzees appear to share many of the same basic social mechanisms as we do, offering themselves as an approximate model for human behavioural evolution, in which studying complex phenomena such as positive behavioural contagion may be more feasible. It is possible to study the social networks of chimpanzees living in semi-captivity, and to study grooming and play as a significant part of all of their social connections (Escribano et al., 2022); furthermore these aspects are generally very well understood, making it possible to generate informed hypotheses and accurately interpret results. It would be more challenging to generate an equally comprehensive understanding of a human's social network and means of positive social interaction, given that these interactions involve multiple groups in both digital and physical spheres. Furthermore, systematic research on positive behavioural contagion in naturalistic scenarios can enable cross-species comparisons with humans and other primates, which are a key way to detect how socio-cognitive differences are realised in behaviour. Chimpanzees are also understood to have highly developed empathic abilities (Clay et al., 2018) with executive function skills equivalent to that of a young human child (Rosati, 2017); therefore, they provide an interesting model for social functioning. More generally, this research enables us to better understand their complex social worlds, which could underpin a variety of future lines of study.

Despite this, behavioural contagion of grooming and play has not yet been studied in chimpanzees. As emphasised in Chapter 1, the expression of emotional and behavioural contagion appears to be highly specific to particular contexts and species (Palagi et al., 2020). We should be cautious to generalise from related research in other species, although this body of literature can inform hypotheses. Understanding grooming and play contagion in chimpanzees would form a useful model for contagion in humans, and the foundation for numerous other lines of research.

PREVIOUS RESEARCH

Whilst positive behavioural contagion remains unstudied in chimpanzees, there is much evidence that chimpanzees' behaviour and emotional state is influenced by those around them. Behavioural contagion is conceptualised as one of three distinct kinds of self-other matching which form the core of affective empathy (Brooker et al., 2021); mimicry, behavioural contagion and emotion contagion.

Mimicry is the involuntary, automatic and fast copying of another's physical appearance (Chartrand & Bargh, 1999; Zentall, 2001). Mimicry differs from behavioural contagion in that it involves single component motor actions, including facial expressions or body postures, rather than entire behaviours. By comparison, *behavioural contagion* is when an individual enacts a species-typical behaviour after observing another perform (Zentall, 2001). *Emotional contagion* is the emotional state matching of one individual with another (de Waal, 2008), and can be revealed by using physiological measures to assess overall emotional arousal, rather than just behavioural observation.

Facial mimicry has been observed in chimpanzees during the context of play: chimpanzees across age, sex and rank mimic the expressions of those they interact with, performing play faces within 1 second, and between 1-5 seconds after observing them (Palagi et al., 2019). There is also evidence for bodily mimicry within social learning of tool use: an observer was found to temporally synch specific motor actions with an individual that they observed (Fuhrmann et al., 2014).

Research on behavioural contagion in chimpanzees has largely focussed on yawn contagion (Palagi et al., 2020). Yawn contagion is when an individual is triggered to yawn after observing another individual yawning in a relaxed context, and although this involves replication of facial expressions, it also involves additional auditory and motor components, and so is generally considered behavioural contagion rather than mimicry (Brooker et al., 2021).

Experimental studies have found a robust effect of stimuli yawn videos eliciting yawns in chimpanzees, with familiarity and similarity playing a role in determining the strength of yawn contagion. Yawn contagion is more pronounced in response to in-group individuals than out-group members (Campbell & de Waal, 2011) and more pronounced with videos of chimpanzees than humans (Amici et al. 2014). However, among stimulus individuals known to the subject, the effect does not appear to improve with relationship quality (Massen et al., 2012). Whilst one experimental study found male yawns were more contagious (Massen et al., 2012), this was not replicated by an observational study, which found females and males were equally likely to trigger and catch yawns (Campbell & Cox, 2019). Overall it seems individuals across demographic dimensions are susceptible to catching yawning, and the effect is not enhanced by familiarity once a certain level of similarity between observer and stimulus individual is reached.

Two studies have addressed how vocal contagion can elicit behaviour, which could indicate emotional contagion. In captive chimpanzees, hearing grooming vocalisations from neighbouring groups led to an increase in grooming (Videan et al., 2005), whilst hearing agonistic vocalisations led to increased aggressive displays and vocalisations (Baker & Aureli, 1996). As this is does not just involve matching the behaviour observed, but a cross-modal response, this suggests that either the contagion of emotions is driving the effect, or that there is a higher order associative process that could involve associated emotions. Emotional contagion has also been studied using infra-red thermal imagery to indicate emotional arousal, whereby chimpanzees show a drop in nasal temperature in response to audio-visual stimuli of chimpanzees fighting (Kano et al., 2016) and aggressive chimpanzee vocalisations (Dezecache et al., 2017).

Although the contagion of affiliative behaviours is understudied in chimpanzees, it has been found in other species, including two species of macaque. Positive contagion was first observed in female Barbary macaques, who were quicker and more likely to initiate grooming after observing others groom (Berthier & Semple, 2018). The nature of this contagion as 'positive' was validated by a simultaneous increase in other affiliative behaviours, and a decrease in behavioural indicators of anxiety, after individuals observed grooming. This is suggestive of a more general transmission of emotional state rather than just behaviour. The grooming contagion effect was replicated in female rhesus macaques (*Macaca mulatta*), and an analysis of influential factors revealed that the effect was more pronounced in higher ranked observers, and that social closeness did not influence the effect (Ostner et al., 2021). The contagion of play behaviour has not been studied in primates, but has been found in young ravens, who were more likely to play when they observed others play. They did not match the particular type of play they observed, suggestive of more general behavioural or emotional contagion, rather than basic motor mimicry (Wenig et al., 2021). As discussed above, although play is generally considered a positive interaction, associated with social cohesion and social bonding (Sommerville et al., 2017; Shimada & Sueur, 2018), there is no established correlation between play and positive emotions (Ahloy-Dallaire et al., 2018). Some play may contain negatively valenced elements, for example play-fights which can escalate to real fights, (Adriaense et al., 2020). The broad range of forms and associated emotions may mean that play contagion follows different trends to grooming contagion, and when interpreting data, the emotional profile of play must not be assumed to be positive.

Overall, there is some evidence that positive behaviours are contagious in other species, although this has not been addressed in chimpanzees, who have been found to exhibit a variety of other contagious processes.

RATIONALE AND RESEARCH QUESTIONS

I sought to establish whether in chimpanzees there is a contagious effect for two purportedly positively-valenced social behaviours -grooming and play - and what influences the strength of the contagion effect.

I tested the hypothesis that chimpanzees would exhibit positive behavioural contagion. I expected this for two reasons. Firstly, contagious processes of motor mimicry, yawn contagion, and emotional contagion have been exhibited by chimpanzees, and I therefore expected that the mechanisms for these kinds of contagion would extend to other contexts, including for grooming and play. Secondly, contagion of grooming and play has been found in other animals who use these behaviours in a similar way to chimpanzees. The transmission of grooming has been established in Barbary and rhesus macaques; primates who groom in much the same way, and same situations, as chimpanzees (Berthier & Semple, 2018; Ostner et al., 2021). Juvenile ravens are thought to use play to strengthen relationships and practise key skills in much the same way as chimpanzees and other primates (Diamond & Bond 2003), and play is contagious in this species (Wenig et al., 2021).

Next, I tested the hypothesis that social closeness would enhance the likelihood of play and grooming contagion. The strength of the behavioural contagion effect has been found and theorised to be influenced by features of the observer and stimulus individuals. Firstly, when observer and stimulus individuals are socially close, there is some evidence for increased yawn contagion (e.g. Palagi et al., 2009; Campbell & de Waal, 2011) and increased facial mimicry (e.g. Mancini et al., 2013). This is thought to be either due to an attention bias towards socially close individuals, or due to increased emotional transfer between close individuals as found in empathy (Norscia et al., 2020).

Individual characteristics may also determine the strength of the contagion effect. Research on facial mimicry and yawn contagion indicates that contagion mechanisms are present from infancy in chimpanzees although some studies have found a heightened effect for juveniles and for adults (reviewed by Palagi et al., 2020). However, the contagion of affiliative processes differs from facial mimicry and yawn contagion as it is a more complex behaviour incorporating multiple components, and its expression is more under voluntary control. As impulse control and executive function improves over adolescence in primates (Weed et al., 2008, Manrique & Call, 2015) the contagion effect for grooming and play were hypothesised to be more pronounced in younger chimpanzees.

Rank has also been shown to influence the expression of contagious behaviour. Higher ranked macaques showed an exaggerated contagion effect, which may be due to their status affording them more freedom to act as they please, rather than for lower ranking individuals who may be unable to safely initiate a behaviour (Ostner et al., 2021). I therefore expected higher ranked individuals to show a greater grooming and play contagion.

Finally, sex has been explored in relation to other behaviours related to socio-emotional sensitivity. Female chimpanzees showing higher rates of consolation (Romero et al., 2010), although multiple studies looking at yawn contagion have not found any sex difference (Palagi et al., 2020). So far, the grooming contagion literature has only assessed females (Berthier & Semple, 2018; Ostner et al., 2021). I tested the hypothesis that female chimpanzees show enhanced socio-sensitivity to others, and therefore may show increased levels of grooming and play contagion.

There is some literature suggesting that individuals who mimic others more are endowed with social favour: tufted capuchin monkeys choose to interact with humans who mimic them (Paukner et al., 2009), and Japanese macaques (*Macaca fuscata*) who mimicked more received higher rates of play and grooming initiations from others (Anderson & Kinnally, 2021). Social favour may be even more enhanced by mimicry that occurs within affiliative contexts, and with contagion of affiliative behaviours themselves. The relationship could also arguably be bi-directional, with individuals who are more socially favoured having more opportunities to mimic, and therefore showing an enhanced tendency to mimic.
However, this proposed relationship is most plausible only at restricted developmental stages, before overall tendencies and temperaments are established, and may be moderated through a number of other variables. The temporal relationship of mimicry inducing social favour is much more direct and has been well established in the human literature (Lakin & Chartrand, 2003), and I therefore anticipated this direction to be more prominent in chimpanzees as well. I expected that individuals who were more inclined to initiate grooming and play when others were engaging in these behaviours would be better at building and maintaining social relationships, and so degree of contagion would predict number of close social partners.

My key questions, hypotheses and predictions are summarised below:

Q1: Detecting evidence of contagion. Do chimpanzees initiate grooming/play more often after having observed it?
H0: Rates of play and grooming initiation are not affected by whether the individual has recently observed others engaging in grooming or play.
H1: Rates of play and grooming initiation are affected by whether the individual has recently observed others engaging in grooming or play.

Prediction 1: A chimpanzee would be more likely to initiate grooming after observation of grooming than in a matched scenario where they had not observed others groom.
Prediction 2: A chimpanzee would be more likely to initiate play after observation of play than in a matched scenario where they had not observed others play.

Q2: What factors moderate the contagion effects?
H0: Social closeness, age, rank, or sex have no influence on whether and when grooming or play is initiated after observation.
H1: Social closeness, age, rank, or sex influence whether and when grooming or play is initiated after observation.

Prediction 1: The contagion effect will be stronger if the observed grooming/play involves individuals who are more socially close to the observer.

Prediction 2: The contagion effect will be stronger in younger individuals than older individuals.

Prediction 3: The contagion effect will be stronger in higher ranked individuals than lower ranked individuals

Prediction 4: The contagion effect will be stronger in females than males.

Q3: Do individual differences in susceptibility to positive behavioural contagion correlate with social integration?

H0: There is no relationship between an individual’s likelihood to “catch” affiliative behaviours and their number of close social partners.

H1: There is a relationship between an individual’s likelihood to “catch” affiliative behaviours and their number of close social partners.

Prediction 1: An individual’s likelihood to “catch” grooming will correlate with their number of close social partners.

Prediction 1: An individual’s likelihood to “catch” play will correlate with their number of close social partners.

PILOT STUDY

INTRODUCTION

Grooming and play contagion have not previously been studied in chimpanzees. Therefore, in order to refine methodological details to decide how best to test my hypotheses, I first conducted a pilot study. I wanted to assess the most accurate and feasible measures to use for chimpanzees, and specifically for chimpanzees living at Chimfunshi Wildlife Orphanage, where I would conduct my main research (see more detail in Methods).

In particular, I used the pilot study to address three areas of methodological uncertainty:

1. I aimed to refine a systematic *behavioural ethogram* to accurately define and distinguish when chimpanzees engaged in grooming and play behaviour, and who initiated it.
2. I aimed to assess *overall incidence of grooming and* play: at which hours these behaviours could be reliably observed, and whether they were more common at a particular time of day. This would enable me to assess what time frame would be needed to collect a substantial amount of data, and when data collection should be carried out.
3. I aimed to establish *what length of focal-video* would be necessary to capture the initiation of grooming and play post-observation. Previous research into grooming contagion in macaques (Berthier & Semple, 2018; Ostner et al., 2021) took place in captive settings, and so individuals were able to be followed for long periods of time (up to sixty/twenty minutes respectively) until they initiated behaviour. However, this is not feasible in the semi-wild setting of Chimfunshi Wildlife Orphanage. Thus, I explored the latency between observing an individual observing a behaviour and then initiating it themselves

METHODS

Data set

We used an existing database of videos collected by members of Dr Marina Davila-Ross's (University of Portsmouth) team at Chimfunshi Wildlife Orphanage. The chimpanzees lived in a large outdoor enclosure similar to their wild habitat, where they could freely range during the day (further details in Main Study Methods).

The database consisted of 835 5-minute focal recordings of individuals in Group 4 (n=11), filmed opportunistically throughout the day, between April and September 2017. The videos followed the focal individual, and the researcher narrated any behaviour the focal engaged in, and which individuals were within 10m. The chimpanzees of Group 4 were all rescued from the illegal wildlife trade, and a demographic breakdown of the individuals in Group 4 is shown in Table 1. Age categories are based on previous research carried out at Chimfunshi Wildlife Orphanage (Cronin et al., 2014).

Table 1: Breakdown of the ages and sexes of chimpanzees making up Chimfunshi Group 4 (2017) which were used in the pilot study

	Males	**Females**	**Total**
Infants (1-2 yrs)	0	0	0
Juveniles (3-7 yrs)	2	0	2
Subadults (8-11 yrs)	1	0	1
Adults (12+ years)	6	2	8
Total	9	2	11

Initial ethogram development

I created a draft ethogram based on definitions used in previous research, specifying what behaviour constitutes grooming and play (Videan et al., 2005; Worch 2012), and a list of gestures used to initiate grooming and play (Hobaiter & Byrne, 2011, 2014). The refined ethogram (discussed below) is included in Appendix I.

I then watched the videos and made note of behaviours that remained ambiguous, and adjusted the ethogram accordingly.

Summary statistics

I watched the focal videos, and recorded which videos included any instance of grooming or play (involving either the focal or any other chimpanzees within 10m). I then calculated the overall proportion of videos that contained grooming and play, per each one hour period of the day (starting at. 7-8am, ending at 3-4pm, and excluding 12-13pm, as there were only 2 observations during this time). I used Microsoft Office Excel to carry out data entry and analysis.

Video coding

As grooming was a more common behaviour than play, within group 4 from my sample video dataset, I focussed just on grooming contagion to address the question of what time-frame potential behavioural contagion happens in.

From all videos where grooming occurred (n= 178), I further selected videos where I could assess potential grooming contagion. I selected only videos where the onset of the grooming bout was filmed, and where at least one individual passed within 5m of the grooming.

I then analysed these videos using ELAN 5.9 software (Wittenburg et al., 2006), an open-source software which allows for the precise recording of the onset and duration of behaviours. I used my newly developed systematic behavioural ethogram to identify and classify the onset of grooming behaviour. For each individual, I calculated the proportion of times they initiated grooming after having observed a grooming bout. For instances when an individual did initiate grooming after observing a grooming bout, I recorded the latency between first observing the grooming and then initiating grooming themselves. Data analysis was carried out using Microsoft Office Excel.

PRELIMINARY RESULTS AND DISCUSSION

Ethogram

I noticed three key areas of ambiguity and so made three key amendments to my ethogram.

Firstly, it was challenging to divide ongoing grooming and play behaviour into separate bouts, which was necessary in order to determine when behaviour was first observed and initiated. I therefore added in clear definitions of ‘bouts’ and ‘episodes of grooming and play, inspired by previous literature (e.g. Manson et al., 2004).

Secondly, it was challenging to objectively judge when grooming and play had been ‘observed’ by an individual. Eye-line was difficult to make out with the focal recordings, so I decided to use facial orientation as a measure of where the chimpanzees were looking. The chimpanzees seemed to show little awareness of individuals as far away as 10m, and so, broadly in line with previous research (7m; Berthier & Semple, 2018), I counted behaviour as ‘observed’ if it took place within 5m.

Thirdly, I noted that my definition of play was too broad, as some forms of play were a lot more salient than others, with my ‘play’ definition including behaviour such as tickling that could be silent and involve little movement, and also rough-and-tumble chasing that took much space and made much noise. I therefore used Fröhlich et al. (2016)’s specification of three kinds of play to distinguish ‘low intensity play’ from other kinds. This would enable me to subsequently not consider observations of ‘low intensity play’ when assessing play contagion.

Play and Grooming incidence over the course of day

I excluded videos before 7:00 (n=4) and after 16:00 (n=6) from the analysis, due to a lack of data; for all other hours, n>40.

As shown in Figure 1, grooming occurred in all hours of the day, although it appeared to occur more frequently in the morning (from 07:00-12:00) than in the afternoon (from 12:00-16:00). I therefore decided to conduct opportunistic focals throughout the day, but ensure that time of day was included in the analysis, as a factor that could influence grooming initiation.

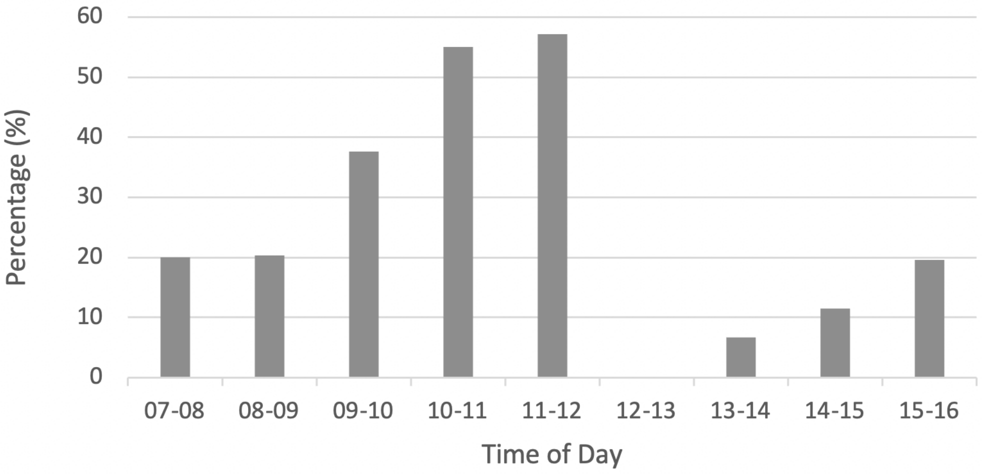

Figure 1: Hourly breakdown of the percentage of focal videos that included footage of grooming (N=834) at Chimfunshi Wildlife Orphanage (recorded in 2017)

Play also occurred in all hours of the day, and was more common in the morning than afternoon, as shown in Figure 2. I therefore decided that when studying play contagion in my main study, I would also collect opportunistic focals throughout the day, but ensure that time of day was included as a factor in the analysis.

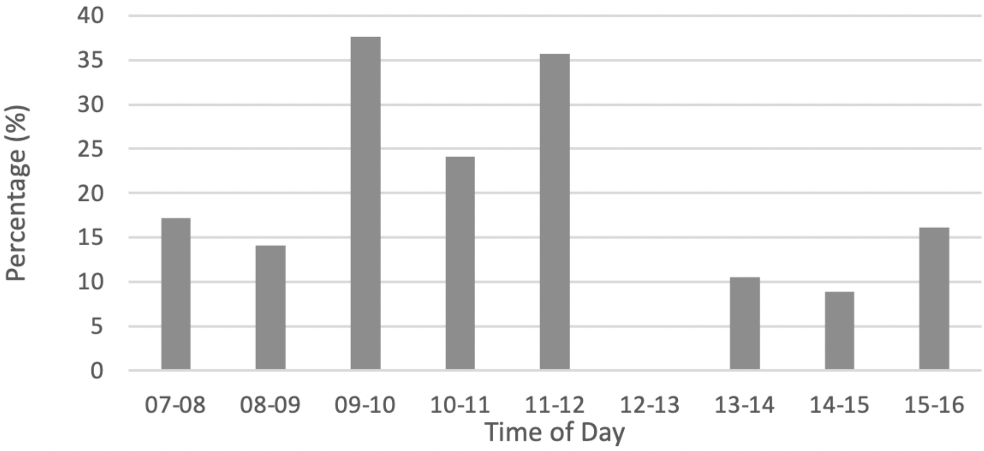

Figure 2: Hourly breakdown of the percentage of focal videos that included footage of play (N=834) at Chimfunshi Wildlife Orphanage (recorded in 2017)

Grooming contagion: Frequency and latency

Overall, chimpanzees in the footage initiated grooming in 17.1% of instances, after observing a grooming bout (15 out of 88 times). However, this is a conservative estimate as the videos were only 5 minutes long and grooming was often observed near the end, meaning observers were not followed for long after observing the grooming. There were large individual differences in the proportion of initiating grooming post-observation: five of the chimpanzees did not initiate grooming in any of the instances studied. Overall, the presence and variation of post-observation grooming was an encouraging indicator that it would be possible to study this behaviour.

In instances where grooming was initiated, latency between first observing grooming and then initiating grooming varied between 2 and 250 seconds (Figure 3), with the majority of initiations happening within the first 120 seconds (Figure 4). It was difficult to draw solid conclusions, as the videos were only 5 minutes long, meaning it was impossible to gauge levels of post-observation grooming at longer latencies. The rough pattern appeared to indicate that post-observation grooming initiations became less likely as time went on, although was not confined to the immediate minutes after observation. Therefore, I decided that following the chimpanzees for 5 minutes after observation would likely capture the majority of behaviour influenced by grooming, as well as being practically feasible in a sanctuary environment. Previous contagion literature has also found that post-observation behaviour happens on a similar time scale: yawn contagion generally peaks within 3.5 minutes (Palagi et al., 2019), and grooming contagion in macaques peaked within 2 (Ostner et al., 2021).

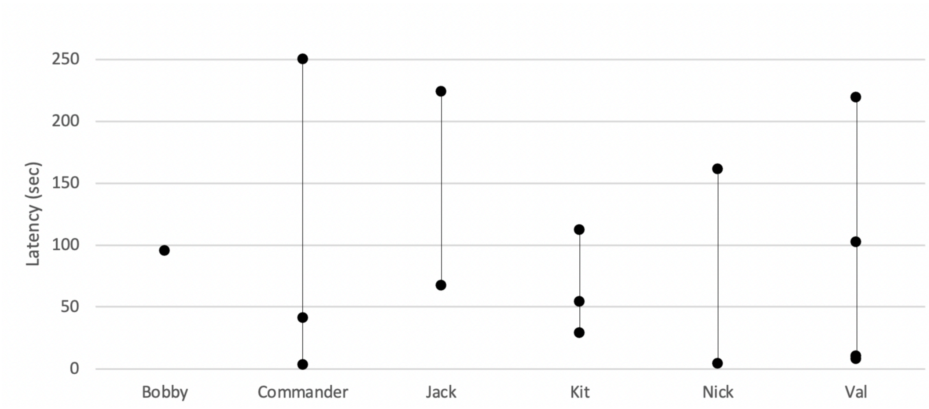

Figure 3: Latencies from first observing grooming to initiating grooming, for each chimpanzee who initiated grooming post-observation (n=15, across 6 chimpanzees). Each individual data point is represented. All data is from Chimfunshi Group 4 (recorded in 2017).

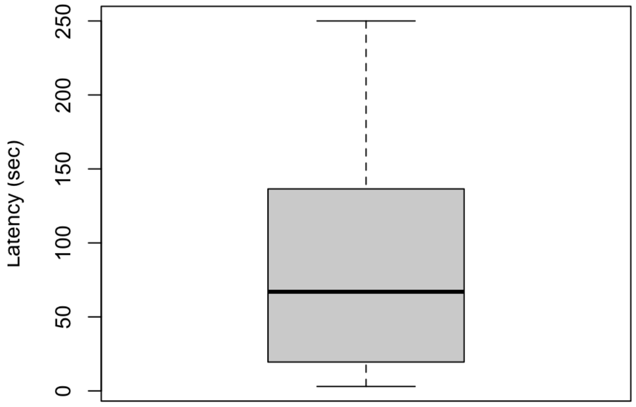

Figure 4: Box plot of the overall distribution of latencies from observing to initiating grooming, across all identified contagious grooming instances (n=15). Box boundaries indicate upper and lower quartiles, and whiskers indicate the full range. All data is from Chimfunshi Group 4, recorded in 2017.

Conclusions

Overall, the pilot study demonstrated encouraging evidence that in the chimpanzees of Chimfunshi Wildlife Orphanage, grooming and play initiation was frequent enough to be studied through opportunistic focal videos, and that post-observation grooming and play occurred frequently enough in the minutes after observation that 5 minute focals could be used to study contagion.

METHODS

STUDY SITE AND SUBJECTS

Observations were collected from the chimpanzees in Group 2 at Chimfunshi Wildlife Orphanage, a sanctuary in the Copperbelt region of north-western Zambia. The chimpanzees who live there were either rescued from the illegal wildlife trade, or born and mother-reared within the sanctuary. They live in a 160-acre enclosure, consisting of dense miombo forest and grassland, and an attached indoors handling facility which they can sometimes enter for supplementary feeding or occasional veterinary checks. Group 2 is a stable and relatively tolerant social group (DeTroy et al., 2021), consisting of 58 individuals. A demographic breakdown is shown in Table 2, and a list of individuals is shown in Appendix I. The chimpanzees were provisioned with supplementary food next to or inside the indoors enclosure twice each day, at around 11:30 and 13:30, at which times the majority of the group would congregate. They spent the rest of the day freely ranging the enclosure, and nested outside overnight.

Table 2: Breakdown of the ages and sexes of chimpanzees making up Chimfunshi Group 2 (2021)

	Males	**Females**	**Total**
Infants (1-2 yrs)	5	6	11
Juveniles (3-7 yrs)	4	6	10
Subadults (8-11 yrs)	4	1	5
Adults (12+ years)	23	9	32
Total	36	22	58

Data was collected between 29th May and 31st July 2021, at the start of the dry season of the year, where seasonal average temperatures have a high of 26° and low of 10°, and average rainfall is 0mm (Brandenburg, 2013). Each day, data was collected in the morning and afternoon periods, from when chimpanzees were first visible to when they left for nesting. All data was collected within a defined area next to the indoor enclosure, where chimpanzees were most visible. Observations were not carried out immediately before and after the supplementary feeding times, as then the chimpanzees were artificially encouraged to congregate, with social tensions increased due to competition for food. Each day data collection took place from approximately 08:00 to 11:00, and from 14:00 to 17:00, logging a total of 237 hours of observation.
I aimed to collect data for all chimpanzees in the group aged above 3 years old (n=47), choosing not to study infants, due to their low rates of grooming initiation (Nishida, 1988), and lack of independent social connections from their mother (Horvat & Kraemer, 1981). Some individuals (n=5) spent most of their time

deeper inside the enclosure where they were out of sight, meaning I was not able to collect enough data for them to include in the final analyses.

ETHICS

This study was entirely observational and non-invasive, strictly adhering to all legal requirements. Ethical approval for this study was obtained from Durham University's Animal Welfare Ethical Review Board, and research was also approved by the Chimfunshi Research Advisory Board.

DATA COLLECTION

Post-observation – Matched Control Focals

I collected behavioural data using a procedure adapted from the post-conflict/-matched control (PC-MC) Method, developed by de Waal and Yoshihara (1983) to study post-conflict behaviour, and recently adapted to study behavioural changes post-observation of grooming (Berthier & Semple, 2018; Ostner et al., 2021). The PC-MC method involves recording the behaviour of an individual for a set amount of time immediately after they observe a conflict, and then comparing this to behaviour recorded during a control period of time, in which they have not just observed a conflict, but where other conditions are matched. In this study, I collected data for the 5 minute period after an individual observed either grooming or observed play.

I collected all post-observation focals opportunistically, from the start of when an individual observed either grooming or play. I determined whether observation happened by considering the head orientation of the observer, and their distance to the behaviour. When the trigger was within 5m, and happened in the 180^o in front of their face and in direct visual contact, I considered the behaviour as observed. Post-observation focals therefore started either when a grooming or play interaction started within the subject's observational area, or when a subject moved so that they observed the behaviour.
For each PO (play or grooming), I then followed the observer for 5 minutes. I recorded data using a handheld digital video-camera (Panasonic HC V770) and microphone (Sennheiser MKE 400), filming the subject and all other chimpanzees within their observational area, and narrating the IDs of everyone present, and noting any grooming and play behaviour that they observed or were involved in.

I also recorded control focals opportunistically, selecting a focal individual at random if there were multiple available. I ensured that the focal chimpanzee had not just observed play or grooming by following them for 5 minutes before starting the focal, and also that, at the start of the focal, there were at least two individuals present within the 5m around them, so that they had the opportunity to engage in social play or grooming if they wanted. I then followed the focal chimpanzee for 5 minutes as with the post-observation videos, narrating relevant behaviour. Data was originally collected by randomly selecting one of multiple possible individuals to follow if there were multiple options. In the last two weeks of data collection, from 15th -31st July, I then prioritised individuals for whom there were the lowest amount of focals collected. All focal follows were collected by GS.

Social Affiliation Data

To collect data on how socially close the chimpanzees were with each other individual, we collected social scan data. We observed a defined viewing area (approximately 50m squared) in the corner of the outdoor enclosure next to the feeding area and indoor enclosure. Every 5 minutes, we recorded the identities of all chimpanzees present, and dyadic social interactions at that moment. Specifically, we recorded each pair of individuals that engaged in grooming, play, contact sitting, and proximity sitting (sitting within 1m of each other). When there were only a few chimpanzees present, data was entered directly into an excel spreadsheet, and when the scene was busier, data was recorded with a video-camera and then transcribed into the excel spreadsheet afterwards. Data for social scans was collected by GS and JB.

Individual Characteristics Data

Dominance rank data was based on interviews conducted with the chimpanzee keepers (n=4) who were responsible for the care of the group, providing food and observing the chimpanzees every day, and recording details of major aggressions. The keepers were asked to class the chimpanzees into low/medium/high ranking, and all four agreed on every individual's position. This method has been used in previous research looking at the influence of rank on behaviour, carried out at Chimfunshi Wildlife Orphanage (e.g. Cronin et al., 2014. A limitation of this method is that it is not purely data-driven, however as data collection took place over a relatively short time-frame, it was unfeasible to collect dominance data. I could not base rank categories on the outcomes of aggression (e.g. Elo, 1978) or patterns of submissive greetings within dyads (e.g. Bygott, 1979) due to the infrequency of aggressions, and lack of observed interactions between all dyads in the group.

The age and sex of individuals was determined using veterinary records; birth date was recorded for 44 of the chimpanzees who were born within the group, and estimated upon arrival by veterinary staff for the 14 chimpanzees who were born in the wild.

CODING AND DATA CLEANING

Video Coding

The post-observation and control focals were all analysed using ELAN 5.9 software (Wittenburg et al., 2006) which allows the recording the onset and duration of behaviours to millisecond precision. Videos were coded according to the systematic behavioural ethogram (Appendix I) developed in the pilot study. The coding was carried out by GS.

Data was then exported and re-organised using Microsoft Office Excel. Whether contagion occurred or not was considered a binary “yes/no” variable. If another individual initiated the behaviour with the focal chimpanzee, the data from that point on was excluded, as it would not be possible to determine whether the focal’s subsequent behaviour was driven by their experience observing or engaging in the behaviour. In a minority of focals, grooming or play was initiated by the focal individual multiple times. This data was not analysed beyond the first grooming or play interaction they engaged in, as similarly, it would not be possible to determine whether this behaviour was influenced by the focal’s initial observation or ensuing engagement in the behaviour.

Latency data (from the time an individual first observed behaviour to the time they initiated a matching behaviour) was calculated, and expressed as a proportion of the 5 minute focal follow.

Intercoder Reliability

A subset of 15% of the video data, balanced across control, grooming observation and play observation focals, was coded by two further observers. Intercoder reliability mean dyadic agreement was established using Cohen’s Kappa values, for all measures of behaviour conducted and observed which were entered into the model. Kappa values ranged between 0.873 and 1, indicating very good agreement (Cohen, 1960).

Social Affiliation Data Preparation

The social affiliation data was used to compute scores for the strength of relationship between dyads. For each pair of chimpanzees, I totalled the number of scan-points where at least one chimpanzee was in view, and calculated what proportion of these scan-points the pair engaged in each interactive behaviour (playing, grooming, contact sitting or in 1m proximity of each other). The four metrics correlated, and so I integrated them into an overall dyadic composite sociality index. I divided each metric by the average of that metric across all dyads, and then for each individual, averaged their 4 scores (Ostner et al., 2021; Silk et al., 2006). This gave an overall dyad social rate which I used as an indicator of social closeness.

For each individual, I then calculated the total number of their relationships which had a dyad social rate score in the upper quartile of all scores, to indicate how many close social partners they had (Clay & de Waal, 2013).

The data was also used to compute scores for each individual's overall tendency to groom and play. Grooming tendency was calculated as the number of scan-points that the individual groomed in divided by the total number of scan-points they were present for. Play tendency was defined as the number of scan-points that the individual played in divided by the total number of scan-points that they were present for.

DATA ANALYSIS

Question 1: Is there a behavioural contagion effect?

In order to assess whether there was a contagion effect, each post-observation follow ("PO") was paired with a matched control ("MC"). The videos were matched in a way that maximised the number of pairs matched by time of day (within 1 hour of each other), and then also by number of individuals present if possible (19% of videos), or if not by the approximate number of individuals.

Following de Waal and Yoshihara (1983), a PO-MC pair was counted as 'attracted' if the focal individual initiated the relevant behaviour in the PO but not MC, 'dispersed' if the focal individual initiated the behaviour in the MC but not the PO, and 'neutral' if the behaviour was initiated in both or in neither.

To detect evidence of a contagion effect as I predicted (indicated by 'attracted' pairs), I compared rates of attracted and dispersed pairs of focals, for the grooming videos and play videos separately. I used a Wilcoxon matched pairs test, using the function 'wilcox_test' of the statistics package R (version 4.1.2; R Core Team 2022).

Question 2: Which factors moderate the contagion effect?

I explored the factors that could predict the occurrence and latency of grooming and play contagion through fitting four General Linear Mixed Models (GLMM; Baayen, 2008). All models were fitted in R (version 4.1.2; R Core Team, 2022), using the function lmer from the package lme4 (version 1.1-27.1; Bates et al., 2015), and the function glmmTMB from the package glmmTMB (version 1.1.1; Brooks et al. 2017).

I originally intended to include rank as a fixed effect, but inspecting the data revealed a very uneven distribution, with only 8 datapoints (5.13%) for high ranked individuals, and so rank was not included.

I first assessed model stability. This was determined by dropping the random factors (focal ID and event) one at a time from the data and comparing the estimates derived from the subsets, using functions kindly provided by Roger Mundry. I obtained confidence intervals of model estimates by using a parametric bootstrap (N=1,000 bootstraps), and tested overdispersion with functions also provided by Roger Mundry. I used Variance Inflation Factors (VIF; Field 2005) to assess collinearity, using the function vif from the package car (version 3.0-11; Fox and Weisberg, 2011)

In order to assess the overall strength of the model without cryptic multiple testing (Forstmeier and Schielzeth, 2011), I then conducted full-null model comparisons, comparing each full model with a null model which lacked the fixed effects but included all control effects and random effects. For each model, I then tested the effect of individual fixed effects (age, sex and social closeness) by comparing the full model with reduced models which dropped the fixed effect terms one at a time (Barr et al., 2013). All model comparisons were done using a likelihood ratio test (Dobson, 2002).

Model 1: Grooming Contagion Occurrence

I used a GLMM model with Binomial error structure and logit link function (Zuur et al., 2009) to examine which factors and covariates predicted whether or not grooming occurred post-observation. As fixed effects, I entered age, sex and social closeness into the model. I included four control effects: time of day, overall grooming tendency, number of other individuals present, and number of grooming bouts observed. I did not include any interaction terms owing to lack of hypotheses for these. As random intercept effects, I included the ID of the focal chimpanzee (as I had multiple observations of the same individuals), and the ID of the event (as sometimes multiple post-observation follows were carried out for the same grooming bout).
I also included all theoretically identifiable random slopes, in order to keep type 1 errors at the nominal level of 5%, and to avoid being overconfident with regard to the precision of fixed effects estimates (Schielzeth and Forstmeier 2009; Barr et al. 2013). There were two theoretically identifiable slopes: the number of others present within focal ID, and the social closeness within focal ID. All fixed and random effects entered into the model are displayed in Table 3. I originally began with a maximal model (Barr et al., 2013) that included the correlations among random intercepts and slopes. However, this led to a ‘singular fit’ warning message, and so I subsequently excluded the three correlation terms, which only led to a small decrease in model fit (Log-likelihoods: Model with correlations = -71.47486, Model without correlations = -72.82198).

Before fitting the model, I inspected the distribution of all the covariates, to check that they were roughly symmetrical and free of outliers. This was the case for all covariates except for grooming tendency and context, which I subsequently log transformed (base e). I then z-transformed all covariates, to ease model convergence and interpretability. Model stability tests had no convergence issues and revealed fair stability for all fixed effects (see Results), there was no evidence for overdispersion (=0.795), and there was no issue with collinearity (maximum vif: 1.405). The final data set analysed comprised of 156 observations, of 40 individuals (with 1 to 12 follows each), across 110 events (with 1 to 4 follows each).

Table 3: The structure of fixed and random effects entered into Model 1- a GLMM with Binomial error structure, used to test the predictors of grooming contagion occurrence.

	Predictor	**Type**
Fixed effects	Age	Continuous
	Sex	Categorical (levels: m/ f)
	Social closeness	Continuous
Control effects	Time period	Categorical (levels: am/pm)
	Grooming tendency	Continuous
	No. others present	Continuous
	No. bouts observed	Continuous
Random intercepts	Focal ID	--
	Event ID	--
Random slopes	No. others present within Focal ID	--
	Social closeness within Focal ID	--

Model 2: Grooming Contagion Latency

I constructed a GLMM with a beta error structure and a logit link function (McCullagh and Nelder 1989; Bolker 2008) to explore, when grooming occurred post-observation, what factors and covariates predicted the latency of when an individual first observed grooming to when they initiated it themselves. I entered the same fixed effects, control effects and random intercepts as in Model 1 (see Table 4). There were no theoretically identifiable random slopes.

Before fitting the model, I again inspected the distribution of all the covariates, to check that they were roughly symmetrical and free of outliers. This was the case for all covariates except for ‘social closeness’ and ‘number of grooming bouts observed’ which I subsequently log transformed (base e). I then z-transformed all covariates, to ease model convergence and interpretability. Model stability tests revealed good stability (see Results), the model was only minorly overdispersed (= 1.133), and there was no issue with collinearity (maximum vif: 1.714). The final data set analysed comprised of 49 observations, of 20 individuals (with 1 to 6 follows each), across 41 events (with 1 to 3 follows each).

Table 4: The structure of fixed and random effects entered into Model 2- a GLMM with Beta error structure, used to test the predictors of grooming contagion latency.

	Predictor	Type
Fixed effects	Age	Continuous
	Sex	Categorical (levels: m/ f)
	Social closeness	Continuous
Control effects	Time period	Categorical (levels: am/pm)
	Grooming tendency	Continuous
	No. others present	Continuous
	No. bouts observed	Continuous
Random intercepts	Focal ID	--
	Event ID	--

Model 3: Play Contagion Occurrence

I used a GLMM with Binomial error structure and logit link function (Zuur et al., 2009) to test what factors and covariates predicted whether or not play occurred post-observation (Y/N). As per Model 1, I entered three fixed effects (age, sex and social closeness), four control effects (time of day, overall play tendency, number of other individuals present, and number of grooming bouts observed), and two random intercepts (ID of the focal chimpanzee, and the ID of the event). As previously, I included all theoretically identifiable random slopes; here there was just one: the number of others present within focal ID. All effects tested are displayed in Table 5.

I used a maximal model (Barr et al., 2013) that included the correlations among random intercepts and slopes. I used the nloptwrap optimizer to ease convergence. Before fitting the model, I inspected the distribution of all the covariates, to check that they were roughly symmetrical and free of outliers. This was the case for all covariates except for play tendency and social closeness, which I subsequently log transformed (base e). I then z-transformed all covariates, to ease model convergence and interpretability. Testing assumptions revealed multiple issues with the model. There was no issue with collinearity (maximum vif: 2.831). However, overdispersion was tested, revealing a parameter of 0.001. This represents substantial underdispersion, indicating the model is hyper-conservative (R. Mundry, personal correspondence).

Model stability was determined by dropping the random factors (focal ID and event) one at a time from the data and comparing the estimates derived from the subsets, revealing that the model was not stable, and therefore results must be interpreted with great caution. Confidence intervals also indicated trouble with the model (see results). The final data set analysed comprised of 139 observations, of 41 individuals (with 1 to 12 follows each), across 85 events (with 1 to 5 follows each).

Table 5: The structure of fixed and random effects entered into Model 3- a GLMM with Binomial error structure, used to test the predictors of play contagion occurrence.

	Predictor	**Type**
Fixed effects	Age	Continuous
	Sex	Categorical (levels: m/ f)
	Social closeness	Continuous
	Rank	Categorical (levels: l/m/h)
Control effects	Time period	Categorical (levels: am/pm)
	Play tendency	Continuous
	No. others present	Continuous
	No. bouts observed	Continuous
Random intercepts	Focal ID	--
	Event ID	--
Random slopes	No. others present within Focal ID	--

Model 4: Play Contagion Latency

As with Model 2, I used a GLMM with beta error structure and a logit link function (McCullagh and Nelder 1989; Bolker 2008) to explore what factors and covariates predicted the latency from when an individual first observed play to when they initiated play themselves. I entered the corresponding fixed effects, control effects and random intercepts, shown in Table 6. There were no theoretically identifiable random slopes.

Before fitting the model, I again checked that the distribution of all covariates was roughly symmetrical and free of outliers. This was the case for all covariates except for 'social closeness' which I subsequently log transformed (base e). I then z-transformed all covariates, to ease model convergence and interpretability. Model stability tests revealed fair stability (see Results), the model was only minorly overdispersed (= 1.368) and there was no issue with collinearity (maximum vif: 2.398).

The final data set analysed comprised of 48 observations, of 26 individuals (with 1 to 5 follows each), across 37 events (with 1 to 3 follows each).

Table 6: The structure of fixed and random effects entered into Model 4- a GLMM with Beta error structure, used to test the predictors of play contagion latency.

	Predictor	Type
Fixed effects	Age	Continuous
	Sex	Categorical (levels: m/ f)
	Social closeness	Continuous
Control effects	Time period	Categorical (levels: am/pm)
	Play tendency	Continuous
	No. others present	Continuous
	No. bouts observed	Continuous
Random intercepts	Focal ID	--
	Event ID	--

Question 3: Does susceptibility to contagion correlate with number of social partners?

I used linear multiple regression models to assess whether number of close social partners was influenced by how susceptible an individual was to grooming and play contagion effects.

For each chimpanzee, I calculated a 'grooming contagion score' from the Post Observation – Matched Control grooming dataset, only using data from chimpanzees who I had at least 3 matched PO-MC follows for. Contagion scores were calculated as the proportion of attracted video pairs (where the focal initiated grooming in the PO but not the MC) minus the proportion of dispersed video pairs (where the focal initiated grooming in the MC but not the PO), as in previous literature (Palagi et al., 2018). I calculated a 'play contagion score' using the same method, from the play PO-MC dataset. This resulted in a total of n=25 individuals for grooming and n=19 individuals for play.

For both models, I tested the significance of the contagion score predictors by comparing the fit of the full model with that of a model comprising only of the control variables, using a likelihood ratio test (Dobson, 2002). I fitted the models using the function 'lm' of the statistics package R (version 4.1.2; R Core Team 2022). Model diagnostics were determined using the functions 'vif' (R package 'car'; version 3.0-11; Fox and Weis- berg 2011) and 'dfbeta'(kindly provided by Roger Mundry).

Grooming Contagion & Social Integration

I used number of close social partners as the dependent variable, and grooming contagion score as a predictor, as well as three control variables previously demonstrated to predict social integration: sex, rank and age (e.g. González et al., 2021). A qq-plot of the of residuals and residuals plotted against fitted values did not show any obvious deviations from the assumptions of normality and homogeneity of residuals. Collinearity was not an issue (maximum vif =1.491). However, I checked model stability using DFBetas which revealed the model to be quite unstable (see results).

Play contagion & Social Integration

I entered number of close social partners as the dependent variable, and play contagion score as a predictor, as well as three control variables: sex, rank and age. A qq-plot of the of residuals and residuals plotted against fitted values did not show any obvious deviations from the assumptions of normality and homogeneity of residuals Collinearity was not an issue (maximum vif =1.927). However, again, a check of model stability using DFBetas revealed the model to be fairly unstable (see results).

RESULTS

Question 1: Is there a contagion effect?

Grooming

For the grooming videos, out of an original 149 PO-MC pairs, 31 were attracted, 1 dispersed, 92 neutral and 25 were excluded (due to another individual initiating grooming which the focal engaged with). To run the analyses, I only included individuals for whom there were at least 2 matched pairs. This resulted in a total of 119 PO-MC pairs (for N=32 individuals), of which 30 were attracted, 1 was dispersed, and 88 were neutral. A Wilcoxon matched-pairs test revealed that across individuals, the average proportion of attracted PO-MC pairs was significantly higher than the average proportion of dispersed pairs (N=32, Z = 3.31, r = 0.66, $p < 0.001$). This supports my first prediction; that chimpanzees initiate grooming more often just after they have observed it.

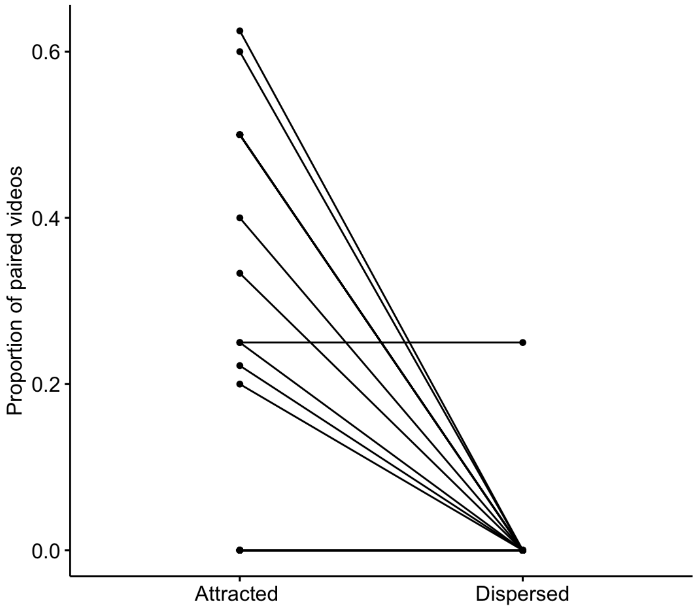

Figure 5: Proportions of attracted and dispersed pairs of grooming PO-MC videos (n=149 pairs), from n=32 individuals in Chimfunshi Group 2.

Play

Out of an original 119 PO-MC pairs of play focals, 40 were attracted, 1 dispersed, 65 neutral and 13 were excluded (due to another individual initiating play which the focal engaged with). To run the analyses, we only included individuals for whom there were at least 2 matched pairs. This resulted in a total of 97 PO-MC pairs (for N=25 individuals), of which 33 were attracted, 1 was dispersed, and 62 were neutral.

A Wilcoxon matched-pairs test revealed that across individuals, the average proportion of attracted PO-MC pairs was significantly higher than the average proportion of dispersed pairs (N=25, Z = 3.81, r = 0.76, p < 0.001). This supports my first prediction; that chimpanzees initiate play more often just after they have observed it.

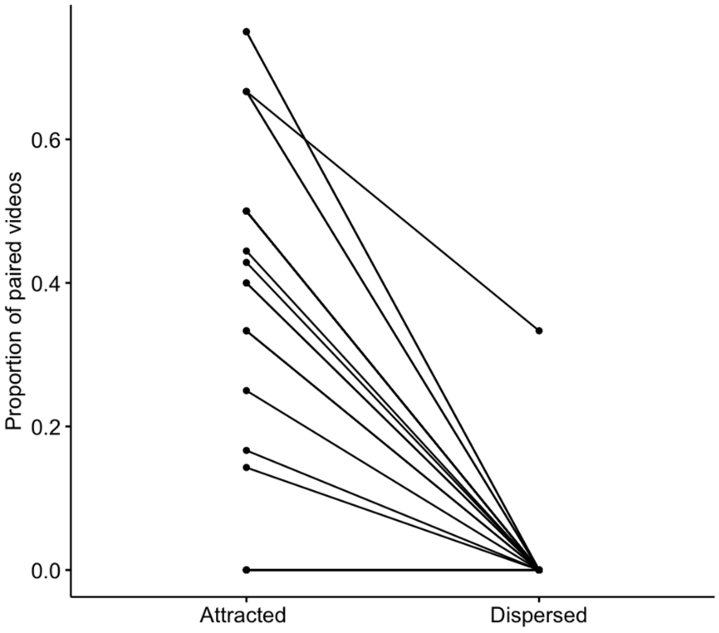

Figure 6: Proportions of attracted and dispersed pairs of play PO-MC videos (n=119 pairs), from n=25 individuals in Chimfunshi Group 2.

Question 2: Which factors moderate the contagion effect?

Grooming contagion occurrence

Overall, the model fitted the data significantly better than the null model (χ^2=11.612, df =3, P= 0.008). There was a significant positive effect of social closeness (χ^2=4.459, df=1, p=0.035). As shown in Figures 7 and 8, the more socially close the observer was to the stimulus individuals that they observed, the more likely they were to then initiate grooming with anyone. The effect of sex also approached significance (χ^2=3.115, df=1, p=0.078): Males tended to be less likely than females to initiate grooming post-observation, as shown in Figure 9. There was no clear effect of age.

There were also significant influences from the control effects. Individuals with a higher baseline grooming tendency were significantly more likely to initiate grooming (χ^2=6.065, df=1, p=0.01), and the more grooming bouts they observed, the more likely they were to initiate grooming (χ^2=6.688, df=1, p=0.010). The effect of the number of others present also approached statistical significance: there was greater tendency for the focal to initiate grooming the more individuals present, (χ^2=3.533, df=1, p=0.060). There was no significant influence of time period. Full results are shown in Appendix II, along with the contributions of the random intercepts and slopes.

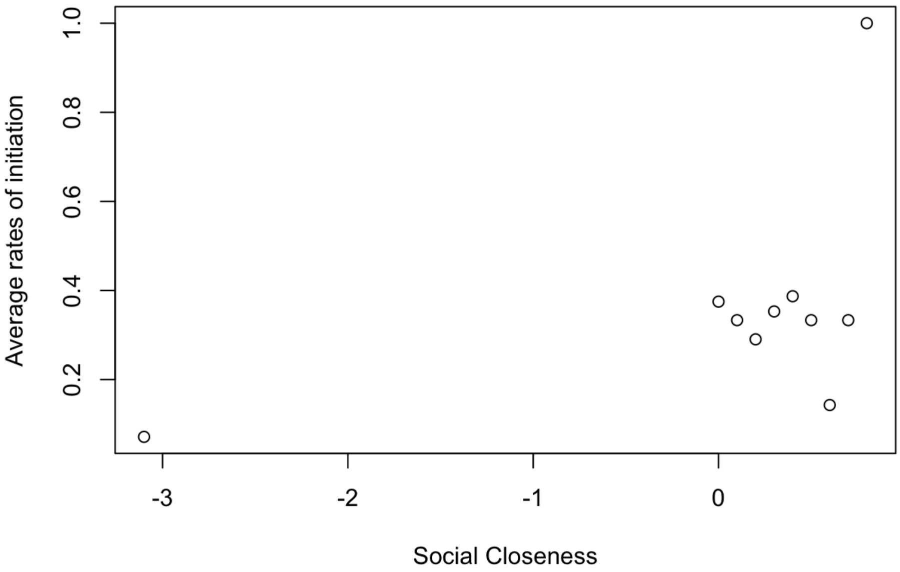

Figure 7: Rates of post-observation grooming initiation. Dots represent the values averaged across every 0.1 increment of the z transformed and logged DSI of observer-stimulus individuals. Data comprised of 156 observations of 40 chimpanzees in Chimfunshi Group 2.

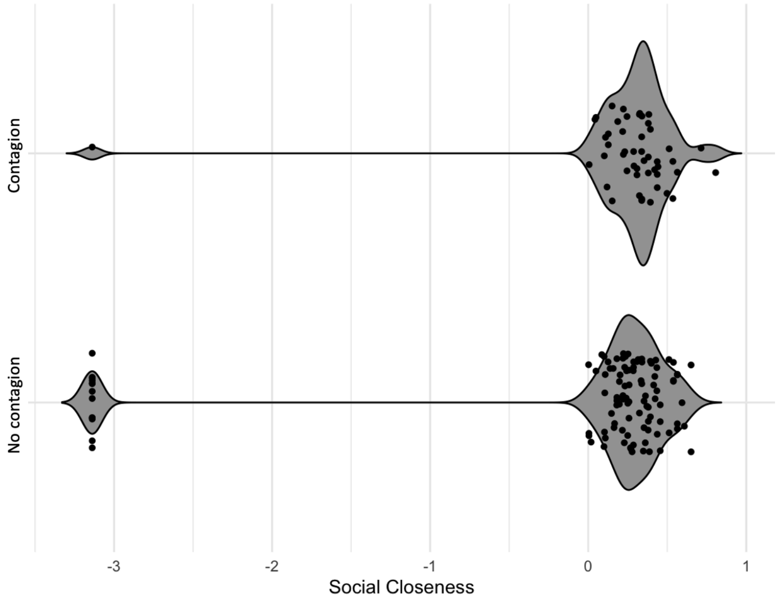

Figure 8: Violin plot of the z transformed and logged DSI of the observer-stimulus individuals, for focals where contagion did and did not take place. Shading represents the density of datapoints collected at different values of social closeness. Data comprised of 156 observations of 40 chimpanzees in Chimfunshi Group 2.

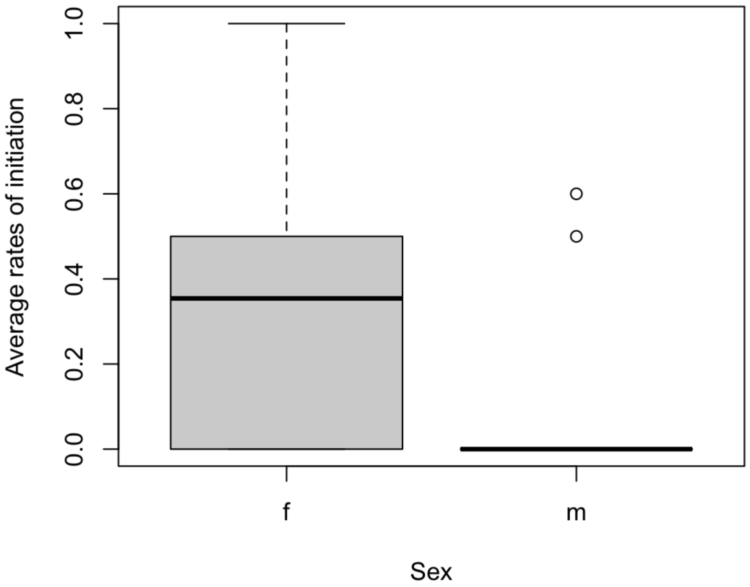

Figure 9: Box plot of post-observation grooming initiation rates of males (49 observations of 13 individuals) and females (107 observations of 26 individuals), in Chimfunshi Group 2. Upper and lower quartiles are indicated by the box boundaries, and dots indicate outliers.

Grooming contagion latency

Results showed that post observation grooming was not immediate, although grooming peaked within the first minute (Figure 10). There was a median latency of 83.1 seconds, lower quartile of 26.4 seconds, and upper quartile of 119.5 seconds.

Overall the model did not significantly differ from the null model (χ^2=3.651, df =3, P= 0.302 There was not a significant contribution of any of the fixed effects; the only control effect that was a significant predictor was time of day (χ^2=4.493, df=1, P=0.034): individuals initiated grooming faster in the afternoon, as shown in Figure 11. Full results and the contributions of random intercepts are shown in Appendix III.

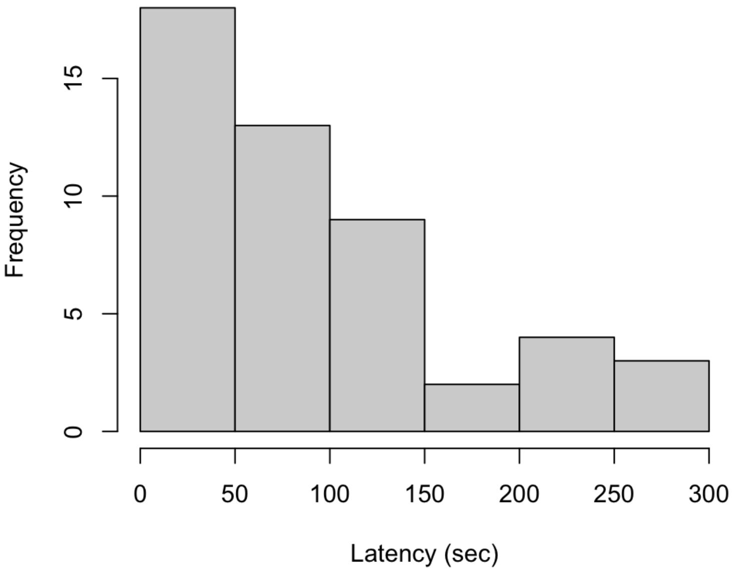

Figure 10: Histogram of latencies from observing grooming to first initiating grooming. Data comprised of 49 observations of 20 individuals in Chimfunshi Group 2.

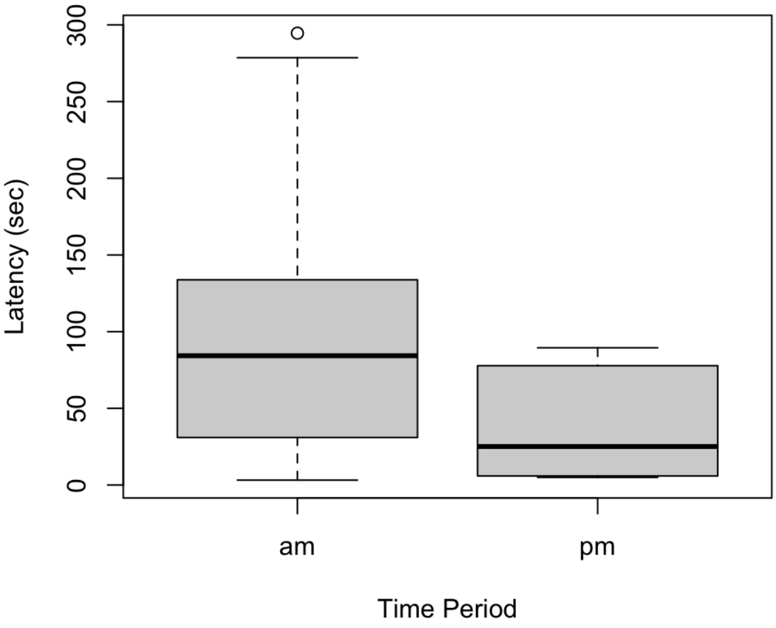

Figure 11: Box plot of post-observation grooming latencies in the morning (n=43) and afternoon (n=6). Upper and lower quartiles are indicated by the box boundaries, and dots indicate outliers. Data was collected from 20 individuals in Chimfunshi Group 2.

Play contagion occurrence

Stability tests revealed that this model was highly unstable, especially with regard to random effects. Therefore, results must be interpreted with caution. The model overall significantly differed from the null (χ^2=27.67, df =3, P<0.001). There was a highly significant effect for age (χ^2=25.730, df =1, P<0.001): younger individuals were more likely to initiate play after observation, as shown in Figure 12. Stability tests revealed that although the size of effect varied over a large range, it was consistently negative, suggesting a genuine effect. There was no discernible effect for the other fixed and control effects, although these may have been masked by the model's underdispersion. Full results of the fixed and random effects are reported in Appendix IV.

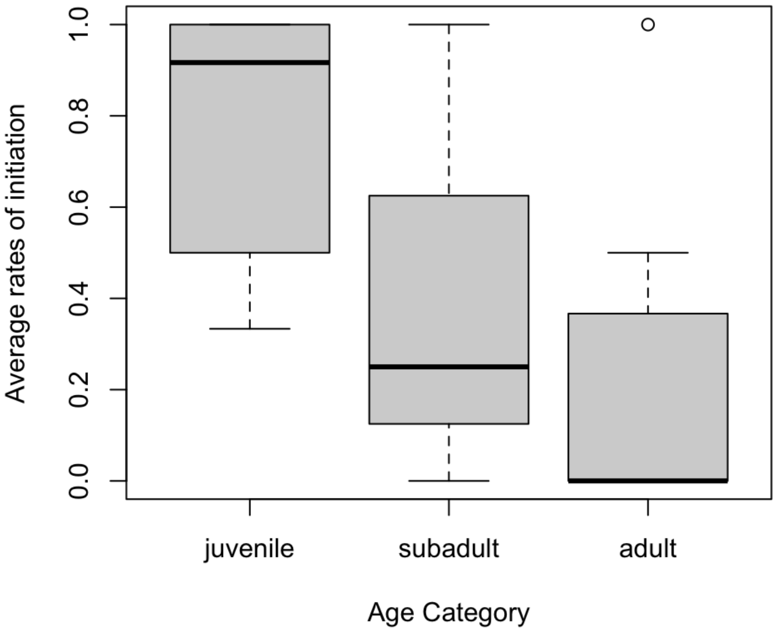

Figure 12: Mean rate of post-observation play across age categories, for juveniles (36 observations of 10 chimpanzees), subadults (20 observations of 4 chimpanzees) and adults (83 observations of 27 chimpanzees). Upper and lower quartiles are indicated by the box boundaries, and dots indicate outliers. Total data comprised of 139 observations.

Play contagion latency

Analysis revealed that post observation play was not immediate, but faster than grooming, and the vast majority of play happened within the first minute, as shown in Figure 13. There was a median latency of 18.0 seconds, lower quartile of 3.5 seconds, and upper quartile of 45.4 seconds.

The model did not significantly differ from the null (χ^2= 3.9379, df =3,P= 0.2682). None of the fixed or control effects reached significance, although there was a slight trend for age (χ^2=1.93662, df=1, P=0.16404), wherein younger individuals were faster than older individuals to initiate play post-observation, as depicted in Figure 14. Full results are shown in Appendix V.

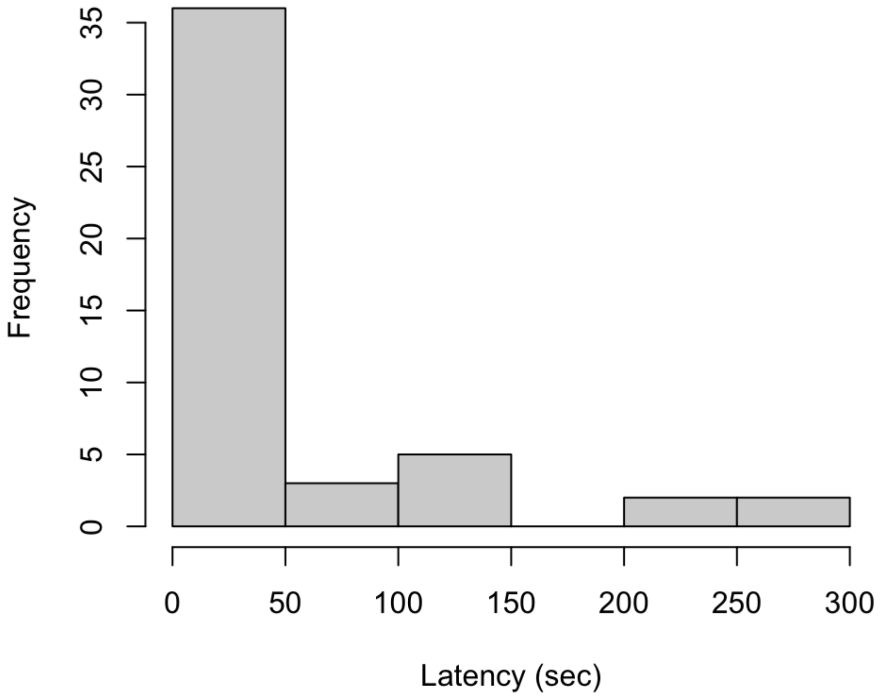

Figure 13: Histogram of latencies from observing play to first initiating play. Data comprised of 48 observations across 28 individuals in Chimfunshi Group 2.

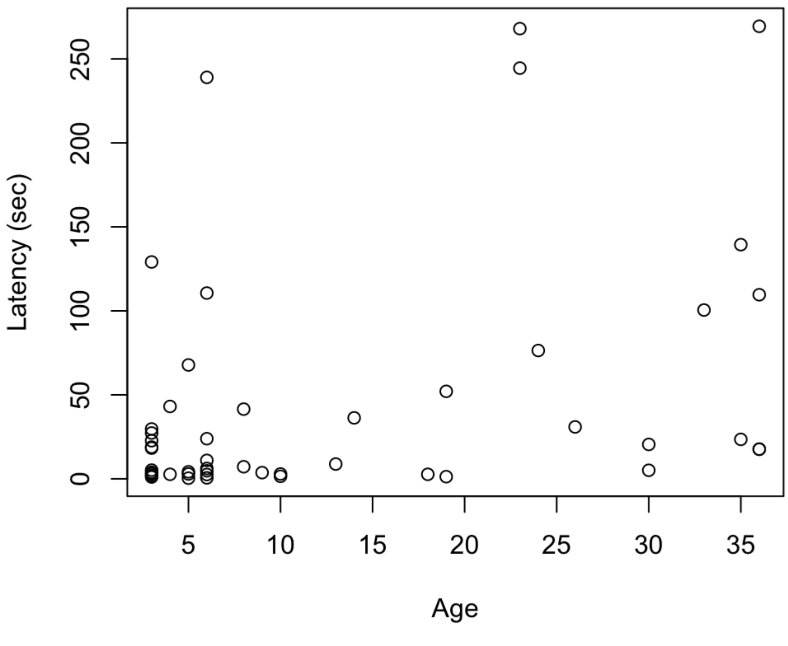

Figure 14: Latencies from first observing play to initiation play, plotted against the age of the observer. Data comprised of 48 observations of 28 individuals in Chimfunshi Group 2

Question 3: Does susceptibility to contagion correlate with number of social partners?

Grooming Contagion & Social Integration

Overall, the model did not significantly predict number of grooming partners (full-null comparison: F(4, 19)=1.9, P=0.1519). A drop-wise comparison revealed no significant influence of grooming contagion score, and no significant influence of the control variables (age, sex and rank).

In particular, there was no significant relationship between contagion score and number of close social partners, as predicted (estimate±SE: 1.256 ± 4.196, t(19)= 0.299, P =0.768). Figure 15 illustrates this lack of clear relationship, and full results are reported in Appendix VI.

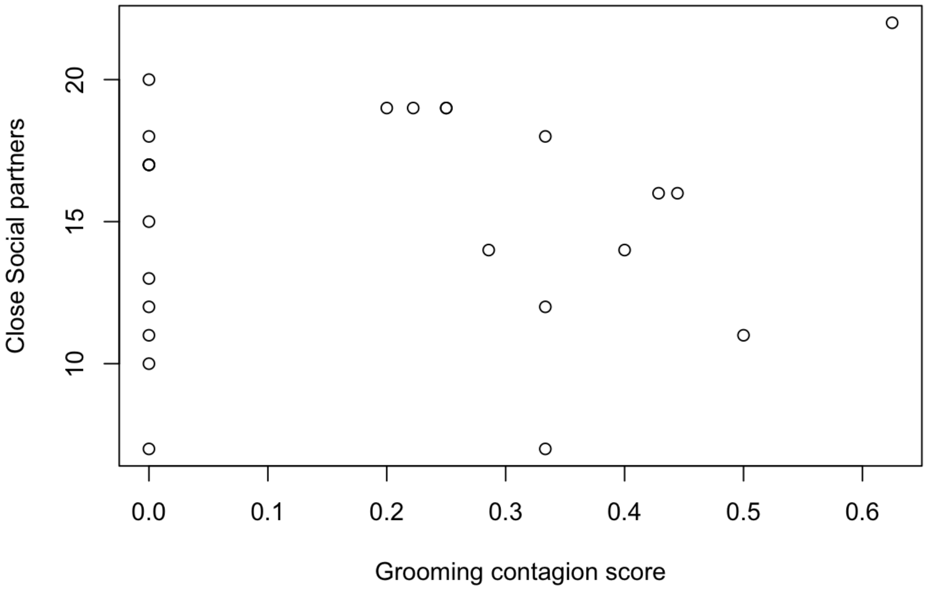

Figure 15: Number of close social partners plotted against grooming contagion score of each chimpanzee (n=24). Close social partners are defined as relationships with a DSI score in the upper quartile of all dyads in Chimfunshi Group 2.

Play Contagion & Social Integration

Stability tests indicated that the model was unstable, and so results must be interpreted with caution. The model did not significantly predict the number of social partners (full-null comparison: F(4, 14)=0.3179, P=0.8613), and a drop-wise comparison revealed no significant individual predictors. There was no clear relationship between play contagion score and number of social partners (estimate±SE: 7.049 ± 7.067, t(14)=- 0.997, P =0.335). This data is shown in Figure 16, and full results are reported in Appendix VII.

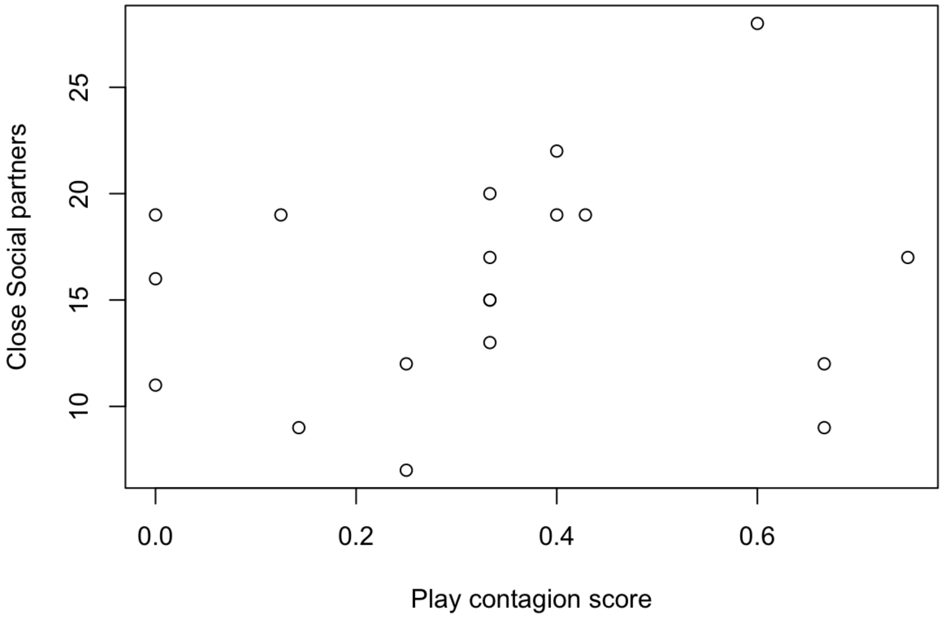

Figure 16: Number of close social partners plotted against play contagion score (n=19). Close social partners are defined as relationships with a DSI score in the upper quartile of all dyads in Chimfunshi Group 2.

DISCUSSION

This study sought to establish whether grooming and play is contagious in chimpanzees, and if so, to explore what individual characteristics influence this, and whether individual differences in contagion are linked to number of close social partners. Evidence for a contagion effect was found for both grooming and play. I also found evidence that grooming contagion is moderated by the social closeness of observer and stimuli individuals, whilst play contagion may be moderated by age. No significant association between degree of contagion and number of close social partners was found. I discuss findings in response to each of my research questions below.

GROOMING CONTAGION

Question 1: Is there a contagion effect?

I found that, as hypothesised, chimpanzees were more likely to initiate grooming after having observed others groom than in a matched control time period. This contagion effect has previously been found in macaques (Berthier & Semple, 2018; Ostner et al., 2021), but is reported in chimpanzees for the first time here. The effect was significant for a sample that included all ranks and sexes, and chimpanzees aged 3-44 years old. This extends our understanding of social contagion in chimpanzees: not only do they instantaneously mimic facial expressions and catch yawns from one another (Palagi et al., 2020), but they also catch affiliative social behaviours.

A challenge of conducting this research in sanctuary living chimpanzees is that our lack of control over their immediate social environment, and limited opportunities for observation. This meant that it was not feasibly possible to match the post-observation videos (POs) and control focal videos (CFs) to all desirable criteria. Although they were matched for time period and approximate number of individuals present, ideally they would also be matched in terms of identity of the individuals present, and other factors such as the focal individual’s activity at the start of the focal. It therefore remains possible that the significant difference in grooming initiation between POs and CFs could be driven in part by these other sources of variance. However, as both POs and CFs were filmed opportunistically and at random, there would be no reason for a systematic bias of unaccounted for factors, presumably resulting in limited interference.

Question 2: What factors moderate the contagion effect?

Results revealed that, as hypothesised, grooming was more likely to be initiated after observation of grooming involving individuals who were socially close to the observer. However, there were no significant effects of sex or age, and we had to exclude rank from the analysis.

The finding that contagion was enhanced by social closeness has several explanations and implications. Heightened contagion between close individuals has been reported for yawn contagion and facial mimicry, as well as in many empathy studies (Palagi et al., 2020), although one recent contagion study has found an opposite effect (Laméris et al., 2020). Palagi et al. (2020) contrast 2 explanations as to why this bias is generally found. Contagion could be biased towards familiar individuals as social closeness facilitates emotional transfer ('Emotional Bias Hypothesis', Palagi et al., 2020). Alternatively, it is also possible that this effect may be driven by an attention bias towards socially close individuals ('Attention Bias Hypothesis'). We accounted for a baseline level of attention by only including instances where the chimpanzee was close by and visually oriented to the grooming behaviour, although did not include any further analysis. Degree of attention could be measured by recording the total time spent orienting towards the behaviour, although even this is an approximate measure that cannot convey to what degree the individual is processing the visual scene in front of them. To unpick degree of processing and subsequent arousal, additional methodologies such as pupillometry or thermography could be used. Pairing these indicators of emotional arousal with data on varying attention levels, and studying the time profile of emotional arousal, would clarify if emotional transfer was enhanced only when attention is sustained towards any individual, or only with socially close individuals

Another explanation for the finding is that the instances where individuals observed grooming involving someone they were socially close to necessarily involved the presence of a preferred grooming partner, and their presence would increase the likelihood of the observer initiating grooming. To differentiate between these explanations, we would need a larger dataset, and to include the presence of a preferred grooming partner as a separate control variable in the analysis, and compare grooming rates when observing non-close individuals groom with a close individual present, vs observing close individuals groom with a non-close individual present.

The prediction that grooming contagion would be more pronounced in younger individuals, due to weaker executive function skills meaning reduced top-down inhibition (Manrique et al., 2015), was not supported. This is most likely driven by the low frequency of younger individuals initiating grooming in the PO focals, and at general baseline, meaning there was insufficient data to detect patterns. It is still possible that the younger individuals were influenced in other ways after observing grooming: future research could address whether observing grooming increased rates of affiliative behaviour (such as contact sitting or play).

There was also no evidence for a sex effect: both males and females were as likely to initiate grooming in the PO focals. This is in-line with a lack of sex difference found in the yawn contagion literature (e.g. Campbell & Cox, 2019). Some research has suggested that males are more sensitive to using grooming as a social currency (in the short term at least) (Schroepfer-Walker et al., 2015), and that females may monitor grooming patterns overall rather than based on a single instance. Comparing the different time-frames that grooming contagion happens in, for males and females, may therefore be an interesting direction for future research. Unfortunately, we did not have enough data to assess the impact of rank on post-observation grooming levels, and so could not test our final prediction.

Finally, two of the four control variables included in the model had a significant effect. As expected, baseline grooming tendency increased likelihood of initiating grooming. Total number of grooming bouts observed also increased likelihood of initiating grooming, presumably because as more grooming was observed, this increased activation to reach the threshold for grooming behaviour being expressed in the observer. There was no significant difference of whether the PO took place in the morning or afternoon, despite the pilot study showing overall higher rates in the morning. There was also no effect of total others present, perhaps because the individual identities of the chimpanzees present mattered more than their total number. Overall, the initiation data suggested that the social closeness between the observer and stimulus individuals is a more important predictor of grooming contagion than individual differences (age and sex). This is in keeping with previous yawn contagion and facial mimicry research.

The latency data revealed no evidence supporting the predictions that sex, age and social closeness would impact the speed of contagion. Post-observation grooming was not instantaneous (median latency = 83.1 sec, SD=81.2 sec). This is comparable to the previous research of grooming contagion in macaques (mean latency = 167 sec, range = 3-841 sec; Ostner et al., 2021), and yawn contagion in chimpanzees (where there is a peak in contagion within the first 1.5min; Campbell & Cox, 2019). This delay in response, compared to more immediate mimicry processes such as rapid facial mimicry, suggests an involvement of more indirect cognitive pathways (Ferrari et al., 2009): the threshold for expression of contagious grooming may only be reached with a specific combination of facilitative factors, or behaviour may initially be inhibited by top-down cognitive pathways.

The only control factor that significantly influenced latency was time of day, with chimpanzees “catching” grooming faster in the afternoon than the morning. Time period was included as a control effect as the chimpanzees are generally more active in the morning, with increased levels of grooming and play (as found in the Pilot Study). It is possible that a lack of other activity in the afternoon meant that there were less distractions and grooming bouts attracted more attention, and so post-observation grooming was initiated faster. Future studies could perhaps address this by including a measure of total other distractions, or more precisely controlling for attention.

In contrast to my hypothesis, there was no evidence that grooming contagion happened faster when a chimpanzee observed a socially close individual grooming. This may just be because the effect was not strong enough to be detected in the reduced dataset (grooming occurred in only N = 49 focals). Alternately, whilst social closeness may influence the overall presence of contagion, it is possible that the exact time profile of when contagion occurs is governed by other factors specific to the interaction. Physical proximity and grooming rates are generally correlated (e.g. Langergraber et al., 2009), but the specific positioning of potential grooming partners may also have an influence on the timing of grooming, with the expression of grooming behaviour becoming more likely when a partner is within arm's reach. The positioning and involvement of other individuals may also play a role: if favoured grooming areas are being blocked by another body, an individual may be less likely to initiate grooming. Such variation in the immediate social surroundings could impact the time profile more than the hypothesised contagion effect, although a larger data-set may still indicate a contagion effect.

Question 3: Does susceptibility to contagion correlate with number of social partners?

I did not find any evidence to support the prediction that likelihood to catch grooming predicted number of close social partners. It is possible that the measures I used to generate a 'contagion score' did not adequately reflect true individual differences. I had limited data-points per individual, (from n=3 to n=12), and as established by Q2, the probability of contagion happening in each instance varied according to multiple situational factors, and so to establish a reliable indicator of overall contagion, more data may have been required. It is also possible that grooming contagion, which appears to be driven by a social closeness bias, only acts to facilitate grooming between already socially close individuals, thereby re-enforcing existing bonds, rather than generates new ones. Therefore, there may not in fact be a correlation between contagion index and number of close social partners, but between contagion index and strength of close bonds. Further research could address the wider implications of individual differences in contagion by conducting a full social network analysis to consider the relationship statuses of individuals on a more fine-grain scale. Additionally, the possible bi-directional relationship could be further explored, using a longitudinal study to unpick the simultaneous positive influences that contagion and overall sociality may have on each other.

PLAY CONTAGION

Question 1: Is there a contagion effect?

As hypothesised, chimpanzees were more likely to initiate play after having observed others play than in a matched control time period. An effect of play contagion had previously been found in ravens (Wenig et al., 2021) but never in primates, and is reported in chimpanzees for the first time here. As with grooming contagion, the effect was significant for a sample that included all ranks and sexes, and chimpanzees aged 3-44 years. Spontaneous mimicry has previously been established within play in chimpanzees, but this finding extends our understanding of social contagion, demonstrating that contagious processes can happen on a larger scale and longer time-frame, in terms of entire affiliative behaviours. As discussed above, a drawback of using sanctuary housed chimpanzees meant that the POs could not be entirely matched to CFs, although this would not have led to systematic biases affecting the results.

Question 2: What factors moderate the contagion effect?

I explored whether sex, age, and social closeness predicted the occurrence of post-observation play. This was a fairly unstable model and so any results drawn from it must be tentative. As hypothesised, there was a negative relationship between age and play initiation, consistent across all iterations involved in the model stability tests. Younger individuals were more likely to initiate play post-observation, controlling for baseline tendency. This offers preliminary support to the idea that the contagion of interactive behaviours that are under voluntary control may be heightened in younger individuals who have weaker executive function - as found in humans, apes, and macaques (Anderson et al., 2002; Manrique et al., 2015; Weed et al., 2008). This pattern was not found within the grooming contagion dataset, and this may be because play is a much more common way of affiliating for juvenile chimpanzees (Shimada & Sueur, 2014), and so more salient to them than grooming. Additionally, play typically involves more movement and physical disturbance of the surroundings, and so may attract more attention than grooming bouts, leading to an increased unsuppressed contagious response.

None of the other predictors showed a significant influence in the model. There was no evidence to support the prediction of a social closeness bias; perhaps due to play bouts being more salient than grooming bouts, high levels of attention are already directed to the interaction, and so an attention bias towards socially close individuals has no additional effect. It was surprising that control variables did not also have an influence. The lack of effect of additional play bouts increasing contagion is reminiscent of some of the yawn contagion literature: number of yawns observed does not increase likelihood of contagion in chimpanzees and humans, although does in bonobos (Campbell & Cox, 2019; Norscia & Palagi, 2011; Norscia et al., 2022).

It could be that the threshold for play contagion (like yawn contagion) in chimpanzees is lower than that of grooming contagion, and is reached after observing just one bout of play.

A possible lower threshold for play contagion than grooming contagion is also suggested by the latency data: the median latency for post observation play was only 18.0 seconds (vs 84.3 seconds for grooming). The latency data revealed the same pattern of results as the overall occurrence analysis. The model, which was fairly stable, showed no statistically significant predictors, although there was a trend that as age increased, latency to play initiation increased too. This adds further support to the idea that younger individuals have a stronger impulse to “catch” play behaviour from others. Older individuals may wait longer until circumstances suit their joining the play - perhaps until another individual moves towards them, or until there is a lapse in the play intensity which makes it easier for them to join. Younger individuals however appear to initiate play more immediately (median latency: Juveniles = 6.2 sec, Adults = 33.6 sec). This suggests that either play is less costly to younger individuals and their threshold for engaging in the behaviour is lower, or that there is less top-down inhibition meaning that arousal is greater and the impulse to play is immediately carried out. This could be further explored by pairing behavioural measures of contagion with parallel emotional contagion measures: we would expect that younger individuals who “caught” play quickly would experience higher and more persistent of arousal and greater emotional transfer, whereas individuals who didn’t would perhaps demonstrate an initial increase but then subsequent decrease in arousal. Emotional contagion could be measured through combining multiple modalities of behavioural and vocal observations to give an indicator of underlying emotional state (e.g. Reimert et al., 2017). To detect more subtle changes in arousal, facial thermal imagery, detecting changes in blood flow, could be used. There is an established nasal temperature effect in primates in response to negative emotional stimuli (Kano et al., 2016; Dezecache et al., 2017; Chotard et al., 2018), although further research may be needed to validate what thermal changes occur in the context of play, and other positive emotional situations. Until then, integrating physiological and behavioural measures will remain important for interpretation. The play latency model, as with Model 3, indicated no significant effect of any of the other predictors, although it is possible that these were masked by a limited sample size and large influence of age.

Question 3: Does susceptibility to contagion correlate with number of social partners?

I did not find any evidence to support the prediction that likelihood to catch play predicted an individual’s number of close social partners. As with the grooming data, it is probable that the measures I used to generate a ‘contagion score’ did not adequately reflect true individual differences, as again I had limited data-points per individual, (from n=3 to n=12), and more data may have been required.

Alternatively, it is possible that there is no overall positive or negative relationship between sensitivity to play contagion and number of close social partners. Although forms of social favour have been previously found to be predicted by facial mimicry (Paukner et al., 2009) and environment-directed mimicry (Anderson & Kinnally, 2020), this relationship may not extend to play contagion. It may be that individuals who have multiple strong social connections, and are more socially competent and confident, are more likely to spontaneously initiate play of their own accord, which would reduce the degree to which they show evidence of play contagion. This would counteract the hypothesised relationship of increased play contagion resulting in more close social relationships. To untangle these conflicting proposed relationships, longitudinal research could be conducted to elucidate the direction of effects, and overall initiation of play could be considered as a factor alongside play contagion and social integration.

OVERALL CONCLUSIONS

The present study finds the first evidence for the contagion of positive social behaviours in chimpanzees. This widens the social contagion literature, where on a behavioural level, only yawn contagion has been studied in chimpanzees previously (Palagi et al., 2020). The wider emotional contagion literature has so far focussed largely on negatively-valenced emotional states (Kano et al., 2016; Dezecache et al., 2017), but the presence of positive behavioural contagion indicates the importance of including the entire spectrum of emotions when considering the function and importance of social contagion. The differing patterns of influential effects and timeframes of contagion that we found within play and grooming further emphasise the importance of not generalising between behavioural contexts. It is clear that contagion of affiliative behaviours is not a universal automatic response, but rather may be underpinned by both bottom-up attention processes and top-down control.

Future research should further explore these processes. Including more precise measures of visual attention could further clarify the nature of a social-closeness bias, and the differences between grooming and play contagion due to their differing saliences. The influence of top-down control could be studied by parallel measures of emotional arousal, which could reveal the time frame of any inhibitory processes. Potential top-down control processes could be specifically studied within scenarios where there are reasons an individual ought not to join an interaction: for example, if a grooming or play bout changes after observation to involve higher ranking individuals who would be less receptive to being joined. Using measures of emotional transfer alongside more precise measures of behavioural synchrony (such as facial mimicry or mimicry of stereotyped behaviours, e.g. as a foot stomp in play) could reveal to what extent behavioural contagion is driven by a more general transfer in mood or by motor mimicry mechanisms. Future research could explore the influence of factors such as age and social closeness on both aspects of contagion, to ascertain at which level they exert an effect. Further individual and interaction level factors could also be considered, such as kinship in addition to social closeness, or an individual's centrality within the social network, to understand more comprehensively what gives rise to individual differences in contagion.

It is also possible that there is further variation within different types of grooming and play, as different instances of the behaviour may entail differing levels of arousal, and may not even be wholly positive. Although play is considered as a uniform behaviour in this analysis, some play can escalate to negative interactions (Adriaense et al., 2020). The surrounding context and the outcomes of the interaction, or parallel measures of emotional arousal such as thermal data, could be used to categorise play into subgroups that involve particular emotional states. Previous research into grooming contagion has used concurrent behavioural measures (self-directed behaviours indicative of anxiety) to suggest a positive emotional state (Berthier & Semple, 2018), and overall a link with pleasurable emotions is established (Russell & Phelps, 2013). However, it is entirely possible that some grooming bouts result in more positive emotions than others, and grooming on the whole is not uniform. Categorising interactions by emotional valence is useful when assessing general patterns in data and identifying areas of missing research, but a consideration of the exact emotional profile of individual interactions may be key to fully understanding them.

In order to understand how the behavioural contagion of positive interactive behaviours then fits into the wider social life of individuals, longitudinal research could be key. Within the human literature, it is established that behavioural mimicry and emotional contagion bolster social success, leading to increased cooperation and affiliation (Barsade et al., 2002; Lakin & Chartrand, 2003; Lakin et al., 2003). Across primates, it is recognised that strong social bonds and increased social integration lead to fitness benefits (Ostner et al., 2018), although how different forms of contagious processes impact sociality and these subsequent evolutionary advantages is not understood. Research could address how differences in likelihood to "catch" affiliative behaviours predict social outcomes including overall integration, changes in rank, and other empathic behaviours such as prosociality. Whether an individual is more likely to spontaneously initiate positive behaviours could also play a role in these social outcomes, and should be considered as a separate influential factor. Other forms of behavioural contagion, including scratch and yawn contagion, could also be considered: understanding the relative influence of these different types of contagion would further our understanding of their differences.

Overall, the present study finds initial evidence that chimpanzees catch both play and grooming from each other. In my sample, the process appears to be biased by social closeness in grooming but not in play contagion, and could be determined by individual factors, with grooming contagion being more pronounced in females, and play contagion being more pronounced in younger individuals. These patterns could serve as a model for our early hominid ancestors: sharing a sensitivity and propensity to catch the positive behaviours of others, additionally to negative behaviours and emotions, may have shaped their social relations and adaptive fitness.

APPENDICES

APPENDIX I: ETHOGRAM

BEHAVIOURS:

Grooming: Picking through the hair of another chimpanzee, searching for and/or removing debris from their body. Involves the use of hands or mouth. May involve any body posture (i.e. sitting, lying down). (Videan et al 2005).
NOTE: does not include genital inspection.
If grooming pauses for <5 secs, ignore the pause, and treat the grooming as continuous.
If grooming stops for >5 secs and <30 secs, record the grooming bout as having ended. The next grooming is a new *grooming bout*.
If grooming stops for >30 secs, or another individual joins the grooming, then any more grooming is a new *grooming episode*.

Social Play: Non-aggressive social interaction involving two or more individuals. Never accompanied by pilo-erection. The pattern of behaviour may resemble those used in serious functional contexts (e.g. fighting, mounting, fleeing), but has no obvious immediate benefit to the players (Worch 2012).

- **Low intensity play:**
  Involves low intensity, stationary actions (touching and tickling) (Fröhlich et al 2016), OR any play that is not accompanied by play faces/laughter.
- **Higher intensity play ("Play"):**
  Accompanied by play faces and/or laughter OR involves high-intensity actions (wrestling, chasing, rough and tumble) (Fröhlich et al 2016).

INITIATION OF BEHAVIOURS:

An individual initiates a behaviour either if:
(i) they approach another individual and start enacting a behaviour (without their partner performing an initiation gesture)
(ii) they approach another individual and use a particular gesture (see below) which results in the desired behaviour.

The gesture must be an intentional, goal-directed, mechanically ineffective movement, indicated by one or more of the following:

1. Audience checking via eye-gaze
2. Response waiting
3. Sensitivity to recipient's attentional state
4. Persistence to a goal

Initiate grooming: Instigate grooming behaviour through one of the following gestures: (Hobaiter & Byrne; 2011, 2014).

- Big loud scratch: A loud exaggerated scratching movement on the signaller's own body
- Present grooming: Body is deliberately moved to expose an area to the recipient's attention, which is immediately followed by grooming of the area
- Bite: recipient's body is held between the teeth of the signaller

Initiate play: Instigate play through on of the following gestures: (Hobaiter & Byrne; 2011, 2014)

(*most common are in italics)*

- Arm shake: Raise arm/hand vertically in the air
- Arm wave: Large repeated back and forth movement of arm raised above the shoulder
- Dangle: To hang from one or both arms from a branch above another individual (audible)
- Drum object palms: Short hard audible contact of alternate palms against an object
- Feet shake: Repeated back and forth movement of feet from the ankles
- *Gallop: An exaggerated running movement where the contact of hands and feet is deliberately audible*
- Hand shake: Repeated back and forth movement of hand from the wrist
- Head nod: Repeated back and forth movement of the head
- *Head stand: Signaller bends forward and places head on the ground*
- Kick: Foot is brought into short hard contact with the recipient's body in a movement from the hip with a horizontal element
- Knock object: Back of the hand or knuckles are brought into short hard audible contact with an object
- Leg swing: Large back and forth movement of the leg from the hip
- Object in mouth approach: Signaller approaches recipient while carrying an object in the mouth (e.g. a small branch)
- Poke: Firm, brief push of one or more fingers into the recipient's body
- Pounce: Signaller displaces through the air to land quadrupedally on the body of the recipient
- *Roll over: Signaller rolls onto their back, exposing their stomach, normally accompanied by repeated movements of the arms and/or legs*
- Stomp other: Sole of the foot/feet is lifted vertically and brought into a short had audible contact with the recipient.

APPENDIX II: FULL RESULTS OF MODEL 1 (GROOMING OCCURRENCE)

		Model estimates			Chi squared test	
	Term	Estimate	SE	Z	X 2	P (chi)
	Intercept	-0.6254	0.3682	-1.698		
Fixed Effects	Age	0.116	0.3055	0.38	0.1547876	0.694001517
	Sex	-1.2999	0.7947	-1.636	3.115036	0.077572764
	Social Closeness	0.663	0.3835	1.729	4.4594771	0.034708121
Control Effects	No. bouts observed	0.521	0.2567	2.029	4.910411	0.026695288
	No. others observed	0.5191	0.3057	1.698	3.5328955	0.060162637
	Time period	-0.8244	0.6703	-1.23	1.7248605	0.189068596
	Grooming tendency	0.6768	0.3148	2.15	6.6882616	0.009704979

		Confidence intervals		Stability tests	
	Term	Lower CI	Upper CI	min	max
	Intercept	-14.09711	0.017694	-1.073351	-0.500627
Fixed Effects	Age	-2.286027	4.089754	0.004372	0.305954
	Sex	-26.170005	0.151942	-2.126231	-1.021706
	Social Closeness	0.084033	14.292556	0.547344	2.158699
Control Effects	No. bouts observed	0.048506	13.303949	0.408331	0.761391
	No. others observed	-0.070007	11.095689	0.378269	0.711864
	Time period	-19.670315	0.627323	-1.405413	-0.5916
	Grooming tendency	0.174417	13.8194	0.529035	0.904126

		Model estimates	Stability tests	
Grouping factor	**Effect**	**SD**	**min**	**max**
Focal ID	Intercept	0.378596	0	0.644454
Focal ID	Total others	0.593555	0	0.805233
Focal ID	Relationship Quality	0.000018	0	0.930686
Event	Intercept	0.414766	0	0.757935

APPENDIX III: FULL RESULTS OF MODEL 2 (GROOMING LATENCY)

		Model estimates			Chi squared test	
	Term	**Estimate**	**SE**	**Z**	**X 2**	**P (chi)**
	Intercept	-0.57359	0.19774	-2.901		
Fixed Effects	Age	0.07824	0.20939	0.374	0.1376359	0.71064263
	Sex	-0.47737	0.65219	-0.732	0.5448881	0.46041396
	Social Closeness	-0.24154	0.15696	-1.539	2.4706227	0.11599197
Control Effects	No. bouts observed	0.1685	0.15954	1.056	1.1173798	0.29048334
	No. others observed	-0.25564	0.16927	-1.51	2.2968096	0.12964004
	Time period	-1.08435	0.52307	-2.073	4.4926189	0.03404149
	Grooming tendency	-0.21293	0.19855	-1.072	1.1161736	0.29074387

		Confidence intervals		Stability tests	
	Term	**Lower CI**	**Upper CI**	**min**	**max**
	Intercept	-1.057438	-0.196525	-0.792	-0.469
Fixed Effects	Age	-0.347008	0.528406	-0.171	0.501
	Sex	-1.950493	0.797571	-0.748	-0.155
	Social Closeness	-0.543371	0.048106	-0.855	-0.217
Control Effects	No. bouts observed	-0.163703	0.535719	0.084	0.357
	No. others observed	-0.630746	0.091472	-0.399	-0.2
	Time period	-2.281972	-0.134075	-1.816	-0.907
	Grooming tendency	-0.634543	0.201204	-0.423	-0.114

		Model estimates	Stability tests	
Grouping factor	**Effect**	**SD**	**min**	**max**
Focal ID	Intercept	0.302	0	0.484
Event	Intercept	0	0	0.993

APPENDIX IV: FULL RESULTS OF MODEL 3 (PLAY OCCURRENCE)

		Model estimates			Chi squared test	
	Term	**Estimate**	**SE**	**Z**	**X 2**	**P (chi)**
	Intercept	-11.178	21.082	-0.53		
Fixed Effects	Age	-17.6	19.147	-0.919	25.729681	0
	Sex	-10.84	29.796	-0.364	-0.126387	1
	Social Closeness	4.171	15.439	0.27	-1.102128	1
Control Effects	No. bouts observed	2.19	12.363	0.177	0.123745	0.725008
	No. others observed	-3.549	21.75	-0.163	0.319232	0.572069
	Time period	-10.485	29.878	-0.351	9.892669	0.001659
	Play tendency	5.086	16.14	0.315	-0.772458	1

		Confidence intervals		Stability tests	
	Term	**Lower CI**	**Upper CI**	**min**	**max**
	Intercept	-22.670529	7.21268	-15.059172	-3.682852
Fixed Effects	Age	-22.372658	0.30468	-30.621382	-8.850106
	Sex	-27.709957	12.1668	-20.293908	2.74746
	Social Closeness	-5.163319	10.73356	-2.297348	11.008501
Control Effects	No. bouts observed	-6.181304	8.58839	-1.251373	6.519389
	No. others observed	-17.358982	11.96298	-6.143123	10.291099
	Time period	-32.4155	20.15087	-23.448473	0.020234
	Play tend	-5.747805	10.24268	-0.63167	9.573481

		Model estimates	Stability tests	
Grouping factor	**Effect**	**SD**	**min**	**max**
Focal ID	Intercept	0.000019	0	22.303191
Focal ID	Total others	69.193066	27.951385	107.822652
Event	Intercept	53.943876	28.181379	96.128484

APPENDIX V: FULL RESULTS OF MODEL 4 (PLAY LATENCY)

		Model estimates			**Chi squared test**	
	Term	**Estimate**	**SE**	**Z**	**X 2**	**P (chi)**
	Intercept	-1.49474	0.24151	-6.189		
Fixed Effects	Age	0.33629	0.23854	1.41	1.93661901	0.1640361
	Sex	-0.31423	0.35788	-0.878	0.77888813	0.3774814
	Social Closeness	-0.10647	0.15739	-0.676	0.43713819	0.508507
Control Effects	No. bouts observed	0.11528	0.1679	0.687	0.46237991	0.4965138
	No. others observed	0.20162	0.18739	1.076	1.11011843	0.2920562
	Time period	0.17492	0.36717	0.476	0.22174067	0.6377168
	Play tendency	0.02402	0.20376	0.118	0.01386635	0.9062614

		Confidence intervals		**Stability tests**	
	Term	**Lower CI**	**Upper CI**	**min**	**max**
	Intercept	-2.103082	-1.128018	-1.653792	-1.417261
Fixed Effects	Age	-0.124957	0.875853	0.215338	0.498616
	Sex	-1.087609	0.414141	-0.514391	-0.171541
	Social Closeness	-0.487709	0.240746	-0.197711	-0.033729
Control Effects	No. bouts observed	-0.235435	0.550678	0.04062	0.18296
	No. others observed	-0.160514	0.589837	0.025783	0.382219
	Time period	-0.559233	1.017465	-0.096633	0.392659
	Play tend	-0.414533	0.468915	-0.071337	0.128081

		Model estimates	**Stability tests**	
Grouping factor	**Effect**	**SD**	**min**	**max**
Focal ID	Intercept	0.000023	0.000016	0.000031
Event	Intercept	0.00001	0.000005	0.000017

APPENDIX VI: FULL RESULTS OF MODEL 5 (GROOMING CONTAGION & SOCIAL INTEGRATION)

	Model Estimates		**Significance Testing**		**Stability Estimates**	
Term	**Estimate**	**SE**	**t(19)**	**P**	**Min**	**Max**
Intercept	17.09953	3.22731	5.298	0.000	16.126	18.152
Contagion score	1.2555	4.19648	0.299	0.7681	0.248	4.663
Sex	-1.54013	1.94222	-0.793	0.4376	-2.793	-0.818
Rank	-0.13773	0.07908	-1.742	0.0977	-0.175	-0.097
Age	0.07643	0.08788	0.87	0.3953	0.019	0.112

APPENDIX VII: FULL RESULTS OF MODEL 6 (PLAY CONTAGION & SOCIAL INTEGRATION)

	Model Estimates		**Significance Testing**		**Stability Estimates**	
Term	**Estimate**	**SE**	**t(14)**	**P**	**Min**	**Max**
Intercept	10.932598	6.214392	1.759	0.100	7.673	13.291
Contagion score	7.048978	7.067324	0.997	0.335	3.668	11.008
Sex	1.407621	3.404542	0.413	0.686	-0.171	3.792
Rank	-0.001648	0.14175	-0.012	0.991	-0.082	0.078
Age	0.126244	0.138835	0.909	0.379	0.08	0.194

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