Social biases affecting self–other matching in Japanese macaques

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Abstract

A phenomenon in which a state of one individual triggers a congruent state in another is called "self–other matching." For group-living animals, the capacity to match one's states with those of conspecifics is advantageous for survival and reproductive success. Studying the mechanisms of self–other matching will provide some insights into how animals cope with the problems they face in group life. Some classical studies assumed that self–other matching is based on a reflex-like response. However, recent studies have shown that the likelihood of self–other matching is not equal among all individuals but is affected by social biases. These studies suggested that self–other matching involves not only a reflex-like mechanism but also more complex mechanisms that are regulated by social context.

In this thesis, I addressed the following three issues raised in previous studies. First, previous researches on social biases in behavioral matching focused primarily on positively valenced behaviors (e.g., play signals) and ones with neutral valence (e.g., yawning). However, little research has been done on negatively valenced behaviors. The way in which individuals act on the emotional states of others may depend on the type of emotional valence of the behavior. Hence, there is a good reason to believe that the effects of social biases on contagious matching vary with the valence of the behavior. The second problem with previous studies is that they have exclusively focused on the matching of an instant, event-like behavior such as yawning. Some types of self–other matching can be maintained over time. Social biases on the maintained self–other matching remain unknown. Third, individuals sometimes fail to maintain self–other matching. Social play provides a clear example of the failure of matching. In some rare cases, previously shared playful states can dissociate, and playful interaction escalates into overt conflict. Studying factors associated with the failure of self–other matching can illuminate the mechanisms of successful matching from a different angle. However, social biases affecting the failure of maintenance of self–other matching remain largely unknown. I addressed these issues by using data of vigilance and play fighting in a group of Japanese macaques.

In the first study (Chapter 2), I examined social biases in the contagion of vigilance, which is considered an emotionally negative behavior. Studies have shown that several social factors (e.g., familiarity, dominance, the mother–offspring relationship) affect behavioral contagion. Our findings revealed that vigilance exhibited by a given individual was more contagious to lower-ranked than to higher-ranked individuals. In addition, vigilance was more contagious to mothers from their offspring than vice versa. Thus, the susceptibility to vigilance exhibited by others varies according to the social status of each individual and the relationship between each pair of individuals. By contrast, we did not find any effects of kinship on vigilance contagion. This implies that familiarity bias, which is often reported to be associated with the contagion of yawning and play signals, does not influence vigilance contagion. Overall, our findings indicate that social bias may not affect all types of contagious matching in the same way, but rather contagious matching is affected by the interplay of the adaptive meaning of behavior and social biases.

In the second study (Chapter 3), I focused on play fighting and examined the relationship between the maintenance of shared playful state and facial signal (i.e., play face). I found that male juveniles were more likely than females to express play face before initiating play with other males and that juveniles were more likely to express play face before playing with others closer in age. Considering that Japanese macaque males have stronger motivation to play than females and that juveniles prefer to play with individuals of the same age, play face

before play initiation may reflect the individual's motivation for the interaction that is about to start. The observation that play bouts preceded by play face lasted longer than those not preceded by play face supports this interpretation. Also, we found that the expression of play face by an individual before play prolonged the time during which the partner attacked the expresser unilaterally. This implies that receivers of play face might be able to deliver playful attacks more vigorously. Overall, our results indicate that play face expression before play initiation functions to display the expresser's play motivation and maintain a shared state over a period by promoting active engagement of the recipients.

In the third study (Chapter 4), I examined social factors affecting the failure of maintenance of playful state matching. When play escalated, I defined the individual expressing negative responses (e.g., screaming and bared-teeth displays) as the "victim" and the other individual as the "aggressor." I found that individuals with a lower social rank than their playmates were more likely to be victims in escalations in same-age dyads. Furthermore, individuals that were younger and smaller than their playmates were more likely to be victims in escalations in mixed-age dyads. These results suggested that inter-individual differences determined by dominance relationships and developmental stages affect how self–other matching breaks down. In addition, I found that individuals that subsequently became aggressors had maintained an advantage for a longer duration during the preceding bout of play fighting compared to individuals that became victims. The results imply that escalation might have occurred because one individual (i.e., a higher-ranked or older individual) held an excessive advantage, and play lost its reciprocity. Overall, our results suggested that inter-individual differences may have led to asymmetries in play interactions, and these asymmetries may have caused the failure of maintenance of shared playful states.

In conclusion, this thesis suggests that self–other matching should be viewed as a more complex process than has been assumed by previous studies. Prior studies have focused primarily only on whether instant state matching occurs, with little attention to the adaptive meaning that varies from behavior to behavior and the time range of matching. The overlap between oneself and others is not simply determined by emotional closeness and social contexts. Instead, the overlap will depend on which behavioral and emotional states the researcher focuses on, each with a different adaptive meaning. Also, the self–other overlap can change over time: interactants manage their state matching with signals, and sometimes state dissociation occurs. In addition, ecological and social conditions, which vary from species to species, may affect patterns of self–other matching. A comparative study that takes into account the complex nature of self–other matching suggested by this thesis is expected to shed further light on the evolutionary background of basic social cognitive skills.

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Chapter 1: General introduction

1.1. Self–other matching across various domains

For group-living animals, the capacity to match one's states with those of conspecifics is advantageous for survival and reproductive success. Several findings have especially motivated researches on inter-individual state matching from proximate and ultimate perspectives. One of such motivating researches is the study of mirror neurons, which are activated when an individual performs an action and observes a conspecific performing the same action (Di Pellegrino et al., 1992). A phenomenon in which an observer's motor system is activated when the observer sees someone else executing an action is called "motor resonance" and is considered the sub-personal mechanism underlying behavioral matching (see also Iacoboni, 2009). Studies of empathy also inspire investigation on state matching. de Waal (2008) has promoted empathy researches from an evolutionary perspective based on the assumption that elaborate empathetic phenomena that humans exhibit, such as perspective-taking and targeted helping, are underlain by automatic and non-reflective state matching processes shared among non-human animals, such as mimicry and emotional contagion.

Researchers use various kinds of terms in the context of inter-individual state matching, such as *contagion* (Thorpe, 1963), *imitation* (Zentall, 2001, 2003), *copying* (Nielsen, 2006), *self–other merging* (Batson et al., 1997), *self–other overlapping* (Galinsky et al., 2005), *self–other matching* (Hecht et al., 2012), *matching with others* (Yamamoto, 2017). The words "contagion" and "imitation" tend to be used to refer to specific types of matching processes (see below), and the word "copy" to refer to a more general phenomenon in which multiple entities have the same or similar state. Also, the term "self–other merging" focuses on subjective and inter-subjective experiences that state matching brings about, and the term "self–

other overlapping” refers to a product of the state matching rather than the process of state matching itself. In this thesis, I consistently use the term “self–other matching” as the umbrella term to refer to processes of state matching triggered by the perception of the state of others who is socially and physically close to the observer.

Self–other matching encompasses various phenomena and can be classified in several ways. For example, self–other matching can be classified based on the domains in which matching occurs (Hecht et al., 2012; Adriaense et al., 2020). Self–other matching occurs across various domains, such as behavior, emotion, neural system, physiology, and cognition. Regarding the matching in behavioral domains, many studies have reported cases in which another individual’s motor pattern triggers the same motor pattern in the observer. For example, a phenomenon in which observing someone else’s yawning elicits yawning in the observer (i.e., yawn contagion) is well studied not only in humans (Massen et al., 2015) but also in many other species, including non-human primates (chimpanzees, *Pan troglodytes*: Campbell and de Waal, 2011; geladas, *Theropithecus gelada*: Gallo et al., 2021; orangutans, *Pongo pygmaeus*: van Berlo et al., 2020) and carnivores (dogs, *Canis lupus familiaris*: Silva et al., 2012; wolves, *Canis lupus*: Romero et al., 2014). Also, facial expressions are contagious in various species like humans (Bourgeois and Hess, 2008), chimpanzees (Davila-Ross et al., 2011), geladas (Mancini et al., 2013a, b), Tonkean macaques (*Macaca tonkeana*: Scopa and Palagi, 2016), domestic dogs (Palagi et al., 2015), and meerkat (*Suricata suricatta*: Palagi et al., 2019). Other examples of behaviors in which inter-individual matching occurs include posture (Tia et al., 2011), self-scratching (Feneran et al., 2013), vigilance (McDougall and Ruckstuhl, 2018a, b), and stretching (Miller, 2012; Gallup et al., 2017) (for review, see Zentall, 2001, 2003; Hecht et al., 2012; Yamamoto, 2017; Prochazkova and Kret, 2017; Adriaense et al., 2020).

As studies on empathy suggest, when one observes someone else's emotional expressions, the observer can experience the same emotion in oneself (Preston and de Waal, 2002). Emotional contagion, the automatic transmission of emotion between individuals (e.g., Hatfield et al., 1993), has been proposed as a core mechanism of empathy that is found not only in humans but also in non-human animals (Preston and de Waal, 2002; de Waal, 2008; de Waal and Preston, 2017). Emotional contagion in non-human animals is well studied on rodents: mice (*Mus musculus*) that witness conspecifics in distress and pain express distress-like (Kavaliers et al., 2001) and fear-related behaviors (e.g., freezing; Jeon et al., 2010) (for review, see Sivaselvachandran et al., 2016). Also, after observing fearful conspecifics, laboratory-reared rhesus macaques (*Macaca mulatta*) learn to fear the objects of conspecifics' fear (Mineka and Cook, 1993).

Neural matching between individuals underpins self–other matching in the behavioral and emotional (for review, see Prochazkova and Kret, 2017). The so-called "perception–action mechanism (PAM)" is considered to be the basis for behavioral and emotional matching (Prinz, 1992; Preston and de Waal, 2002; Preston, 2007). This mechanism links the perception of another individual's behavior and emotional expression to the brain areas that serve to execution of those behaviors and expressions and consequently leads to the observer's behaviors and emotions congruent with the other's (Prinz, 1992). Some researchers view the discovery of mirror neurons as empirical evidence of PAM (de Waal and Preston, 2017). Also, inter-individual coordination of neural activity is facilitated by communication and information afforded by a shared environment, and the resulting tight brain-to-brain coupling may act as a basis for self–other matching in other domains (Hasson et al., 2012).

Inter-individual matching in the physiological domain may enhance and be enhanced by the matching in behavioral and emotional domains (Prochazkova and Kret, 2017). For example, 3-month-old human infants and mothers synchronize their heart rhythms, and the concordance of heart rate increases with vocal and affect synchrony (Feldman et al., 2011). Also, heart rate and cortisol levels are concordant when preschool friends are playing together (Goldstein et al., 1989). The pupil size change, which is related to changes in the autonomic nervous system, is synchronized between socially interacting chimpanzees (Kret et al., 2014). Prairie voles (*Microtus ochrogaster*) concordantly increase corticosterone levels when observing conspecifics in distress (Burkett et al., 2016). Zebrafish (*Danio rerio*) show concordant increase cortisol levels when conspecifics display antipredator behaviors (Oliveira et al., 2017).

Self–other matching also occurs in the cognitive domains. In humans, the way in which friends process the information in the environment is matched to one another, so their perception of reality is very similar (Parkinson et al., 2018; Hyon et al., 2020). This may be explained by the fact that shared experience leads to similar neural responses (Echterhoff et al., 2009). These mechanisms may contribute to establishing a so-called "sense of shared reality," which is the subjective experience of the commonality of inner states (e.g., feelings and beliefs) with an interaction partner (Rossignac-Milon et al., 2018, 2021; Higgins et al., 2021).

It should be noted that there are interactions between self–other matchings in different domains. As noted above, inter-individual matching in neural and physiological domains may be the basis for the matching in behavioral, emotional, and cognitive domains. Also, the relationship between emotional contagion and behavioral contagion has long been discussed from the biopsychological perspective (e.g., James, 1884). As each behavior is underlain by its emotional valence (i.e., positive, neutral, or negative), separating emotion from behavior is fraught with fundamental difficulties. Therefore, it is important to note that categorization by domain does not provide a clear-cut classification of self–other matching.

Another way of classification of self–other matching focuses on the mechanisms. Some researchers assume that matching can be classified according to the involvement of cognitive, inferential, and reflective mechanisms. Imitation and mimicry provide contrasting examples from this perspective (note that this thesis uses the terms behavioral contagion and mimicry inter-changeably). The term "imitation" is generally defined as a process of behavioral matching based on a cognitive understanding of the others' intentions and goals (Carpenter and Call, 2009) and is controlled reflectively (Hecht et al., 2012). By contrast, mimicry can occur even without any understanding of the intentions or goals of others (Carpenter and Call, 2009) and is an automatic and non-reflective process in which the observed behavior of others is matched with one's own behavior (Hecht et al., 2012). In the emotional domain, the same distinction can be found between cognitive empathy (e.g., perspective-taking) and emotional empathy (e.g., emotional contagion) (de Waal and Preston, 2017). The former is characterized by explicit understanding of self–other distinction and inferential attribution of mental states (de Waal and Preston, 2017; Hecht et al., 2012). For example, human adults can cognitively understand that young children fear the dark without fearing the dark themselves (Zahavi and Rochat, 2015). By contrast, the latter is an involuntary and non-reflective process triggered by other individuals' emotional expressions (de Waal and Preston, 2017).

1.2. Social biases on self–other matching

Some classical studies assumed that self–other matching is based on a reflex-like response (Provine, 1986; Hatfield et al., 1993). However, recent studies have shown that the likelihood of self–other matching is not equal among all individuals but is affected by social biases (e.g., Bourgeois and Hess, 2008; Jeon et al., 2010). These studies suggested that self–other matching involves not only a reflex-like mechanism but also more complex mechanisms that are regulated by social context (Fig. 1; Moody et al., 2007; Palagi et al., 2009; Hess and Fischer, 2013). There are two ways in which social factors affect self–other matching. On the one hand, factors related to an individual's social attributes (e.g., absolute dominance rank, social network centrality) may set a baseline for the likelihood of contagious matching to/from the individual. On the other hand, factors related to social relationships with others (e.g., relative dominance rank, familiarity, kinship) may lead to variations or fluctuations from the baseline in the likelihood of matching. It is expected that these two types of social factors involve different mechanisms and serve different functions; the former can be recognized as promoting canalized reactions and the latter as allowing for more flexible responses. However, in this thesis, both factors related to the social attributes of an individual and factors associated with the social relationship between an individual and their partner are simply referred to as "social biases."

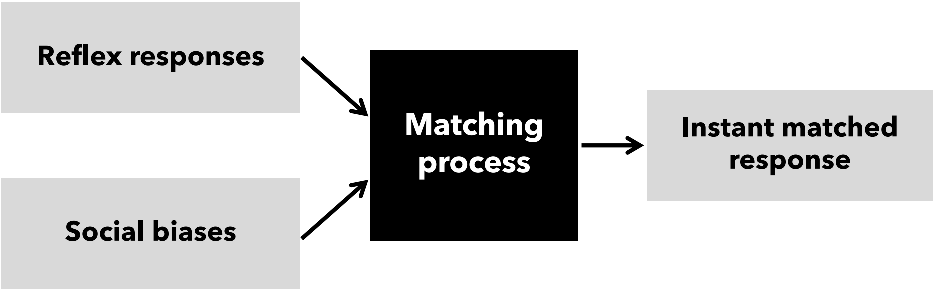

Fig. 1 Mechanisms of self–other matching proposed in previous studies

Social biases in self–other matching is especially well studied in emotional and behavioral domains (review, see Sivaselvachandran et al., 2016; Massen and Gallup, 2017; Palagi et al., 2020). Some researchers considered that emotional connectedness between individuals is a crucial factor for the occurrence of emotional contagion (de Waal, 2008; Palagi et al., 2009) as some studies have shown that social bonds and familiarity enhance empathic-like responses (e.g., Jeon et al., 2010). Mice display more pain- and fear-related behaviors when witnessing close relatives and familiar conspecifics in pain or distress than when witnessing unfamiliar conspecifics (Jeon et al., 2010; Jeon and Shin, 2011; Langford et al., 2006; Gonzalez-Liencres et al., 2014; Martin et al., 2015). Dogs maintain a higher level of cortisol after hearing familiar conspecifics' whines than strangers' whines (Quervel-Chaumette et al., 2016). In humans, emotional contagion of pain is stronger in friends than in stranger dyads (Martin et al., 2015).

Familiarity bias has also been reported in behavioral matching such as yawn contagion and play signal mimicry. In humans, contagious yawning is more likely to occur between kin and friends than between strangers and weakly bonded pairs (Norscia and Palagi 2011; Palagi et al., 2014; Norscia et al., 2016). Studies in non-human animals also indicate that contagious yawning (chimpanzees: Campbell and de Waal, 2011, 2014; bonobos, *Pan paniscus*: Demuru and Palagi 2012; Palagi et al., 2014; geladas: Palagi et al., 2009) and play signal mimicry (geladas: Mancini et al., 2013b; dogs: Palagi et al., 2015; meerkats: Palagi et al., 2019) are more likely to occur between familiar and ingroup individuals than between unfamiliar and outgroup individuals. Also, studies of yawn contagion in dogs using human yawning as stimuli showed that yawning by familiar humans is more likely to trigger yawn responses in dogs than yawning by unfamiliar humans (Silva et al., 2012; Romero et al., 2013).

It should be noted that a significant number of studies have failed to find familiarity bias in behavioral matching (Kapitány and Nielsen, 2017). Studies have not found the effects of relationship quality and familiarity on yawn contagion (chimpanzees: Massen et al., 2012; budgerigars, *Melopsittacus undulatus*: Gallup et al., 2015; orangutans: van Berlo et al., 2020; dogs: Madsen and Persson, 2013; Neilands et al., 2020). Rather, some studies have shown that contagion and mimicry are more likely to occur between unfamiliar or weakly bonded individuals (yawn contagion in rats, *Rattus norvegicus*: Moyaho et al., 2015; yawn contagion in geladas: Gallo et al., 2021; play face mimicry in chimpanzees: Davila-Ross et al., 2011; play face mimicry in lowland gorillas, *Gorilla gorilla gorilla*: Bresciani et al., 2021).

Other studies have indicated that dominance relationships can affect behavioral matching, but the results have not been consistent. In chimpanzees (Massen et al., 2012) and bonobos (Demuru and Palagi, 2012), yawning is more contagious from the dominant sex (i.e., males in chimpanzees and females in bonobos). By contrast, a human study combining photos of politicians (high-status condition vs. low-status condition) and auditory clips (breathing vs. yawning) showed that yawning was more contagious when subjects viewed photos of low-status politicians (Massen et al., 2015). Another study on wolves did not find the effect of social rank on yawn contagion (Romero et al., 2014).

In this thesis, I addressed the following three issues raised in previous studies. First, previous research on social biases in behavioral matching focused primarily on positively valenced behaviors (e.g., play signals: Palagi and Mancini, 2011; Palagi et al., 2015) and ones with neutral valence (e.g., yawning: Campbell and de Waal, 2011; Romero et al., 2013). Many studies focusing on emotional contagion have examined observers' responses, such as freezing, when demonstrators receive foot shocks (Jeon et al., 2010; Jeon and Shin, 2011; Gonzalez-

Liencres et al., 2014). These studies did not focus on the matching of specific behavioral patterns because individuals who receive foot shocks also exhibit behaviors other than freezing, such as running, screaming, and jumping (Jeon et al., 2010; Jeon and Shin, 2011; Gonzalez-Liencres et al., 2014). Studies that specifically focused on the mimicry of freezing behavior did not consider the influence of social factors on the likelihood of behavioral matching (Burkett et al., 2016; Han et al., 2020; although Han et al. 2019 examined the familiarity bias in the behavioral matching of freezing and found no significant effect of familiarity). Hence, research on the social bias of matching of negatively valenced behaviors is still relatively limited. The way in which individuals act on the emotional states of others may depend on the type of emotional valence of the behavior (dogs: Huber et al., 2017; common ravens, *Corvus corax*: Adriaense et al., 2019). Hence, there is a good reason to believe that the effects of social biases on contagious matching vary with the valence of the behavior. The second problem with previous studies is that they have exclusively focused on the matching of an instant, event-like behavior such as yawning and play signals. Some types of self–other matching can be maintained over time. For example, social play can be regarded as the case in which maintained matching is required because individuals must keep each other's playful state to play together for a certain amount of time. Social biases on the maintained self–other matching remain unknown. Third, individuals sometimes fail to maintain self–other matching. Again, social play provides a clear example of the failure of matching. In some rare cases, previously shared playful states can dissociate, and playful interaction escalates into overt conflict. Studying factors associated with the failure of self–other matching can illuminate the mechanisms of successful matching from a different angle. However, social biases affecting the failure of maintenance of self–other matching remain largely unknown.

1.3. Objectives of my thesis

In this thesis, I conducted the following three studies to address the issues mentioned in the last section. In Chapter 2, I examined how social factors affect the contagion of vigilance, which is a negatively valenced behavior (Laundré et al., 2001, 2010, Welp et al., 2004). Although many studies have shown that vigilance is contagious among individuals (e.g., Pays et al., 2007), social factors affecting vigilance contagion remain largely unknown (but see McDougall and Ruckstuhl, 2018a). By focusing on vigilance, which has a different emotional valence than yawning and play signals, I discussed whether social biases apply to all types of contagious matching or vary by the type of behavior and adaptive meaning thereof.

In Chapter 3, I addressed the issue of the maintenance of self–other matching that persists over a period by focusing on play fighting behavior. Play is spontaneous and endogenously motivated behavior (Held and Špinka, 2011). Therefore, social play, such as play fighting, cannot occur unless both individuals voluntarily participate and are readily engaged in the interaction. If one of the players becomes reluctant, the play is terminated immediately. It is suggested that individuals use signals in a play context to share and maintain playful states among participants (van Hooff, 1972). In this study, I examined whether facial signals that Japanese macaques (*Macaca fuscata*) express before initiating a play session function to maintain shared playful states and to whom these signals are used.

In Chapter 4, I addressed the issue of the failure of maintenance of self–other matching. The failures in self–other matching have received much less attention than successful state matching between individuals. We defined “self–other dissociation” as the process of differentiating previously matched states between individuals and examined factors affecting self–other dissociation by focusing on play fighting. In play fighting, individuals use motor patterns that are also used in severe aggression, such as biting, grabbing, and wrestling (Bauer and Smuts, 2007; Burghardt, 2005). Although animals usually perform these pseudo-aggressive motor patterns gently so as not to injure the playmates, play sessions can sometimes escalate into overt conflict (Palagi et al., 2016). I regarded play escalation as a case of self–other dissociation and examined social factors affecting play escalation.

Chapter 2: Social biases in vigilance contagion

2.1. Introduction

For group-living animals, coordinating one's behavior to that of other group members is associated with essential functions such as facilitating group cohesion (Conradt and Roper, 2000) and information acquisition (Danchin et al., 2004). Behavioral contagion, which is a type of self–other matching and is defined as the phenomenon in which one's behavior automatically triggers similar behaviors in others (Zentall, 2003, Massen et al., 2016), is an example of such coordination. As noted in several studies, behavioral contagion is a mechanism in which the behaviors of group members are synchronized (McDougall and Ruckstuhl, 2018a, 2018b). Some of the most studied topics of behavioral contagion are yawning (humans: Provine, 2005; bonobos: Demuru and Palagi, 2012; chimpanzees: Massen et al., 2012; dogs: Madsen and Persson, 2013; budgerigars: Gallup et al., 2015) and emotional behaviors (e.g., laughter in humans: Provine, 1992, 2005; emotional vocalizations in common marmosets, *Callithrix jacchus*: Watson and Caldwell, 2010; play faces and play bows in dogs: Palagi et al., 2015; play faces in Tonkean macaques: Scopa and Palagi, 2016).

Studies of contagious behavior, mainly in Western, educated, industrialized, rich, and democratic (WEIRD) human populations (Henrich et al., 2010), have shown that the likelihood of behavioral contagion is not equal among all individuals but is influenced by social biases (familiarity, dominance, and so forth: e.g., Weyers et al., 2009, Niedenthal et al., 2010, Hess and Fischer, 2013). It is essential to understand how social biases affect behavioral contagion in non-human animals to elucidate how they cope with the problems they face in group life. Despite significant research, it is unclear whether these social biases apply to all types of contagious behavior. This is partly because previous research has focused mostly on emotionally positive and neutral behaviors, such as play signals (Palagi and Mancini, 2011, Palagi et al., 2015) and yawning (Campbell and de Waal, 2011, Romero et al., 2013). It is therefore important to examine the effects of social biases on other types of contagious behaviors that vary in adaptive meaning. Based on the above, this study examined how social biases affect vigilance behavior, which is contagious among individuals (e.g., Pays et al., 2007) but has a distinctly different adaptive meaning compared to other well-studied contagious behaviors, such as yawning and play signals.

When engaging in vigilance behavior, animals scan their surroundings to obtain environmental and social information on actual and potential threats posed by predators or conspecifics (Favreau et al., 2010). Some researchers hypothesize that vigilance is associated with negatively valenced emotions such as fear and anxiety (e.g., Welp et al., 2004; Sapolsky and Share, 2004). Although it had been theoretically assumed that group members engage in vigilance independently of one another (Pulliam, 1973, Bednekoff and Lima, 1998, Scannell et al., 2001), empirical research over the last two decades has shown that vigilance is rather contagious and synchronous among individuals (e.g., Fernandez et al., 2003). For group-living animals, neighbors can be a useful source of information (Danchin et al., 2004). Thus, observing vigilant neighbors and contagiously engaging in vigilance might enable individuals to share information about their surroundings and coordinate behaviors among group members. Moreover, being vigilant simultaneously with neighbors increases each individual's fitness benefits more directly because vigilant individuals can escape from predators' attacks faster than non-vigilant ones (Lima, 1994; Quinn and Cresswell, 2005). When there are both vigilant and non-vigilant individuals, predators preferentially target the latter (Fitzgibbon, 1989). By advertising their awareness of the presence of predators, prey can also deter predators from attacking (Diana monkeys, *Cercopithecus diana*: Zuberbühler et al., 1997; black capuchin monkeys, *Sapajus nigritus*: Wheeler et al., 2008). Therefore, synchronously engaging and disengaging in vigilance is an adaptive tactic for successfully avoiding threats.

Although there is much evidence to indicate that animal vigilance is contagious (e.g., greater rheas, *Rhea americana*: Fernandez et al., 2003; degus, *Octodon degus*: Ebensperger et al., 2006; eastern grey kangaroos, *Macropus giganteus*: Pays et al., 2007; red-necked pademelons, *Thylogale thetis*: Pays et al., 2009; ring-billed gulls, *Larus delawarensis*, herring gulls, *Larus argentatus*, and greater black-backed gulls, *Larus marinus*: Beauchamp 2009; common eiders, *Somateria mollissima*: Öst and Tierala, 2011; greater kudus, *Tragelaphus strepsiceros*: Pays et al., 2012; bighorn sheep, *Ovis canadensis*: McDougall and Ruckstuhl, 2018a), research on the social biases associated with vigilance contagion is quite limited. Furthermore, results from the few studies examining how social biases affect vigilance contagion are not consistent. Take the so-called "familiarity bias" that behavioral contagion is promoted among individuals who are socially bonded by friendship, kinship, and so forth (e.g., Campbell and de Waal, 2011, Palagi et al., 2015; but see Massen and Gallup, 2017). Regarding vigilance contagion, one study showed that vigilance contagion was enhanced among familiar individuals (McDougall and Ruckstuhl, 2018a), while another indicated that vigilance synchrony was not increased, even among related individuals (Quirici et al., 2013).

Inconsistent support for such social biases in studies of vigilance contagion may be due to methodological problems, such as those associated with quantifying the degree of behavioral contagion. Each vigilance bout begins when an individual raises her/his head and ends when the individual lowers her/his head (Bekoff, 1995b, McDougall and Ruckstuhl, 2018b). Nevertheless, most studies that had investigated vigilance contagion did not clarify whether both head-up and head-down movements or either of them are contagious because they only focused on the proportion of time spent in a state of vigilance (e.g., Fernández et al., 2003; Öst and Tierala, 2011; Pays et al., 2012) or whether there was a tendency for vigilance to overlap (e.g., Pays et al., 2009, Quirici et al., 2013). As both head-up and head-down contagion can enhance the degree of vigilance overlap, we cannot tell whether one or both of these occur during animal vigilance in cases where these two behaviors are not distinguished. Besides, even in cases where researchers directly investigated contagion related to head movement, they focused only on vigilance onset but not on its offset (McDougall and Ruckstuhl, 2018a, 2018b). In this study, we focused on the contagiousness of both the onset and offset of vigilance bouts between two nearest neighbors by analyzing data from a group of Japanese macaques.

By focusing on Japanese macaques, it is possible to avoid the problem of ambiguity regarding the target of vigilance, which is a common issue raised in vigilance studies (e.g., Treves, 2000, Allan and Hill, 2018). Despite the general difficulty of determining the target of a gaze in the natural environment (Emery, 2000; Watson et al., 2015), several studies have suggested that vigilance is used not only to find predators but also to monitor within-group threats (Chance, 1967, Carter et al., 2009). This multifunctionality may lead to confounding results regarding the social biases associated with vigilance contagion. However, as some researchers have noted, vigilance in Japanese macaques is unlikely to be directed towards predators and is predominantly used to monitor group members (Kazahari and Agetsuma, 2010; Suzuki and Sugiura, 2011). This is consistent with the hypothesis that because within-group aggression in primates is considered to occur more frequently than in other taxa (Treves, 2000) and sometimes causes serious or even lethal injuries (e.g., Japanese macaques: Soltis et al., 2000; chimpanzees: Muller, 2002; chacma baboons, *Papio ursinus*: Kitchen et al., 2003), primate vigilance primarily serves to monitor within-group threats rather than predators (Treves, 2000; Busia et al., 2016).

We conducted behavioral observations of a free-ranging wild Japanese macaque group with no predators to test the following predictions regarding social biases associated with behavioral contagion:

Prediction 1: Vigilance is more contagious to subordinate individuals than to dominant ones

Japanese macaque society is highly despotic, and subordinate individuals face a constant risk of being attacked by dominant individuals (Thierry, 2000). Therefore, it is assumed that subordinates (i.e., individuals with low absolute dominance ranks) are more susceptible to vigilance behaviors by other individuals compared to dominant individuals (i.e., ones with high absolute dominance ranks). Hence, we predicted that head-up and head-down movements by a given individual are more contagious to subordinates than to dominant individuals.

Prediction 2: Vigilance is more contagious from higher-ranked to lower-ranked individuals

The dominance hierarchy of Japanese macaque society is strict and linear (Chaffin et al., 1995). Hence, if a given individual is a threat to higher-ranking individuals, the former is also a threat to lower-ranking ones, but not necessarily vice versa. We expected that individuals would pay more attention to the vigilance of those who are more highly ranked. Therefore, we predicted that contagion of head-up and head-down movements is more likely to occur from higher-ranked to lower-ranked individuals (i.e., rank difference > 0; see Methods) than from lower-ranked to higher-ranked individuals (i.e., rank difference < 0).

Prediction 3: Mothers are more likely to contagiously synchronize vigilance with their immature offspring than vice versa

In Japanese macaques, mothers are highly protective of their immature offspring (Thierry, 2000). They restrict contacts between their offspring and others and frequently retrieve their offspring (Thierry, 2000). Therefore, it is expected that mothers would pay special attention to their offspring's vigilant state and that offspring, on the contrary, leave the appraisal of the surrounding situation to their mothers. Based on the above assumptions, we predicted that head-up and head-down movements would be more contagious in the direction from the offspring to the mother, but less contagious from the mother to the offspring compared to a non-mother–offspring pair.

Prediction 4: Kinship enhances vigilance contagion

The degree of behavioral contagion and synchrony is enhanced by social bonds among individuals. In humans, mothers are more likely to synchronize their behavior with their own children than with other children (Bernieri et al., 1988). In bonobos, yawn contagion is more likely to occur among related individuals than among unfamiliar individuals (Demuru and Palagi, 2012). As for vigilance, familiarity enhances vigilance contagion in bighorn sheep (McDougall and Ruckstuhl, 2018a), whereas kinship does not affect vigilance contagion in degus (Quirici et al., 2013). Considering that in Japanese macaque society, there is a high degree of nepotism such that related individuals form strikingly strong social bonds (Chapais et al., 1997), we predicted that the degree of contagion regarding head-up and head-down movements would be greater between two related individuals than between unrelated individuals.

2.2. Methods

Study sites and subjects

A free-ranging provisioned group of Japanese macaques was studied in Shiga Heights, Nagano Prefecture, Japan. S.I conducted behavioral observations from July to October of 2018 and from

July to September of 2019. The total observation time was about 1,008 h. Demographic records have been kept since 1962, and all individuals are identifiable. Because the study site is regularly visited by tourists, the individuals in the subject group are fully habituated to humans. Although it was not possible to determine the exact number of individuals in the group because mature Japanese macaque males migrate between groups, and some individuals were located at the periphery of the group (Sprague et al., 1998), the group comprised approximately 240 individuals. As mature males leave the natal group, there are fewer mature males than mature females (Sprague et al., 1998). In September 2019, there were 82 adult females (> 4 years old), approximately 20 adult males (> 4 years old), approximately 110 juveniles (1–4 years old), and 32 infants (0 years old). Each day, the study group came to Jigokudani Monkey Park just before the park opened (09:00) and went back to the forest when the park closed (17:00). The group was fed barley, soybeans, and apples four times daily (09:00, 12:00, 15:00, and 16:30) by the staff of the park. Our subject group was the only group that regularly visited the park, and other groups rarely approached the park. For a detailed description of the research site, see Wada and Ichiki (1980).

Data collection

Dominance rank

To estimate the dominance ranks of members of the subject group, we observed unidirectional aggressive interactions between pairs of adult individuals using the *ad-lib* sampling method. We considered an interaction to be unidirectional when individual A approached B, and B expressed submissive behavior (e.g., bared teeth display) or fled, or when A unilaterally attacked B. Because the Japanese macaque is a highly despotic species, most aggressive interactions are completely unidirectional (Thierry, 2000). Therefore, it was easy for the observer to discern between the winner and loser in an aggressive interaction. Because maternal dominance rank is passed from mother to offspring in the Japanese macaque (Chapais, 1988; Kutsukake 2000), we considered immature individuals to have the same ranks as their mothers. In a study of rhesus macaques, which are phylogenetically close to Japanese macaques and have a similarly despotic society, Berman (1980) provided a further rationale for assigning immature offspring the same rank as their mothers. The study found that infants of higher-ranked mothers are less likely to be threatened and attacked by other group members than infants of lower-ranked mothers are. Overall, we observed 1,112 events of unidirectionally aggressive interaction. There were no cases of mature males being defeated by females in aggressive interactions. As Japanese macaques form matrilineal linear dominance hierarchies (e.g., Chaffin et al., 1995), dominance was indexed by an ordinal rank based on the outcome of these interactions. Due to the small number of mature males in the dataset ($N = 4$ responders; see '*Video coding*') and a lack of instances of multiple males foraging in a patch simultaneously, we assigned all mature males the highest rank (i.e., 0).

Vigilance behavior

We established a regular hexagonal patch within the park area (Fig. 2). At three feeding times, i.e., 09:00, 12:00, and 15:00, the observer put barley in the patch, as indicated in Figure 1. No food was placed within 5 m around the patch. Using two digital video cameras (HDR-TD10 and HDR-PJ40V; Sony, Tokyo, Japan) recording from different angles, the observer videotaped the behaviors of individuals that entered the patch, stayed at one of the seven locations in a sitting posture, and engaged in foraging in 15-min sessions. Any instances of vigilance behavior were recorded. During all sessions, no non-group member intrusion was observed. We did not conduct the experiment on rainy days.

Following previous studies (e.g., Beauchamp, 2017, McDougall and Ruckstuhl, 2018b), we classified vigilance behaviors into two types to investigate contagiousness and synchrony in a reliable way. The first type is 'threat-induced' vigilance. This type of vigilance occurs as a response to external threats. In this case, even if vigilance by multiple individuals is seemingly synchronous, this is mere pseudo-synchrony that occurs just because the external event makes individuals vigilant simultaneously. The second type of vigilance is 'pre-emptive' vigilance. Pre-emptive vigilance occurs without any external threat being present. Therefore, if pre-emptive vigilance is synchronized across multiple individuals, we can say that this is genuine synchrony because one individual's vigilance contagiously and directly elicits another individual's vigilance. In this study, we disregarded threat-induced vigilance and analyzed only pre-emptive vigilance (see also '*Video coding*').

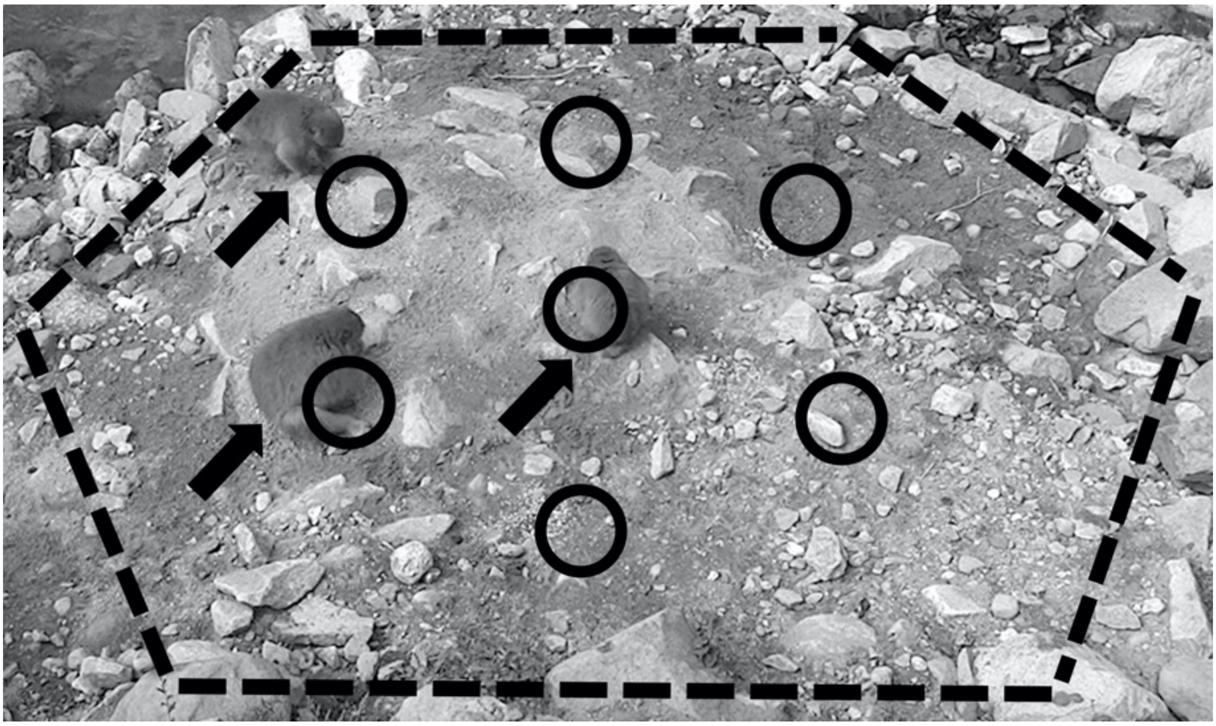

Fig. 2 We established a patch (dotted line) in an area of the park below the area that human visitors were allowed to enter. Hence, visitors were not allowed near the patch and could only look down on it from a distance of more than 5 meters. The length of each side of the hexagonal patch is 2 m. The observer put 25 g barley at each of the seven locations circled in the image. In the figure, three individuals are foraging in the patch (indicated with arrows).

Video coding

We conducted video analyses using Behavioral Observation Research Interactive Software (BORIS; Friard and Gamba, 2016). We recorded the identities of all individuals who entered the experimental patch and foraged in it. We considered that each experimental session consisted of several phases during which group composition in the patch and each individual's position remained unchanged. If an individual changed their position or moved out of the patch, or new individuals entered the patch to forage, this was considered a new phase. All phases that lasted less than 30 s were discarded from the analyses. Every phase during which fewer than two individuals were foraging in the patch was also discarded. For each phase, we chose two individuals situated the closest together in the patch. When three or more individuals were located at almost the same distance from one another, we randomly selected two individuals from this group. We examined each phase frame-by-frame (30 fps) and noted instances of vigilance onset (i.e., the time point when an individual raised her/his head) and offset (i.e., the time point when an individual lowered her/his head). For each vigilance event, we considered the first individual that raised or lowered her/his head as the initiator and the other individual as the responder. We classified the initiator's relationship to the responder into three categories: mother, offspring, and other (non-mother-offspring pair).

The time window for behavioral contagion varies considerably across studies. In general, studies of yawn contagion tend to use a relatively wide time window (e.g., 3 min: Demuru and Palagi, 2012; Romero et al., 2014, Norscia et al., 2016); studies of play face contagion use a narrower one (e.g., 1 s: Davila Ross et al., 2008; Palagi et al., 2015; Maglieri et al., 2020). Since vigilance contagion involves the collection of information on the immediate surroundings, a narrow time window was considered necessary in this study. Indeed, studies of vigilance contagion have used a narrow time window of 5 s (McDougall and Ruckstuhl, 2018a, 2018b). In general, studies of behavioral contagion suffer from Type I error inflation, in which researchers falsely regard behaviors as contagious when they are really not (e.g., Kapitány and Nielsen, 2017). Since the vigilance rate in our subject group (0.13/s; Iki and Kutsukake, 2021), which was much higher than that in McDougall and Ruckstuhl (2018a), can increase the risk of false positives, we considered it necessary to use a more conservative time window. Based on the above, we considered vigilance contagion to have occurred when the responder congruently moved her/his head within 1 s of the initiator's head-up or head-down movement. We did not analyze data from instances in which the initiator was behind the responder because the initiator was presumably out of the responder's line of sight. To calculate the probability of vigilance contagion, we analyzed only data on an initiator's head-up and head-down movements performed while the responder's head was already lowered and raised, respectively. To distinguish pre-emptive vigilance events from threat-induced ones, we recorded whether external events (e.g., aggression among group members, approach by other monkeys, screaming, appearance of other species, and the voices of park staff or visitors, or other noise) were present. We considered an approach by another individual to have occurred when his/her body entered the patch. All vigilance events that might have been induced by these external events were considered threat-induced vigilance. Data pertaining to threat-induced vigilance events were discarded from the analyses, and only those pertaining to pre-emptive vigilance were analyzed.

Overall, we conducted 60 sessions of 15-minute behavioral experiments. In 111 nearest neighbor dyads, 78 individuals were considered responders in front of whom the initiators performed head-up or head-down movements at least twice in a phase. Each responder appeared in 2.94 phases on average (standard deviation 3.22).

Statistical analyses

We analyzed the data using generalized linear mixed models (GLMMs; *glmer* function in the package *lme4*; Bates et al., 2015) in R version 3.6.3 (R Development Core Team, 2020). In all GLMM analyses, we included phases and the identities of the responders and initiators as random effects to deal with pseudo-replication. To obtain reliable estimates, we restricted our analyses to responders in front of whom the initiator performed head-up or head-down movements at least twice in a phase. Using a subset of the data consisting only of mother-offspring pairs, we used ANOVA to compare a model that differentiated between infants and juveniles and included responder's and initiators' age class and control factors (see below), with a model including only control factors based on the likelihood ratio test. We found that the former model did not explain more variance than the latter one (head-up: $\chi^2 = 5.61$, $df = 4$, $p = 0.23$; head-down: $\chi^2 = 5.62$, $df = 4$, $p = 0.23$), so categorized juveniles and infants as immature individuals.

To investigate whether and what social factors affect vigilance contagion, we ran GLMMs with a binomial error structure and a logit link function. The dependent variables were the probabilities of contagion for head-up and head-down movements. The probability of contagion was calculated by dividing the number of congruent head movements by the responder within 1 s of the initiator's head-up or head-down movement by the total number of head-up or head-down movements by the initiator. We included the following social factors as fixed variables: the responder's absolute dominance rank (continuous; relevant to Prediction 1), rank difference between the responder and initiator (continuous; relevant to Prediction 2), the relationship between the responder to the initiator (categorical: mother, offspring, and other; relevant to Prediction 3), and kinship (categorical: yes or no; relevant to Prediction 4). A responder–initiator pair was considered kin if they had a close maternal relationship (i.e., mother–offspring, grandmother–grandoffspring, or maternal siblings; relatedness [r] ≥ 0.25). In addition, to control for possible confounding effects, we included the following individual factors as fixed variables: the responder's age (categorical: mature or immature), the responder's sex (categorical), the initiator's age (categorical: mature or immature), the initiator's sex (categorical), a two-way interaction between the responder's age and sex, and a two-way interaction between the initiator's age and sex. The physical distance between each responder and initiator, and the number of individuals in the patch other than the responder and initiator (continuous) were also included as fixed effects. To test for multicollinearity among the fixed effects in the global models, we calculated variance inflation factors (VIF) using the *vif* function in the *car* package (Fox and Weisberg, 2019). All of the resulting VIF values were < 1.5, suggesting no multicollinearity. We fitted all possible combinations of fixed effects. For all models, we calculated and compared Akaike information criterion (AIC) scores using the *dredge* function in the package *MuMIn* in R (Bartoń, 2019). The model with the lowest AIC score was considered the best model; i.e., one that provides a satisfactory explanation of the variation in the data. However, models with a ΔAIC (difference between model AIC score and that of the best model) ≤ 2 are considered to have a similar level of statistical support as the best model (Burnham and Anderson, 2002). To deal with this uncertainty in model selection, we used a multi-model inference method (Burnham and Anderson, 2002). Akaike weights represent the relative likelihood of each model (Burnham and Anderson, 2002). Using Akaike weights, we calculated the relative variable importance (RVI) of models with $\Delta\text{AIC} \leq 2$ (Burnham and Anderson, 2002). This procedure allows us to estimate the strength of the relationship between each explanatory variable and the response variables while simultaneously taking into account the relative likelihood of each model. Figures were created with the *ggplot2* package (Wickham, 2016).

2.3. Results

In terms of the contagiousness of head-up and head-down movements, the models with the lowest AIC scores contained two social factors (the responder’s rank and relationship of the responder to the initiator; Tables 1 and 2). Regarding these two factors, the best models implied the following: regarding the responder’s dominance rank, head-up and head-down movements were more contagious when the responder’s absolute dominance rank was lower (Figs. 3a and 4a; Prediction 1 supported). In terms of the responder-initiator relationship, head-up and head-down movements were more contagious when the responder was the initiator’s mother, whereas they were less contagious when the responder was the initiator’s offspring (Figs. 3b and 4b; Prediction 3 supported). However, rank difference and kinship did not remain in the best models (Predictions 2 and 4 not supported).

Table 1. The best model explaining the variation in the probability of head-up contagion.

Best model	**estimate**	**SE**
Intercept	–1.242	0.329
Responder’s rank	0.014	0.002
Relationship of the responder to the initiator		
Mother	0	
Non-mother-offspring pair	–0.315	0.296
Offspring	–1.568	0.471
Responder’s sex		
Female	0	
Male	–0.434	0.219
Initiator’s age		
Mature	0	
Immature	–0.350	0.201

Model: Responder's rank + Relationship of the responder to the initiator + Responder's sex + Initiator's age. Log likelihood = -257.408. Akaike information criterion = 532.8. Sample size: *N* = 109 dyads (18 mother–offspring dyads, 91 nonmother–offspring dyads), *N* = 77 responders (53 females, 24 males), *N* = 82 initiators (58 females, 24 males).

Table 2. The best model explaining the variation in the probability of head-down contagion.

Best model	**estimate**	**SE**
Intercept	0.514	0.667
Responder’s rank	0.013	0.009
Relationship of the responder to the initiator		
Mother	0	
Non-mother-offspring pair	–0.441	0.649
Offspring	–1.632	0.785

Model: Responder’s rank + Relationship of the responder to the initiator. Log likelihood = -88.010. Akaike information criterion = 190.0. Sample size: $N = 46$ dyads (10 mother–offspring dyads, 36 non-mother–offspring dyads), $N = 43$ responders (29 females, 14 males), $N = 39$ responders (29 females, 10 males).

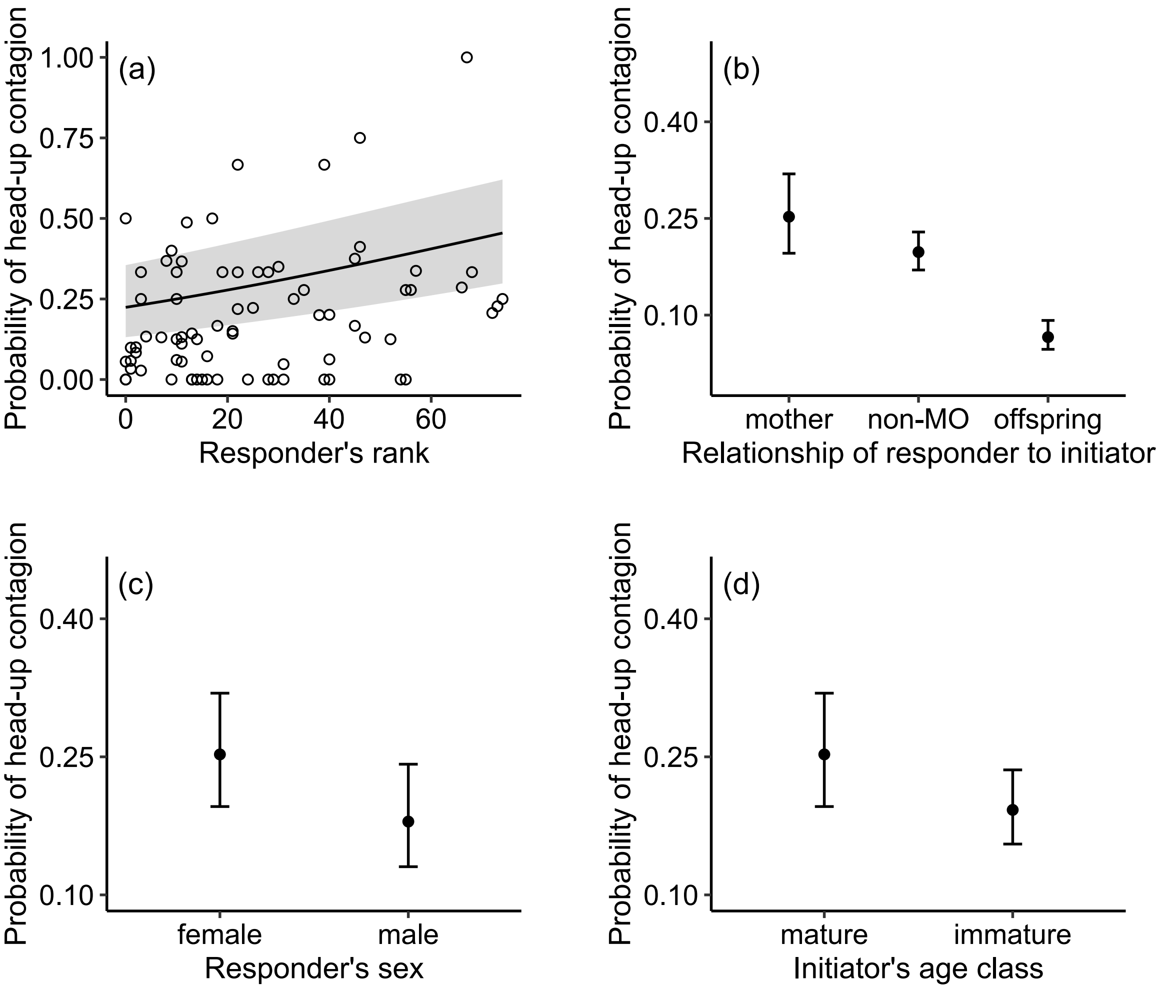

Fig. 3 The predicted probabilities of head-up movement contagion according to the following fixed effects: the (a) responder’s absolute rank, (b) relationship of the responder to the initiator, (c) responder’s sex, and (d) initiator’s age class, based on the best generalized linear mixed model (GLMM). In (a), smaller numbers on the x-axis indicate higher ranks. The black line and

shaded area represent the fitted values and 95% confidence intervals (CIs), respectively. In (b)–(d), the black dots and error bars represent the mean probabilities and standard errors (SEs), respectively. non-MO, non-mother-offspring pair.

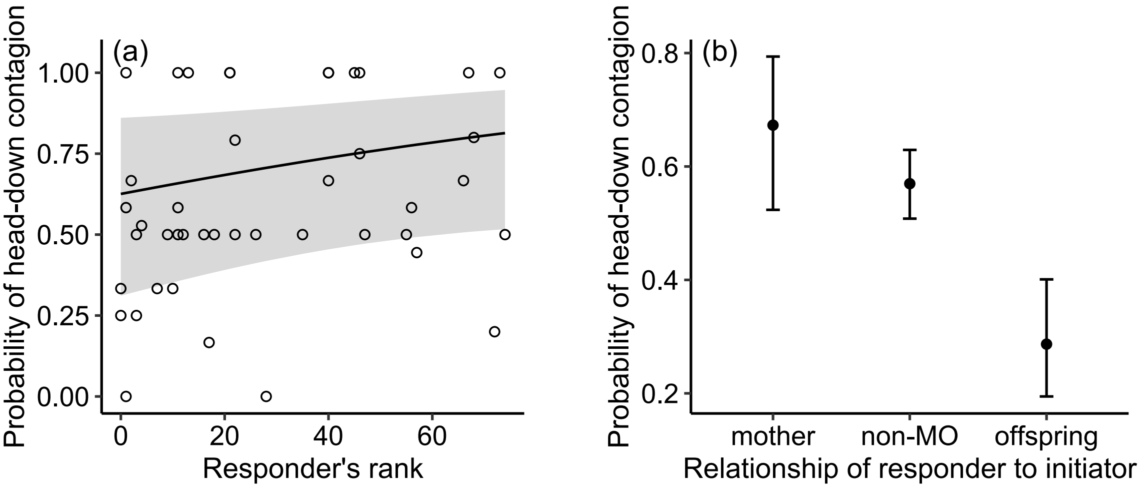

Fig. 4 The predicted probabilities of head-down movement contagion according to the following fixed effects: the (a) responder's absolute rank and (b) relationship of the responder to the initiator, based on the best GLMM. In (a), smaller numbers on the x-axis indicate higher ranks. The black line and shaded area represent the fitted values and 95% CIs, respectively. In (b), the black dots and error bars represent the mean probabilities and SEs, respectively. non-MO, non-mother-offspring pair.

Regarding the contagiousness of head-up movements, two individual factors were also highlighted in the best model (Table 1); head-up movements were more contagious to females than to males (Fig. 3c) and more contagious when exhibited by a mature initiator versus an immature initiator (Fig. 3d).

However, the low Akaike weights produced by the best models ($w_i = 0.17$ for head-up movement and $w_i = 0.07$ for head-down movement) indicate that there was a considerable degree of uncertainty in model selection. Indeed, there were 11 and 25 models with ΔAIC values ≤ 2 (Table 3) for contagion associated with head-up and head-down movements, respectively. The respective null models comprising only the control factors and random effects were not included in the models with ΔAIC values ≤ 2. Despite the uncertainty in model selection, the multi-model inference analyses corroborated the above results and revealed that both head-up and head-down contagion was most strongly influenced by the two social factors mentioned above (i.e., the responder's rank and the relationship between the responder and initiator). The responder's rank and responder-initiator relationship were the two variables with the highest RVI values (Table 4). For head-up movements, the RVIs associated with the responder's rank and responder-initiator relationship were both 1.00. For head-down movements, the RVIs associated with the responder's rank and responder-initiator relationship were 0.51 and 0.97, respectively. These results imply that the probability of contagion for head-up and head-down movements is more strongly affected by these two social factors than by other individual factors. Again, rank difference and kinship had little effect on vigilance contagion, with RVIs of 0.07 and 0.09 for rank difference and kinship, respectively, for head-up movements, and values of 0.16 and 0.03, respectively, for head-down movements.

Table 3. Details of the models with ΔAIC ≤ 2.

Models	**df**	**AIC**	**ΔAIC**	w_i
Head-up contagion				
1. Rank + RS + Rsp sex + Init age	9	532.8	0.00	0.17
2. Rank + RS + Rsp sex + Init age + No indv	10	533.7	0.87	0.11
3. Rank + RS + Rsp sex	8	533.8	0.94	0.11
4. Rank + RS + Rsp sex + No indv	9	533.9	1.04	0.10
5. Rank + RS + Rsp sex + Init age + Kin	10	534.1	1.32	0.09
6. Rank + RS + Rsp sex + Init age + Dist	10	534.6	1.83	0.07
7. Rank + RS + Rsp sex + Init age + No indv + Dist	11	534.7	1.85	0.07
8. Rank + RS + Init age	8	534.7	1.86	0.07
9. Rank + RS + Rsp sex + Init age + Rank diff	10	534.7	1.86	0.07
10. Rank + RS + Rsp sex +Rsp age + Init age	10	534.7	1.87	0.07
11. Rank + RS + Rsp sex + Init sex + Init age	10	534.8	1.95	0.07
Head-down contagion				
1. Rank + RS	7	190	0.00	0.07
2. RS	6	190.4	0.36	0.06
3. RS + Rsp sex + Init sex	8	190.5	0.50	0.06
4. Rank + RS + Init sex	8	190.5	0.50	0.06
5. RS + Rsp sex	7	190.5	0.53	0.06
6. Rank + RS + Init age	8	190.7	0.68	0.05
7. Rank + RS + Rsp sex	8	190.7	0.71	0.05
8. RS + Init sex	7	190.8	0.77	0.05
9. Rank + RS + Rsp sex + Init sex	9	190.8	0.82	0.05
10. RS + Init age	7	191	1.01	0.04
11. RS + Rsp sex + Init sex + Rank diff	9	191.1	1.05	0.04
12. RS + Init sex + Rank diff	8	191.4	1.40	0.04
13. RS + Rsp sex + Init age	8	191.6	1.54	0.03
14. Rank + RS + Dist	8	191.7	1.65	0.03
15. Rank + RS + Rsp sex + Init age	9	191.7	1.67	0.03
16. RS + Rank diff	7	191.7	1.69	0.03
17. Rank + RS + Init sex + Init age	9	191.8	1.75	0.03
18. RS + Rsp sex + Rank diff	8	191.9	1.90	0.03
19. Rank	5	191.9	1.93	0.03
20. RS + Init sex + Init age	8	192	1.98	0.03
21. Rank + RS + Kin	8	192	1.98	0.03
22. Rank + RS + No indv	8	192	1.99	0.03
23. RS + Rsp sex + Init sex + Init age	9	192	1.99	0.03
24. Rank + RS + Rank diff	8	192	2.00	0.03
25. Rank + RS + Rsp age	8	192	2.00	0.03

Models with ΔAIC > 2 are not presented. AIC, Akaike information criterion; df, degrees of freedom; wi, Akaike weight; RS, relationship of the responder to the initiator; Rank, responder's rank; Rsp sex, responder's sex; Rsp age, responder's age; Init sex, initiator's sex; Init age, initiator's age; No indv, number of individuals; Rank diff, rank difference between the responder and initiator; Dist, distance between the responder and initiator.

Table 4. Relative importance of variables in models with ΔAIC ≤ 2.

	Head up	**Head down**
RS	1	0.97
Rank	1	0.51
Rsp sex	0.93	0.37
Rsp age	0.07	0.03
Init sex	0.07	0.37
Init age	0.79	0.24
No indv	0.29	0.03
Kin	0.09	0.03
Rank diff	0.07	0.16
Dist	0.14	0.03

RS, relationship of the responder to the initiator; Rank, responder's rank; Rsp sex, responder's sex; Rsp age, responder's age; Init sex, initiator's sex; Init age, initiator's age; No indv, number of individuals; Rank diff, rank difference between the responder and initiator; Dist, distance between the responder and initiator. Variables that were omitted in the models with ΔAIC ≤ 2 are not shown.

2.4. Discussion

Our results imply that both head-up and head-down contagion are influenced by the dominance relationship, with lower-ranked individuals (in terms of absolute ranking) being more susceptible to vigilance behaviors by other individuals (Figs. 3a and 4a). The Japanese macaque society is highly despotic, and attacks are unilaterally directed from higher-ranked to lower-ranked individuals (Thierry, 2000). Therefore, the lower the rank of a macaque, the more threats there are around her/him to be wary of. Hence, to immediately detect a threat, lower-ranked individuals may pay more attention to what their neighbors are looking at than higher-ranked individuals. Although we also expected that vigilance contagion is more likely to occur from higher-ranked to lower-ranked individuals than vice versa, we failed to observe this effect (Tables 1, 2, and 4). Instead, our results showed that both head-up and head-down movements were likely to be contagious to lower-ranked individuals regardless of the initiator's rank. These results are even more interesting compared to those reported by Scopa and Palagi (2016). They compared Japanese macaques, a despotic species, to Tonkean macaques, an egalitarian species, and showed that behavioral contagion of play face does not occur in Japanese macaques. Since play face is a positively valenced behavior directed toward the interaction partner, while vigilance is a scanning behavior directed toward the surrounding environment, these behaviors obviously differ markedly in terms of adaptive meaning. Combining the findings of the previous study of play faces with ours reinforces the idea that whether behavioral contagion occurs depends on the interplay between the type of behavior and social structures.

In addition, our results showed that both head-up and head-down movements were more contagious from offspring to their mothers than from mothers to their offspring (Figs. 3b and 4b). This implies that mothers were likely to be vigilant when their offspring were vigilant, but not necessarily vice versa. Japanese macaque mothers are highly protective of their offspring (Thierry, 2000). Our results imply that Japanese macaque mothers may pay special attention to their offspring's vigilance. On the contrary, offspring likely leave appraisal of the surrounding environment to their mothers and do not pay attention to their mothers' vigilant state. In contrast to this result, research on the contagion of smiles in humans has shown that these behaviors are contagious not only from immature offspring to their mothers but also from the mothers to their offspring, although cultural differences must be carefully considered (e.g., Wörmanna et al., 2012). This bidirectional susceptibility to contagion between mothers and their offspring can also be observed in play faces in non-human primates (e.g., Mancini et al., 2013b). Taken together, our results indicate that although it is generally believed that mother-offspring dyads are characterized by a high susceptibility to reciprocal and bidirectional behavioral contagion, this is not the case with vigilance. While we did not find any difference between juveniles and infants in the context of vigilance contagion between mothers and offspring (see 'Statistical analyses'), the ontogenetic variation of individual vigilance levels in the early life stages is an interesting question in itself, apart from the context of contagion.

A number of studies have reported on familiarity bias; i.e., behavioral contagion is more likely to occur among individuals with stronger social bonds (Bernieri et al., 1988, Demuru and Palagi, 2012, Campbell and de Waal, 2014, McDougall and Ruckstuhl, 2018a; but see Neilands et al., 2020). Because Japanese macaque societies are characterized by a high degree of nepotism, and related individuals form very strong social bonds (Chapais et al., 1997), we predicted that kinship would enhance vigilance contagion. However, no effects of kinship were observed (Tables 1, 2, and 4). There are several possible explanations for this result. First, this negative result might have been due to our method of examining vigilance contagion between two nearest individuals. In primates, individuals in close proximity tend to have a strong social bond (e.g., bonnet macaque, *Macaca radiata*: Silk, 1994; yellow baboons, *Papio cynocephalus*: Silk et al., 2003; chimpanzees: Langergraber et al., 2009; see Massen et al., 2010 for review). Hence, we might not have detected any effects associated with familiarity because all dyads we examined exhibited a certain level of social bonding, whether they were kin or non-kin. Second, familiarity bias may not affect vigilance contagion, unlike the contagion of play signals and yawning (Demuru and Palagi, 2012, Campbell and de Waal, 2014; but see Massen et al., 2012; Massen and Gallup, 2017). However, this possibility seems unlikely in light of previous studies showing that in some species, negative valence responses (e.g., alertness and escape behavior) increased in familiar pairs when witnessing the distressed state of another individual (dogs: Quervel-Chaumette et al., 2016; mice: Gonzalez-Liencres et al., 2014, Pisansky et al., 2017). In any case, additional detailed studies are needed to further test these possibilities.

Our results also imply that the contagiousness of head-up movements is affected by individual factors related to the initiators and responders, although we did not make any specific predictions about these individual factors. Head-up movements were more contagious to female responders than to male ones and more contagious from mature initiators than from immature ones. Several studies have reported a greater susceptibility to behavioral contagion in females (Romero et al., 2014, Demuru and Palagi, 2016), but many others have reported the absence of this bias (Gallup and Massen, 2016, Massen and Gallup, 2017, Neilands et al., 2020). Further research is needed to clarify whether the sex bias demonstrated in this study applies to the phenomenon of behavioral contagion in general regardless of species and the type of behavior, or whether it is derived from factors specific to Japanese macaques and vigilance. With respect to the age class of the initiators, our results imply that mature initiators are a more reliable source of information in terms of appraising the surrounding situations than immature initiators. For group-living animals, group members can be a useful source of information (Danchin et al., 2004). Japanese macaques inherit their rank from their mothers over the course of ontogeny (Chapais, 1988, Kutsukake, 2000). Hence, mature individuals who are fully incorporated into the dominance relationship and have a fixed rank may be a more reliable source of information.

Although it was not a major focus of this study, the adaptive meaning of contagion may differ between head-up and head-down movements. Considering that vigilant individuals can escape attacks faster than non-vigilant individuals (Lima, 1994; Quinn and Cresswell, 2005), it may cost more not to be vigilant when neighbors are vigilant than not to relax vigilance when neighbors relax vigilance. Unfortunately, our results are of little help in addressing this issue: the same social biases (i.e., responder's rank and the mother-offspring relationship) affected both head-up and head-down movements (Tables 1 and 2). The differences in factors influencing head-up versus head-down movements were also unclear: the initiator's age and responders' sex, which were included in the best model for head-up movement, were not included in the best model for head-down movement (Table 1 and 2). However, the RVI values for these individual factors in the context of head-down contagion were higher than those for almost all other factors (Table 4), which was also the case for head-up contagion. Other indicators, such as foraging efficiency and success rates at avoiding attacks, may provide greater insight into this issue.

It should be noted that we saw social bias only in the context of the contagion of vigilance "behavior," not that of vigilance as an internal state. Although some researchers have assumed that behavioral contagion drives empathic processes such as emotional contagion (yawning in humans: Platek et al., 2003; play signals in dogs: Palagi et al., 2015; play faces in Tonkean macaques: Scopa and Palagi, 2016), the relationship between these processes is still debated (e.g., Tamietto et al., 2009; Massen and Gallup, 2017). In any case, more detailed studies are needed to clarify the relationship between vigilance contagion and emotional contagion.

We did not focus on the possibility that vigilance is contagious among more than two individuals; research on that topic could clarify how individual or dyadic behavior is extended to the group level. Studies on anti-predatory vigilance have assumed that vigilance contagiously spreads out like a wave through the group (Sirot and Touzalin, 2009; Beauchamp et al., 2012). Although predators can be a threat to any individual in a group, threats from conspecifics depend on the social relationships among individuals. Therefore, the way by which social vigilance is spread within a group may be different from that associated with anti-predatory vigilance. Investigations on social vigilance contagion among more than two individuals constitute an interesting area of future research.

As this study focused on the contagion of head movements, we did not analyze gaze direction in detail. However, an important question in ecological and cognitive terms is whether vigilance contagion is merely a copy of head movements or involves more specific mechanisms of gaze direction matching (McDougall and Ruckstuhl, 2018b). Sharing vigilance targets would benefit responders, but augmenting the vigilance of others by looking in a different direction would also be of some benefit. Depending on whether the vigilance is induced or pre-emptive, the benefits of sharing gaze direction may vary. To address these issues, more detailed experiments, such as those used in studies of gaze following, are essential (e.g., Bugnyar et al., 2004; Catala et al., 2017). Based on some evidence of gaze following in *Macaca* species (e.g., Tomasello et al., 1998), our subjects might first check the direction of an initiator's glance and then turn their gaze in the same direction.

In conclusion, this study found that vigilance in Japanese macaques was more contagious among lower-ranked individuals. We also revealed that vigilance was more contagious in the direction from the offspring to the mother, but there was no familiarity bias. These findings suggest that social biases do not apply to all types of behavioral contagion, instead varying by the type of behavior and adaptive meaning thereof.

Chapter 3: Facial signals that contribute to the maintenance of playful state matching

3.1. Introduction

Before initiating a shared activity, animals, including humans, often establish mutual engagement with one another (Gómez, 1994; Susswein and Racine, 2008). Physical proximity is not enough to establish mutual engagement, so animals accomplish it by regulating their behavioral and emotional states and matching them with those of others through the exchange of communicative signals. Greeting behavior in humans is one example that best illustrates such signal exchange (Goffman, 1981; Pillet-Shore, 2012). Studying how non-human animals initiate social interactions collaboratively by exchanging signals is important for elucidating the evolutionary background of elaborate social skills in humans. This study focused on the use and function of facial signals expressed by Japanese macaques when they initiate playful interactions.

In various primate species, animals often initiate a variety of social interactions by facing one another and establishing eye contact. For example, humans usually direct their faces and eyes toward one another before starting a conversation (Cary, 1978; Mondada, 2009). In chimpanzees, eye contact can serve as an introduction to reconciliation (de Waal and Yoshihara, 1983). In mountain gorillas (*Gorilla beringei beringei*), eye contact functions to invite affiliative interactions (Yamagiwa, 1992). Bonobos and stump-tailed macaques (*Macaca arctoides*) invite copulation through eye contact (Savage and Bakeman, 1978; Chevalier-Skolnikoff, 1974). In various species, social play is often initiated through face-to-face and eye-to-eye contact (orangutans: Rijksen, 1978; mountain gorillas: Yamagiwa, 1992; chimpanzees: Fröhlich et al., 2016; Japanese macaques: Iki and Hasegawa, 2020, 2021). By establishing a situation wherein individuals are mutually attentive and intersubjectively engaged (Gómez, 1994, 2010; Stawarska, 2010; Iki and Hasegawa 2021), a face-to-face configuration and eye contact set up the scaffolding on which interactions are subsequently established.

A face-to-face configuration at the start of an interaction can be accompanied by facial expressions, and these facial signals signify the characteristics of the emerging interaction. When initiating an amicable interaction, it may be important to indicate one's friendly stance toward others in advance to successfully manage the subsequent interaction (Pillet-Shore 2012, 2018). In humans, smiling and laughter are facial signals that express affiliation and enjoyment (Niedenthal et al., 2010), although it should be noted that many studies have focused on predominantly Western, educated, industrialized, rich, democratic (WEIRD) human populations (Henrich et al., 2010). These affiliative facial expressions are especially important in play fighting, which involves intense physical contact (Heesen et al., 2017). Human children express smiles and laughter when initiating a play session to communicate to the partner that subsequent physical contact will be playful, not agonistic (Smith and Boulton, 1990). Although the meaning and function of facial signals in non-human animals have also been well studied from evolutionary and comparative perspectives (van Hooff, 1967, 1972; Preuschoft and van Hooff, 1995), how facial signals are used and how they function in the opening of interactions remain unclear.

Play fighting is a form of social interaction commonly observed in immature mammals (Burghardt, 2005), and it often includes facial expressions specific to a play context (van Hooff, 1972). Play fighting in non-human animals involves motor patterns such as "biting" and "grabbing," which are seemingly similar to those used in serious aggression (Palagi et al., 2016; Špinka et al., 2016). Although these motor patterns are used gently enough not to harm playmates, play fighting can sometimes escalate into overt conflict (Palagi, 2018; see Chapter 4). As is the case with smiles and laughter in humans, it is assumed that non-human animals use a variety of play signals, including facial expressions, to convey a friendly stance toward their partner and prevent play escalation (Pellis and Pellis, 1996; Palagi et al., 2016).

Studies on play face and on play signals more generally have mainly focused on signals expressed during play sessions rather than those expressed before the start of play (for a few exceptions focused on mutual gaze and gestures at the opening of play, see Fröhlich et al., 2016; Genty et al., 2020; Heesen et al., 2021). For example, ultrasonic calls by rats during play decrease the likelihood of play escalation (Kisko et al., 2015; Burke et al., 2017). In dogs, reciprocal bowing during play serves to sustain play (Palagi et al., 2015). As for facial signals, although a study of sun bears (*Helarctos malayanus*) suggested that the frequency and mimicry of play face are not correlated with the duration of the play session (Taylor et al., 2019), other studies have reported that (mimicry of) play face during play prolongs play sessions (chimpanzees: Davila-Ross et al., 2011; western gorillas: Waller and Cherry, 2012; geladas: Mancini et al., 2013a; Tonkean macaques: Scopa and Palagi, 2016; meerkats: Palagi et al., 2019). However, these results should be interpreted with caution because in studies of play face expressed during play, it is difficult to control for the possible confounding effects of specific patterns of the unfolding play before play face is expressed on the maintenance of subsequent play interaction and the likelihood of play face expression.

Although some studies have shown that the opening of a play session is not necessarily accompanied by facial signals (chimpanzees: Spijkerman et al., 1996; Tibetan macaques, *Macaca thibetana*: Wright et al., 2018) and facial signals may serve to maintain an ongoing play session rather than to initiate a new one (gelada: Palagi and Mancini 2011), other studies have suggested that animals initiate play fighting with various kinds of play signals (play bows in dogs: Byosiere et al., 2016; play faces in chimpanzees: Hayaki, 1985; gestures in chimpanzees: Fröhlich et al., 2016; also see Heesen et al., 2021). To investigate the use and function of facial signals expressed before play, it is necessary to compare play sessions preceded and not preceded by facial signals. However, no such comparison has been conducted in previous studies. The current study addressed this issue by focusing on dyadic play fighting in juvenile Japanese macaques. Before and during play fighting, Japanese macaques express facial displays (i.e., play face; also called open-mouth display) that are specific to the context of play by opening the mouth in a relaxed way and drawing the corners of the mouth slightly backward (Preuschoft and van Hooff, 1995; Petit et al., 2008; Scopa and Palagi 2016). Because of their morphological and functional similarities, this expression is considered homologous to human laughter (van Hooff, 1967, 1972; de Waal, 2003). This study compared dyadic play fighting sessions preceded by bidirectional or unidirectional play face with ones not preceded by play face. Our key questions were under what situations play face is expressed and how play face at the opening of play affects subsequent interactions. Although a previous study suggested that mirroring of play face does not occur during play fighting in Japanese macaques (Scopa and Palagi, 2016), they do express play face bidirectionally to a considerable extent before initiating play (Fig. 5). Hence, we also addressed the question of whether there is a functional difference between bidirectional and unidirectional play face.

Specifically, we tested the following two hypotheses. Note that we did not attempt to test whether one hypothesis is more plausible than the other. In principle, the predictions derived from these two hypotheses are partially mutually exclusive (i.e., *Prediction 1b* vs. *Prediction 2b*) and also partially compatible.

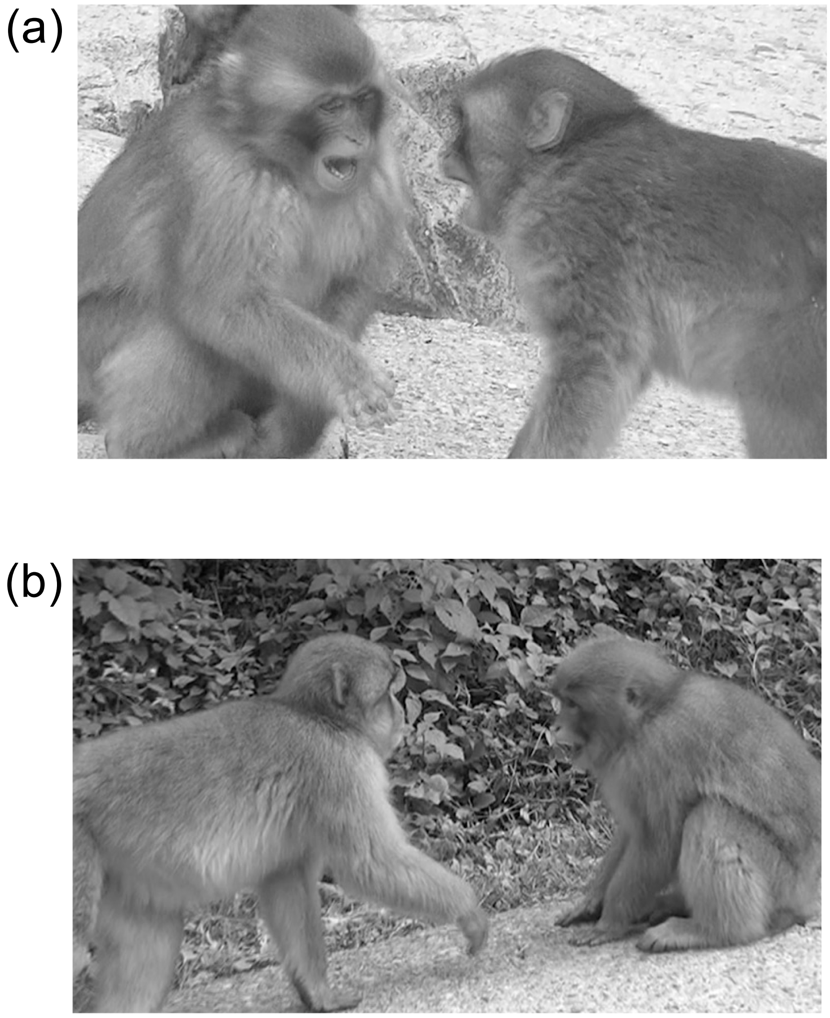

Fig. 5 (a) Bidirectional and (b) unidirectional play face before the start of a play bout.

Hypothesis 1: The expression of play face reflects an individual's motivation to play.

It has been suggested that play face is a spontaneous expression of an individual's internal state, such as a playful propensity and pleasurable emotion (van Hooff, 1972; Demuru et al., 2015; Scopa and Palagi, 2016). Hence, we hypothesized that play face expression immediately before play initiation reflects an individual's motivation for the subsequent interaction. In Japanese macaques, males play more frequently than females (Eaton et al., 1986; Nakamichi, 1989) and they prefer to play with other males (Glick et al., 1986). Therefore, we predicted that play face would be more likely to be expressed by males before initiating play with other males than by individuals before initiating play between pairs representing other sex combinations (*Prediction 1a*). Also, several primate studies have suggested that individuals prefer to play with partners of a similar age and body size (long-tailed macaques, *Macaca fascicularis*: Fady, 1976; Japanese macaques: Mori, 1974; chimpanzees: Mendoza-Granados and Sommer, 1995; western gorillas: Maestripieri and Ross 2004; Palagi et al., 2007; rhesus macaques: Kulik et al., 2015). Hence, we predicted that individuals would be more likely to express play face before initiating a play bout with playmates of a similar age (*Prediction 1b*). Also, if play face displays the expresser's willingness to play, it is expected that the more participants express play face before beginning a play bout, the longer the bout will last. Hence, we predicted that a play bout preceded by bidirectional play face involving both players would last longer than a play bout preceded by unidirectional play face by one of the players, and a play bout preceded by unidirectional play face would last longer than a play bout not preceded by play face (*Prediction 1c*).

Hypothesis 2: Play face is expressed before engaging in a risky situation.

It has been pointed out that play signals are used in risky situations that carry the potential for overt conflict because individuals can express their playful and non-harmful stance toward playmates through play signals (Bekoff, 1972; Matsusaka 2004; Palagi, 2009). In Japanese macaques, the inter-player difference in dominance rank and age may affect the occurrence of play escalation into serious conflict; individuals of higher rank and greater age than their partners are more likely to trigger a negative response (e.g., screaming) in the playmate (see Chapter 4). Hence, we predicted that a higher-ranked (*Prediction 2a*) and older (*Prediction 2b*) individual relative to the partner would be more likely to express play face before initiating play. Also, if individuals communicate by play face that they are about to engage in a risky situation, they may express play face before initiating a bout that would involve intense physical contact. In play fighting, players compete to gain an advantage over their partners by attacking them unilaterally (e.g., Aldis, 1975; Biben, 1986; Bauer and Smuts, 2007). We predicted that individuals would maintain an advantage for a longer time if they expressed play face before a bout started than if they did not do so (*Prediction 2c*).

3.2. Methods

Study sites and subjects

This research was conducted at the same study site, during the same period, and with the same study group as described in Chapter 2.

Data collection

We conducted behavioral observations of agonistic interactions to assess the dominance ranks and play fighting sessions to investigate the function of the play face. See Chapter 2 for the method to assess the dominance rank.

To collect data on play fighting, the observer stood in specific positions in the Park from which almost all individuals of the group were observable and recorded all visible play fighting sessions between juveniles using a digital video camera (HDR-TD10 211; Sony, Tokyo, Japan). The observer regularly changed the observation location to avoid observation bias. We did not adopt focal sampling because focal sampling is not sufficiently efficient for infrequent behaviors such as play fighting (Martin and Bateson, 2007). We did not observe animals for 30 min before and after provisioning time. Following previous studies on play fighting in Japanese macaques (Reinhart et al., 2010; Iki and Hasegawa, 2021), play bouts were required to meet the following requirements: the entire bout took place on relatively flat ground and not in a three-dimensional environment such as trees; the individual did not use objects such as stones and branches; and there was at least one play bite but no negative expressions (e.g., screaming and bared-teeth displays). We excluded cases in which individuals made a continuous transition from grooming, contact-sitting, mounting, or chasing to play fighting.

A total of 578 play bouts met the above requirements. To investigate the function of the play face before a play bout began, we focused only on cases in which both players faced each other when they initiated play and the faces of both players could be clearly seen in the video data. Though only a limited camera angle provided a clear sight of the faces of both individuals, 133 bouts met this requirement. As only 6 bouts involved 4-year-old individuals (bouts in 2018 and 2019: $N = 2$ and 4, respectively), we discarded these bouts. The remaining 127 bouts involved 63 individuals (see Table 5 for detailed information). Each individual was involved in a mean of 4.03 bouts (SD: 3.10; range 1–12). Of the 127 bouts, 96, 23, and 8 bouts involved male–male, male–female, and female–female dyads. In terms of age differences, 80, 33, and 14 bouts were between dyads with age differences of 0, 1, and 2 years, respectively.

Table 5. Overview of the individuals in the dataset

Observation year	**Age**	**No. of males**	**No. of females**
2018	1	7	3
	2	14	6
	3	4	2
2019	1	17	5
	2	5	2
	3	8	4

Video coding

We conducted frame-by-frame video analyses using ELAN software (Lausberg and Sloetjes, 2009). We defined the beginning of each bout as the moment when an individual directed any playful attack (i.e., biting, grabbing, or wrestling) at their partner, and the end as the time when the players stopped playing for at least 10 s. We defined a play bout as being preceded by play face if one or both individuals expressed play faces immediately before the onset of play (i.e., within 5 s). Following previous studies (Biben, 1986; Bauer and Smuts, 2007; Iki and Hasegawa, 2020), we considered a player to have the advantage when he/she pinned down or attacked the partner unidirectionally. A player was considered to have pinned down the partner if the player stood or sat with their weight on the partner, causing the partner to lie down in a lateral, supine, or prone position. A player was considered to have attacked the partner unidirectionally when they bit or grabbed the partner without being bitten or grabbed by the partner. Overall, the mean duration of 127 play bouts in our dataset was 24.79 s (SD: 29.14). In terms of play face expression before play initiation, 56, 30, and 41 bouts were preceded by bidirectional, unidirectional, and no play face, respectively.

Statistical analyses

We analyzed the data using generalized linear mixed models (GLMMs; glmer function in the lme4 package) in R ver. 4.0.5 (R Core Team, 2021). Analyses of play face expression and the duration during which a player held an advantage were conducted by regarding each player in the dyad as a focal individual. The analysis of the duration of play bouts was conducted at the dyadic level.

For the analysis of play face expression, we ran a GLMM with a binomial error structure and a logit link function. The response variable was whether play face was expressed by a focal individual before the onset of a bout. We included the following key predictors as fixed effects: the sex combination between a focal individual and their partner (categorical: male–male, male–female, female–male, female–female; relevant to *Prediction 1a*); the rank difference between players (continuous; relevant to *Prediction 2a*); the age difference between players (continuous; relevant to *Prediction 2b*); and the quadratic term of the age difference (continuous: relevant to *Prediction 1b*). To control for possible confounding effects, we included the following factors as control variables: focal individual's age (continuous); focal individual's absolute dominance rank (continuous); and kinship between players (categorical: kin or non-kin). Individuals were considered kin if they were maternal siblings. This kinship criterion was set with reference to a study by Chapais et al. (1997), which showed a threshold for nepotism in Japanese macaques. To deal with pseudoreplication, we included the identity of the focal individual, play partner, and play bout as random effects.

To analyze the duration of the play bout, we ran a GLMM with a gamma error structure and a log link function. We included the direction of play face before a bout began (categorical: bidirectional, unidirectional, or none) as a key predictor (relevant to *Prediction 1c*). To control for possible confounding effects, we included the following factors as control variables: sex combination of the dyads (categorical: male–male, male–female, female–female); the absolute value of the rank difference between players (continuous); the absolute value of the age difference between players (continuous); and kinship between players (categorical: kin or non-kin). We included the identity of the dyad as a random effect.

For the analysis of the duration during which a focal individual held an advantage, we used a GLMM with a gamma error structure and a log link function. The response variable was the cumulative time during which the focal individual maintained an advantage in a bout. We included play face by a focal individual before the onset of a bout (categorical: present or absent) as a key predictor (relevant to *Prediction 2c*). As control variables, we included the following factors: play face by a partner before the onset of a bout (categorical: present or absent); focal individual's age (continuous); focal individual's absolute dominance rank (continuous); kinship between players (categorical: kin or non-kin); and the sex combination between a focal individual and their partner (categorical: male–male, male–female, female–male, female–female). We included the identity of the focal individual, play partner, and play bout as random effects.

We fitted all possible combinations of fixed effects and compared the Akaike information criterion (AIC) scores using the dredge function in the MuMIn package in R. The model with the lowest AIC score was considered the best model (i.e., the model that provides a satisfactory explanation of the variation in the data). However, models for which the difference between the model's AIC score and that of the best model (ΔAIC) was < 2 were considered to have levels of statistical support similar to the best model (Burnham and Anderson, 2002). To deal with this uncertainty in model selection, we used a multimodel inference method (Burnham and Anderson, 2002). Akaike weights represent the relative likelihood of each model (Burnham and Anderson, 2002). Using Akaike weights, we calculated the relative variable importance (RVI) of models with ΔAIC < 2 (Burnham and Anderson, 2002). This procedure enabled us to estimate the strength of the relationship between each explanatory variable and the response variables, while simultaneously considering the relative likelihood of each model. In cases where categorical fixed effects of more than two levels remained in the best model, we conducted Tukey's post hoc multiple-comparison test to assess statistical significance. For the post hoc analyses, we set our alpha level to 0.05.

3.3. Results

The model for play face expression with the lowest AIC score included the sex combination and the quadratic term of the age difference (Table 6). The post hoc Turkey's test showed that a male was significantly more likely to express play face before initiating play with another male than a female was before initiating play with a male or another female (Table 7; Fig. 6a). There was no significant difference in the probability of play face expression between dyads combining male focal individuals and female partners and those with male focal individuals and male partners (Table 7; Fig. 6a). These results partially supported *Prediction 1a*. In terms of age difference, the best model, which included the quadratic term of the age difference, indicated that the probability of play face expression increased as the age difference decreased, reaching its maximum value when the age difference was zero (Fig. 6b; *Prediction 1b* supported). The rank and age differences between players did not remain in the best model (*Predictions 2a* and *2b* not supported). Although the low Akaike weight produced by the best model (w_i = 0.14; Table 8) indicates a considerable degree of uncertainty in model selection, multimodel inference analyses supported the above results. The RVI for the sex combination exhibited the maximum value (i.e., RVI = 1.0; Table 9), and the RVI for the quadratic term of the age difference had the next-highest value (RVI = 0.81). This implies that the probability of play face expression was affected by these factors more strongly than by others.

The model for the duration of play bouts with the lowest AIC score included the direction of play face and the age difference (Table 6). Post hoc Tukey's tests showed that play bouts preceded by bidirectional and unidirectional play faces lasted significantly longer than play bouts not preceded by play face, whereas no difference in the play duration was found between play bouts with bidirectional and those with unidirectional play faces (Table 7; Fig. 7a; *Prediction 1c* partially supported). Although the Akaike weight produced by the best model ($w_i = 0.22$; Table 8) was low, multimodel inference analyses corroborated the above results. The RVIs for the direction of play face and the age difference reached the maximum value (i.e., RVI = 1.0; Table 9), implying that the duration of play bouts was more affected by these factors than by others.

Table 6. Details of the best models

Best model	Estimate	SE
Probability of play face expression		
Model selection: Age difference^2 + Sex combination LogLik = -145.14, AIC = 306.28		
Intercept	1.449	0.438
Age difference^2	-0.416	0.254
Sex combination (reference: male–male)		
female–female	-3.588	1.352
female–male	-3.630	1.181
male–female	-1.703	0.951
Play bout duration		
Model selection: Play face + Age difference LogLik = -62.0, AIC = 136.01		
Intercept	3.432	0.147
Direction of play face (Reference: bidirectional)		
none	-0.620	0.217
unidirectional	0.143	0.238
Age difference	-0.311	0.133
Duration maintaining an advantage		
Model selection: Partner's play face LogLik = -331.48, AIC = 674.96		
Intercept	1.414	0.189
Partner's play face (absent < present)	0.417	0.253

Sample size: *N* = 254, 127, and 254 for the probability of play face expression, play bout duration, and duration maintaining an advantage, respectively.

Table 7. Results of Tukey's post hoc multiple-comparison tests of the effect of sex combination on the probability of play face expression and the effect of direction of play face on the play bout duration

	Estimates	**SE**	***Z***	***P***
Probability of play face expression				
male–male > female–female	3.588	1.352	2.654	0.040
male–male > female–male	3.630	1.181	3.073	0.011
male–male vs. male–female	1.703	0.951	1.791	0.277
female–female vs. female–male	0.042	1.478	0.029	1.000
female–female vs. male–female	-1.885	1.424	-1.323	0.548
female–male vs. male–female	-1.927	0.974	-1.979	0.196
Play bout duration				
bidirectional > none	0.620	0.217	2.855	0.012
bidirectional vs. unidirectional	-0.143	0.238	-0.599	0.821
none < unidirectional	-0.762	0.246	-3.094	0.006

For the Tukey tests, we used the function emmeans in the R package emmeans.

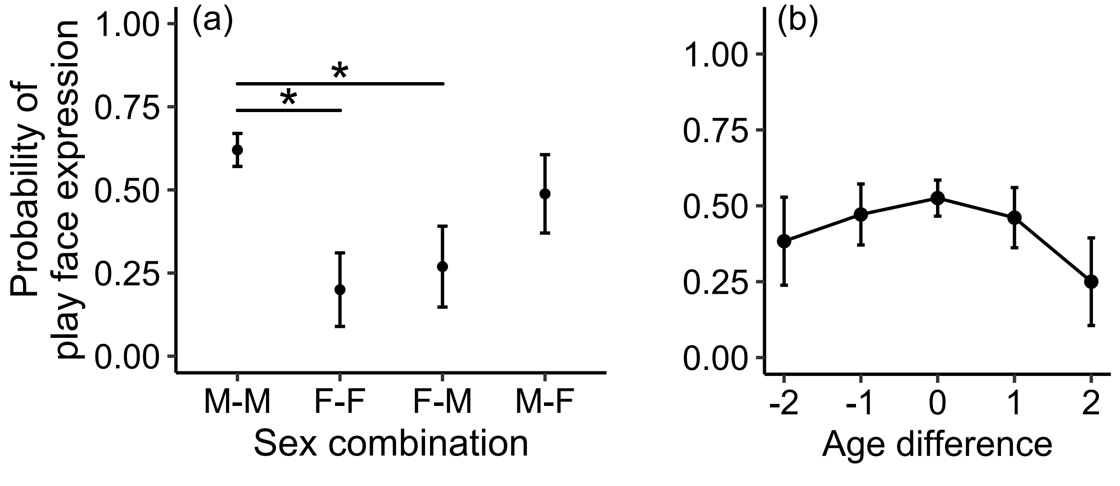

Fig. 6 Probability of the expression of play face according to the (a) sex combination and (b) age difference between a focal individual and a partner. In (a), there was no significant difference between the categories not marked with an asterisk. The black dots and error bars represent the mean values and standard errors, respectively. **P* < 0.05 (Tukey's post hoc test).

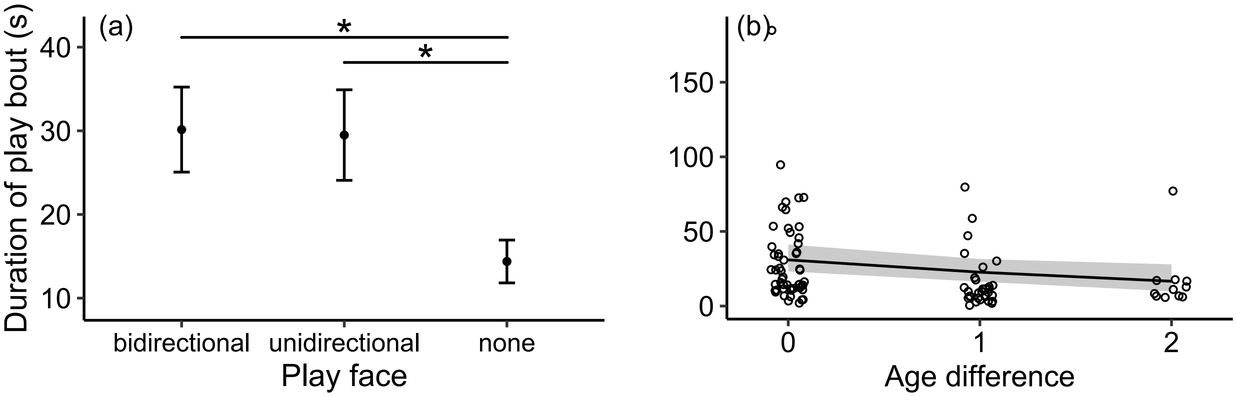

Fig. 7 Duration of a play bout according to the (a) direction of play face and (b) age difference between players. In (a), there was no significant difference between the categories not marked with an asterisk. The black dots and error bars represent the mean values and standard errors, respectively. In (b), for a better view of overlapping data points, we used a jitter plot to add slight, random noise to the data. The black line and shaded area represent the fitted value and 95% CI, respectively. *$P < 0.05$ (Tukey's post hoc test).

Regarding the duration of a focal individual maintaining an advantage, the model with the lowest AIC score only included play face by the partner before initiating a bout (Table 6), implying that a focal individual held an advantage for a longer duration if their partner expressed play face before a bout began (Fig. 8). Play face expression by a focal individual did not remain in the best model, and its RVI was comparatively low (i.e., RVI = 0.07; Table 9; *Prediction 2c* not supported); the RVI for play face expression by a play partner had the highest value (RVI = 0.77).

Table 8. Details of the models with ΔAIC < 2

Models	*df*	AIC	ΔAIC	w_i
Probability of play face expression				
SC + AD^2	8	306.28	0.00	0.14
SC + AD^2 + IA + AD	10	306.29	0.01	0.14
SC + AD^2 + IA	9	306.37	0.08	0.13
SC	7	307.17	0.89	0.09
SC + AD^2 + IR	9	307.62	1.33	0.07
SC + AD^2 + IA + IR + AD	11	307.80	1.52	0.06
SC + AD^2 + IA + IR	10	307.87	1.59	0.06
SC + AD^2 +RD	9	308.16	1.88	0.05
SC + AD^2 + IA + AD +RD	11	308.17	1.89	0.05
SC + Kinship	8	308.17	1.89	0.05
SC + IA	8	308.19	1.91	0.05
SC + AD^2 +Kinship	9	308.28	1.99	0.05
SC + AD^2 + AD	9	308.28	2.00	0.05
Play bout duration				
DPF + AD	6	136.01	0.00	0.22
DPF + AD + SC	8	136.12	0.11	0.21
DPF + AD + RD	7	136.46	0.45	0.18
DPF + AD + RD+ SC	9	136.68	0.67	0.16
DPF + AD + Kinship	7	137.39	1.38	0.11
DPF + AD + Kinship+ SC	9	137.47	1.45	0.11
Duration of the advantage				
PPF	6	674.96	0.00	0.20
Null	5	675.61	0.65	0.15
PPF + IR	7	676.44	1.48	0.10
PPF + SC	9	676.56	1.60	0.09
IR	6	676.74	1.78	0.08
PPF + AD	7	676.81	1.85	0.08
PPF + IA	7	676.85	1.89	0.08
PPF + RD	7	676.88	1.92	0.08
PPF + Kinship	7	676.95	1.99	0.07
PPF + FPF	7	676.95	1.99	0.07

Models with ΔAIC > 2 are not presented. AIC: Akaike information criterion; w_i, Akaike weight; IA: individual age; IR: individual rank; AD: age difference; RD: rank difference; DPF: direction of play face; SC: sex combination; FPF: focal individual’s play face; PPF: partner’s play face.

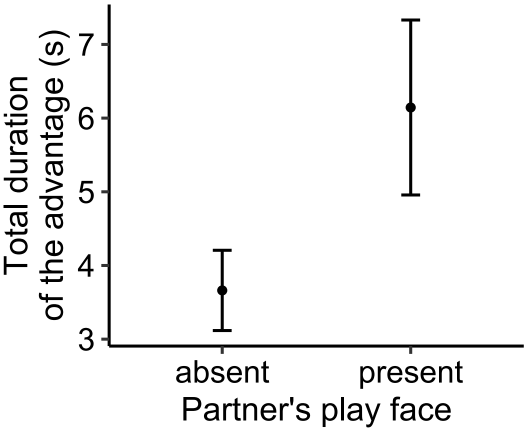

Fig. 8 Total duration of the advantage maintained by a focal individual according to the presence of the play partner's play face before the start of a bout. The black dots and error bars represent the mean values and standard errors, respectively.

Table 9. Relative variable importance (RVI) calculated from models with $\Delta \mathrm{AIC} < 2$

	Play face expression		**Bout duration**		**Advantage duration**
SC	1.00	DPF	1.00	PPF	0.77
AD^2	0.81	AD	1.00	IR	0.18
IA	0.50	SC	0.48	SC	0.09
AD	0.30	RD	0.34	AD	0.08
IR	0.20	Kin	0.22	IA	0.08
RD	0.11			RD	0.08
Kin	0.10			FPF	0.07
				Kin	0.07

IA: individual age; IR: individual rank; AD: age difference; RD: rank difference; DPF: direction of play face; SC: sex combination; FPF: focal individual's play face; PPF: partner's play face.

3.4. Discussion

Overall, our results supported *Hypothesis 1* (i.e., that play face expression reflects an individual's motivation for the subsequent interaction), but not *Hypothesis 2* (i.e., that play face is expressed before engaging in a risky situation). The results imply that play face is more likely to be expressed by individuals with a playful propensity before they play with preferred partners. We showed that a male juvenile was more likely to express play face before initiating a bout with another male than was a female before initiating a bout with another female or a male (Fig. 6a). Although there was no significant difference in the likelihood of play face expression between males before initiating play with another male and males initiating play with a female, these results imply that males were more likely to express play face than females (*Prediction 1a* partially supported). In addition, Japanese macaque juveniles were more likely to express play face before initiating play with others closer in age (Fig. 6b; *Prediction 1b* supported). Considering that males have a stronger motivation to play than females do and that juvenile Japanese macaques prefer to play with individuals of the same age (Mori, 1974; Eaton et al., 1986; Glick et al., 1986; Nakamichi, 1989), our results suggest that play face expression before the start of play signifies the individual's motivation for the interaction that is about to take place. The finding that a play bout preceded by play face lasted longer than a bout not preceded by play face (Fig. 7a; *Prediction 1c* supported) also supports this interpretation. We did not examine whether individuals with a higher play frequency were more likely to express play face, but this remains an interesting question. However, as we did not adopt focal sampling, we could not collect data on the frequency of play fighting. To address this question, additional well-controlled studies are needed.

Relevant to the above results, more detailed consideration is needed to clarify whether play face can directly prolong a play bout by enhancing play partners' engagement or whether the duration of a play bout and play face expression were merely positively correlated because an individual with a highly playful internal state spontaneously expresses play face. Our finding that there was no significant difference in duration between play bouts preceded by unidirectional and by bidirectional play face (Fig. 7a) provides some insight into this issue. This result suggests that even when one player did not express play face, observation of the partner's play face may have led both partners to engage in prolonged play bouts to the same extent as when both individuals expressed play face. Many studies on humans and non-human animals have shown the matching and transmission of internal states such as emotions between individuals via facial signals (e.g., Hatfield et al., 1993; Niedenthal et al., 2010; Adriaense et al., 2020). Extrapolating from previous studies and our results, it may be that merely witnessing a partner's play face induces a playful state in the perceiver, as if they themselves are expressing play face. As studies on emotional contagion in humans imply (Hess and Blairy, 2001), it is not necessary that playful facial expressions be copied for playful states to be transmitted between individuals. Studies showing that a playful propensity can be transmitted between individuals without behavioral copying also support this possibility (Osvath and Sima, 2014; Wenig et al., 2021).

Researchers have hypothesized that play face is likely to be expressed before engaging in a risky situation to avoid escalation into overt conflict (e.g., Bekoff, 1972), but our results did not support this hypothesis (i.e., *Hypothesis 2*). We predicted that higher-ranked or older players, who are more likely to trigger a negative response (e.g., screaming) in the partner (see Chapter 4), would be more likely to express play face before initiating play than would lower-ranked or younger partners, but we found no such effect of rank or age difference on the probability of play face expression (Table 6; *Predictions 2a* and *2b* not supported). Also, although we expected that individuals would express play face before gaining an excessive advantage over the partner, the presence of the focal individual's play face did not affect the total duration during which that individual held an advantage (*Prediction 2c* not supported). These results indicate that at least in our subject group of Japanese macaques, play face might not serve a function of communicating to play partners that the expressers were about to engage in a risky situation.

Although we did not expect it, our result indicates that a partner's play face before a bout prolonged the duration during which focal individuals maintained an advantage over the partner (Fig. 8). Play face may have advertised the expressers' receptive and tolerant stance toward partners, which might in turn enable receivers of the facial signals to deliver playful attacks without hesitation. A study on chimpanzees showed that individuals emit play panting while being attacked (e.g., being grabbed) by partners and suggested that the play signal serves to enhance partners' playful engagement (Matsusaka, 2004). Also, humans initiate daily interactions such as conversations after expressing a positive stance and friendliness toward others by smiling (Pillet-Shore, 2012). Especially in the context of social play involving aggressive motor patterns, it may be important to demonstrate a receptive and friendly stance toward one's partner before starting an interaction to successfully manage the interaction later on.

In conclusion, whereas previous studies have mainly focused on play signals used during ongoing play sessions, our study is unique in that we focused on the use and function of facial signals expressed before the start of play. Our results indicate that Japanese macaques' use of play face before play bouts begin may have two intertwined functions: to display the motivation for subsequent interactions and to display a receptive and tolerant stance toward others.

Chapter 4: Social factors in the failure of maintenance of playful state matching

4.1. Introduction

The essence of play behavior is difficult to capture, so it is often described in contrast to so-called "serious" behaviors with clear adaptive functions, such as anti-predator, agonistic, and sexual behaviors (Palagi et al., 2016; Palagi, 2018). However, the boundary between "playfulness" and "seriousness" is not absolute. For example, many motor patterns used in play behavior are borrowed from serious behaviors (Caillois, 1961; Fagen, 1981; Palagi et al., 2016). Additionally, in both humans (e.g., Cordoni et al., 2016) and non-human animals (e.g., Pellis et al., 2010), playful interactions can sometimes transform into serious behaviors (e.g., Palagi et al., 2016). The phenomenon that best illustrates the transgression of the boundary between playfulness and seriousness is the escalation of play fighting into overt hostility.

Play fighting is a type of social play that is common in immature mammals (Burghardt, 2005) and is generally competitive but non-agonistic. Play fighting can involve motor patterns such as "biting" and "grabbing," which appear similar to those used in the context of aggressive and predation behavior (Bekoff, 1995a; Špinka et al., 2016). Play fighting can be distinguished from agonistic interactions by its affiliative nature and the absence of threats and negative expressions, such as screaming (Fry, 2005; Lewis, 2005). Although animals usually perform these pseudo-aggressive motor patterns in a self-handicapping manner to avoid injuring playmates, play sessions can sometimes escalate into overt conflict, presumably because of miscommunication of intent between participants, loss of reciprocity, etc. (Cordoni et al., 2018; Palagi, 2018).

To initiate and maintain play, individuals match each other's playful state. For instance, in some birds (e.g., common ravens: Osvath and Sima, 2014; Wenig et al., 2021; keas, *Nestor notabilis*: Schwing et al., 2017), play itself or the behavioral patterns accompanying play (i.e., play-call) exhibited by one individual can induce play in others through play contagion (Adriaense et al., 2020; Held and Špinka, 2011). Likewise, chimpanzees watching a video of other chimpanzees engaging in play exhibited play solicitation behavior and displayed play faces, i.e., a relaxed open-mouth display with a slight upward and backward withdrawal of the lip-corners, to the video monitor (Parr and Hopkins, 2000). By contrast, in calves (*Bos taurus*), the presence of less playful individuals decreased the play level of others (Größbacher et al., 2020).

To sustain play fighting sessions, individuals coregulate each other's behavior, match the intensity of the attacks, and maintain the reciprocity of play (Palagi et al. 2016; Lampe et al. 2019). The "50:50 rule" illustrates how animals sustain play reciprocity by allowing their playmates to counterattack, thus making the interaction balanced and symmetrical (Altmann 1962; Aldis 1975; Palagi et al. 2016). This rule indicates that escalation can occur when play loses its reciprocity and becomes unfair (Pellis et al. 2010; Pellis and Pellis 2017; Palagi 2018). Indeed, a study using game theory models suggested that deviations from the 50:50 rule could lead to interruption of play and escalation into conflict (Dugatkin and Bekoff 2003). In addition, observations in degus suggested that individuals that playfully attack a partner subsequently behave in a way that makes it easier for the partner to have an advantage in the next turn (Pellis et al. 2010).

The matching of individuals' playful states and maintaining play without escalation may be enhanced by rapid mimicry of play signals, which are presumably used to share playful intentions among individuals (Davila-Ross et al., 2011; Burke et al., 2017). Multiple studies have shown that rapid mimicry of play faces, which occurs involuntarily in as little as 1 s, prolongs the duration of play sessions (chimpanzees: Davila-Ross et al., 2011; geladas: Mancini et al., 2013a; Tonkean macaques: Scopa and Palagi, 2016; meerkats: Palagi et al., 2019). Likewise, rapid mimicry of a relaxed open mouth and play bowing during play in dogs functions to sustain play (Palagi et al., 2015). In addition, when Japanese macaques adopt a face-to-face configuration at the beginning of play behavior, subsequent play sessions are prolonged (Iki and Hasegawa, 2020) and play symmetry is enhanced (Iki and Hasegawa, 2021). When this face-to-face opening is combined with a play face, the duration of play is further prolonged (see Chapter 3). The relationship between play signals and play escalation has been directly examined in laboratory experiments with rats, which indicated that the reciprocal use of ultrasonic calls by rats during play serves to prevent play escalation (Burke et al., 2017). Indeed, when researchers used surgery to render one of the rats in a pair unable to emit ultrasonic calls, the risk of escalation increased (Kisko et al. 2015).

If the initiation and maintenance of play are based on the matching of playful states between individuals, then the breakdown of play can be viewed as a dissociation of these previously matched playful states. In general, processes of so-called "self–other matching," a phenomenon in which observation of others' behavioral, emotional, or physiological states causes congruent states in the observer (Hecht et al., 2012), have received substantial attention as the basis for successful social interaction (Preston and de Waal, 2002; Hecht et al., 2012; Hess and Fischer, 2013; Duffy and Chartrand, 2015; Massen and Gallup, 2017; Prochazkova and Kret, 2017; Yamamoto, 2017; Adriaense et al., 2020; Palagi et al., 2020). Compared to the strong focus on self–other matching such as behavioral mimicry, emotional contagion, and physiological synchrony, few researchers have examined state dissociation between individuals.

We defined “self–other dissociation” as the process of differentiating previously matched states between individuals. By focusing on the factors associated with self–other dissociation, we can illuminate the mechanisms of successful social interaction from a different angle.

Several studies have suggested that self–other matching is facilitated by inter-individual similarity (Preston and de Waal 2002; Chartrand and Lakin 2013). Extrapolating from this, self–other dissociation, the counterpart of self–other matching, may reflect interindividual differences. In animals with a despotic social structure, group members are differentiated from one another through repetitive dominance–subordination interactions (e.g., Chance 1967; Thierry 2000). Inter-individual differences determined by dominance cause asymmetric interactions (Drews 1993; Thierry 2000) and may affect how previously shared playful states dissociate, i.e., escalate into overt conflict. Regarding the effect of dominance relationships on play fighting, a study showed that dominant dogs delivered a greater proportion of attacks in a play session than subordinates (Bauer and Smuts 2007). Furthermore, another study designed an experimental situation in which male rats encountered one another and found that individuals that behaved more aggressively when play escalated were dominant (Pellis and Pellis 1991). In addition, studies involving captive and free-ranging primate groups have suggested that play is more likely to escalate in despotic species than in egalitarian species (chimpanzees vs. bonobos: Palagi and Cordoni 2012; Japanese macaques vs. moor macaques, *Macaca maura*: Beltrán Francés et al. 2020; see also Cordoni et al. 2018). However, it remains unclear if play escalation reflects dominance relationships between play partners in wild group-living animals.

In addition to dominance relationships, developmental differences may also cause loss of play reciprocity and the dissociation of playful states. A previous study indicated that the degree of play asymmetry is greater in mixed-age dyads than in same-age dyads in wolves, (Essler et al. 2016). In pairs of dogs of different ages, older individuals delivered a higher proportion of playful attacks than younger ones (Bauer and Smuts 2007). However, the effects of age differences on the way play escalates are unclear.

Japanese macaques are considered a valuable model for examining the influence of interindividual differences determined by the dominance rank and development on play escalation. Among the species in the genus *Macaca*, which exhibit a variety of matrilineal dominance styles, Japanese macaques have one of the strictest dominance hierarchies (Thierry 2000). In immature Japanese macaques, there are clear physical differences between individuals of different ages (Fooden and Aimi 2003; Hamada 1994). Play fighting in Japanese macaques involves aggressive motor patterns, such as biting, grabbing, slapping, and wrestling (Petit et al. 2008; Reinhart et al. 2010). Japanese macaques often use play faces (Scopa and Palagi 2016) but do not use play vocalizations. Sessions that remain playful do not show any sign of negative emotions, but when a session escalates into overt conflict, one of the players expresses negative responses (e.g., screaming, bared-teeth displays).

In this study, we examined whether play escalation reflects interindividual differences determined by the dominance rank and development by analyzing data on play fighting in juveniles in a free-ranging provisioned group of Japanese macaques. We hypothesized that deviations from the 50:50 rule caused by interindividual differences lead to escalation into conflict. Specifically, we tested the following predictions.

Prediction 1 is relevant to dominance relationships. We defined an individual that expressed negative responses (e.g., screaming) when play escalated as the “victim,” and the individual that provoked such responses in the partner as the “aggressor.” We predicted that when escalation occurs in same-age dyads (*Prediction 1a*) or mixed-age dyads (*Prediction 1b*), individuals ranked higher than their playmates are more likely to be the aggressors, whereas individuals with lower ranks are more likely to be the victims.

Prediction 2 is relevant to developmental differences between individuals. We predicted that when escalation occurred in mixed-age dyads, individuals older than their playmates would be more likely to be the aggressor, and individuals younger than their playmates would be more likely to be the victim.

Prediction 3 is relevant to play reciprocity and unfairness. In play fighting, players compete for an advantage over their play partners by attacking them without being attacked. We predicted that individuals that subsequently became aggressors would maintain an advantage for a longer total duration compared with individuals that subsequently became victims.

Prediction 4 is relevant to the influence of a dominance relationship on postescalation behaviors of the victim. If dominance relationships affect the way previously shared playful states dissociate, the behavior of individuals immediately after escalation may vary according to the dominance relationship. We predicted that a victim with a higher rank than the aggressor would be more likely to counterattack the aggressor, whereas a victim with a lower rank than the aggressor would be more likely to avoid the aggressor.

4.2. Methods

Study site and subjects

This research was conducted at the same study site, during the same period, and with the same study group as described in Chapter 2.

Data collection

We conducted behavioral observations of agonistic interactions to assess the dominance ranks and play fighting sessions and recorded their outcomes and the participating individuals. See Chapter 2 for the method to assess the dominance rank.

To examine the escalation of play fighting, we observed play fighting sessions and recorded data on the outcome of the sessions (i.e., whether they escalated), the identities of the two individuals participating in the sessions, and their behavior after the escalation. To collect these data, the observer stood in specific positions in the park, from which almost all members of the group could be observed, and recorded all visible play fighting sessions between juveniles using a digital video camera (HDR-TD10 211; Sony, Tokyo, Japan). To observe as many incidents of escalation as possible, we used event sampling (Altmann 1974; Martin and Bateson 2007). If several bouts coincided, we focused on the dyads with the smallest number of observations. To avoid observation bias, the observer regularly altered their standing position. We did not observe animals 30 min before or after feeding times. We did not use focal sampling because only ~3% of all play sessions escalate in primates (chimpanzees and lowland gorillas: Cordoni et al. 2018; bonobos and chimpanzees: Palagi and Cordoni 2012; moor macaques and Japanese macaques: Beltrán Francés et al. 2020). We defined the beginning of each bout of play fighting as the point at which an individual directed any playful attack (i.e., biting, grabbing, wrestling) at a partner, and the end as the point at which both individuals of the dyad stopped playing for at least 10 s. A play session that proceeds without escalation usually ends with individuals staying close together or moving away from each other (Reinhart 2008). There were no "winners" or "losers" in the sessions that remained consistently playful, at least not obviously (Burghardt 2005; Bekoff 2014). In contrast, a session that escalates into overt conflict ends with negative responses (i.e., screaming, bared-teeth displays, grimacing) by one of the players. We defined the individual that expressed the negative response as the victim and the partner as the aggressor. To precisely determine the victim and aggressor roles, we only analyzed cases in which only one individual was in physical contact with a victim when the escalation occurred. To exclude cases of affiliative but non-playful physical contact, only bouts that included at least one instance of biting were analyzed. We did not analyze data from cases in which the first contact between individuals resulted in overt conflict.

We classified the behavior of each victim immediately after escalation into two categories: retaliation and avoidance. We defined retaliation as instances in which the victim lunged, threatened, bit, or grabbed the aggressor within 5 s of the occurrence of the escalation. We defined avoidance as instances in which no retaliation occurred within 5 s of the escalation and the victim moved away from the aggressor or maintained negative responses (i.e., screaming, bared teeth displays, grimacing). There was no case of individuals resuming play immediately after escalation.

In total, we recorded 578 cases of dyadic play fighting sessions that proceeded without escalation and 39 cases of escalation of play fighting that met the above criteria. These cases involved 41 juveniles (10 females, 31 males) as aggressors or victims. Each individual was involved in a mean of 1.9 ± 1.3 cases (range 1–7) of escalation. The difference in the number of males and females in our dataset may reflect the fact that immature Japanese macaque males play more frequently than immature females (Eaton et al., 1986). Two of these sessions occurred between siblings. To exclude confounding effects due to sibling relationships, we excluded these cases from our analysis. Two dyads were included in the dataset twice, and the other dyads were included once. To ensure data independence, we randomly selected one session for each of the former two dyads and omitted them from the analysis. Of the 35 remaining cases, 15 were escalations that occurred in same-age dyads (13 cases in dyads of 1-year-old individuals and 2 in dyads of 2-year-old individuals), and 20 cases occurred in mixed-age dyads (11 cases in dyads with an age difference of 1 year, 8 cases with an age difference of 2 years, and 1 case with an age difference of 3 years). We used the former dataset to test *Prediction 1a* and the latter to test *Predictions 1b* and *2*. For the dataset used for *Prediction 3*, see the "Video coding" section. Immediately after escalation, a victim's behavior may be affected by confounding effects related to the presence of third parties such as potential allies. To rule out this confounding effect, we excluded cases in which siblings, mothers, and other playmates were within 5 m of the aggressor and victim at the time of the escalation from our analysis. As a result, 19 cases of escalation were used as the dataset for testing *Prediction 4*.

Video coding

To compare the amount of time during which individuals that subsequently became aggressors and victims held the advantage over their partner during the prior play bout, we conducted frame-by-frame video analyses (30.3 FPS) using ELAN software (Lausberg and Sloetjes, 2009). Following previous studies (Pellis and Pellis, 1997; Biben, 1986; Bauer and Smuts, 2007; Iki and Hasegawa, 2020), when a player attacked her/his partner unidirectionally or pinned down her/his partner, we defined that player as having the advantage. An attack was defined as unidirectional if an individual grabbed or bit their partner without being grabbed or bitten by their partner. A player was determined to have pinned down their partner if they stood or sat with their weight on their partner, causing the partner to lie down in a prone, supine, or lateral position. We calculated the proportion of time during which each individual maintained the advantage by dividing the total duration during which each individual maintained the advantage by the total duration of the play session. Following previous studies (Reinhart et al., 2010; Iki and Hasegawa, 2020), only play bouts that met the following criteria were included in the analysis to control for confounding factors: the individuals did not use objects such as stones and branches, the entire bout took place on relatively flat ground and not in a three-dimensional environment including fences or trees, and the play bout lasted for more than 5 s. There were 14 cases of play bouts that met the above conditions and escalated to overt conflicts. The mean duration between the start of play and the escalation of play was 21.5 ± 21.4 (range 5.4–89.6) s. We used these cases as the dataset to test *Prediction 3*. A separate coder checked the dataset to assess inter-observer reliability. The resulting Cohen's kappa values were 0.91 for cases in which the player held an advantage, 1.00 when the player became the victim, and 0.89 when the victims counterattacked or evaded aggressors.

Statistical analyses

We randomly labeled one of the two individuals involved in the escalation as the "subject player" and the other as the "subject's partner." We used Fisher's exact test to examine whether higher-ranked and older/larger subject players were more likely to be aggressors than lower-ranked and younger ones (*Predictions 1* and *2*; Table 10) and whether post-escalation behaviors of the victim varied according to the dominance relationship with the aggressor (*Prediction 4*; Table 10). To compare the proportions of time during which individuals that subsequently became aggressors and those that subsequently became victims maintained the advantage (*Prediction 3*; Table 10), we used the Wilcoxon rank-sum test. We conducted analyses using R ver. 4.0.5 (R

Development Core Team, 2021) and created figures using the *ggplot2* package (Wickham, 2016). We set the alpha value at 0.05.

To reassess the results in light of *Predictions 1* and *2*, we conducted follow-up analyses. We evaluated the correlation between the outcome of play escalation and the rank or age difference by calculating point-biserial correlations using the cor.test function in R. We coded the outcome of play escalation dichotomously according to whether a subject player became the aggressor (1) or the victim (0). We calculated the rank and age differences by subtracting the absolute rank and age of the subject's partner from those of the subject player.

Table 10. Overview of the data on play escalation.

Dataset	No. of sessions	Total individuals	Mean (SD/MIN/MAX)	Category		
				Subtotal no. of individuals	**Sex**	**Birth year**
Prediction 1a	15	14 (subject player)	1.07 (0.27/1/2)	3	female	2018
				2	male	2016
				2	male	2017
				7	male	2018
Prediction 1b *Prediction 2*	20	16 (subject player)	1.25 (0.45/1/2)	1	female	2014
				2	female	2016
				3	male	2016
				5	male	2017
				5	male	2018
Prediction 3	14	12 (aggressor)	1.17 (0.39/1/2)	1	female	2018
				1	male	2015
				6	male	2016
				4	male	2018
		12 (victim)	1.17 (0.58/1/3)	1	female	2016
				2	female	2018
				1	male	2016
				3	male	2017
				5	male	2018
Prediction 4	19	16 (victim)	1.19 (0.40/1/2)	1	female	2014
				1	female	2016
				1	female	2017
				3	female	2018
				2	male	2016
				3	male	2017
				5	male	2018

Mean, the mean number of sessions in which each individual participated.

4.3. Results

For escalations that occurred in dyads of the same age, individuals with a higher rank than their playmates were more likely to be aggressors when escalation occurred (Fisher's exact test: p = 0.041; Table 11; *Prediction 1a* supported). However, for escalations that occurred in dyads of different ages, the likelihood of becoming an aggressor did not differ significantly between a subject player with a higher rank than the partner and one with a lower rank than the partner (Fisher's exact test: p = 1.0; Table 11; *Prediction 1b* not supported). In contrast, individuals older than their playmates were more likely to be aggressors when escalation occurred (Fisher's exact test: $p = 0.007$; Table 11; *Prediction 2* supported).

Table 11. The number of play escalations in which a subject player was the aggressor or victim.

Dataset	**No. of sessions**	***p-value***	**Relative rank/age of the subject player**	**Outcome**	
				victim	**aggressor**
Prediction 1a	15	0.041	Higher	2	6
			Lower	6	1
Prediction 1b	20	1.0	Higher	7	3
			Lower	7	3
Prediction 2	20	0.007	Older	2	5
			Younger	12	1

The follow-up analyses using point-biserial correlations corroborated the results. For the escalation that occurred in same-age dyads, a significant correlation was detected between the outcome of play escalation and the rank difference (point-biserial correlation: $r_{pb} = -0.63$, df = 13, $p = 0.012$), suggesting that the higher the rank of the subject player relative to their partner, the more likely the subject player was to be the aggressor. In contrast, the correlation between the outcome of play escalation and the rank difference was not significant for escalations that occurred in mixed-age dyads (point-biserial correlation: $r_{pb} = -0.19$, df = 18, $p = 0.426$). For those cases, the correlation between the outcome of play escalation and the rank difference was significant (point-biserial correlation: $r_{pb} = 0.63$, df = 18, $p = 0.003$), suggesting that the older the subject player was relative to the partner, the more likely the former was to be the aggressor.

With respect to the proportion of time during which each player maintained an advantage over their partner, a player that subsequently became the aggressor maintained an advantage in the preceding play session for a greater proportion of time than a player that subsequently became the victim (Wilcoxon rank-sum test: $W = 167.5$, $p < 0.001$; Fig. 9;

Prediction 3 supported).

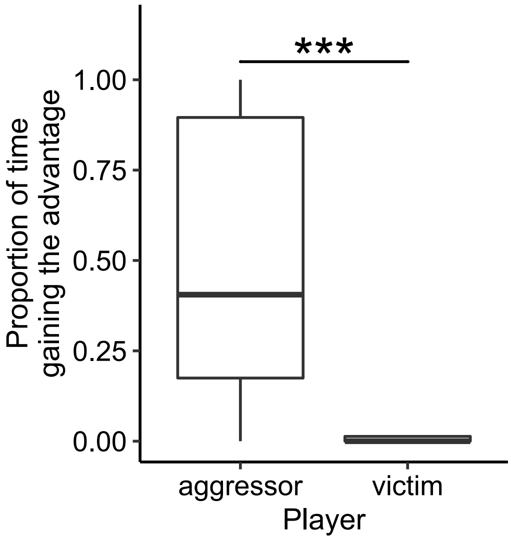

Fig. 9 The proportion of time during which the aggressor or victim maintained the advantage over their partner during the play session. Sample size: N = 14 escalations involving 12 individuals that were subsequently aggressors, and N = 12 individuals that were subsequently victims. ***p < 0.001.

With regard to post-escalation behaviors, victims with higher rankings than aggressors were more likely to retaliate immediately after the escalation, whereas those with lower rankings than aggressors were more likely to avoid the aggressors (Fisher's exact test: p = 0.01; Table 12; *Prediction 4* supported).

Table 12. The number of play escalations in which the victim exhibited retaliation or avoidance.

Dataset	**No. of sessions**	***p-value***	**Relative rank of the victim**	**Victim's behavior**	
				retaliation	**avoidance**
Prediction 4	19	0.01	Higher	5	2
			Lower	1	11

4.4. Discussion

Overall, our results show that play escalation can reflect inter-individual differences between play partners. Specifically, in dyads of the same age, individuals with a lower rank than their playmates were more likely to be victims during play escalation (Table 11; *Prediction 1a* supported). The results of our field observations are consistent with the findings of a laboratory study showing that dominant rats behaved more aggressively when play escalated (Pellis and Pellis, 1991). Many studies have identified social factors affecting the process of self–other matching, such as behavioral mimicry (yawning: Campbell and de Waal, 2011; vigilance: see Chapter 2; scratching: Laméris et al., 2020), emotional contagion (Bourgeois and Hess, 2008; Weisbuch and Ambady, 2008; for a review, see Hess and Fischer, 2013), and physiological synchrony (Feldman et al., 2011). However, whether self–other dissociation, which is the counterpart of self–other matching, is associated with social factors remains unclear. Our results indicate that inter-individual differences determined by dominance relationships may influence the way previously shared playful states dissociate. Follow-up analyses also indicated that the higher the rank of the subject player relative to the partner, the more likely the subject player was to be the aggressor. This result further supports the above interpretation that inter-individual differences may affect play escalation.

Our results also showed that play escalation reflects developmental/physical differences between individuals. In play escalation that occurred in dyads of different ages, those that were more likely to express negative responses (i.e., victims) were younger than their playmates (Table 11; *Prediction 2* supported). As there are clear physical differences between juvenile Japanese macaques of different ages (Fooden and Aimi, 2003; Hamada, 1994), attacks by an older/larger individual might have caused the play breakdown. In contrast to escalations that occurred in dyads of the same age, the relatively higher-ranked individuals in dyads of different ages were not significantly more likely to become aggressors during escalations than the relatively lower-ranked individuals (Table 11; *Prediction 1b* not supported). This indicates that the dissociation of playful states between individuals of different ages may follow a pattern that reflects developmental differences, but not rank differences. The follow-up analyses using point-biserial correlations were consistent with the above results, indicating that for escalations in mixed-age dyads, the age difference was more influential than the rank difference. Also, it remains possible that body size differences might influence the outcome of escalation even in same-age dyads. Offspring of higher-ranked mothers may be able to gain more weight than those of lower-ranked mothers (rhesus macaques: Bercovitch et al., 2000; although Hinde et al., 2009 found no effect of mother's rank on infant weight in rhesus macaques). Hence, there may be a link between offspring body size and maternal rank. To examine the influence of rank while controlling for physical differences, future studies need to collect data on body size and/or weight.

Individuals that subsequently became aggressors maintained an advantage for significantly longer during the preceding play compared to individuals that subsequently became victims (Fig. 9; *Prediction 3* supported). This implies that escalation might have occurred because one individual held an excessive advantage and play lost its reciprocity. This is consistent with previous studies that indicated that asymmetry in the chances of gaining an advantage between players can cause play escalation (Dugatkin and Bekoff, 2003; Pellis and Pellis, 2017; Palagi, 2018). As other researchers have noted, maintaining play reciprocity may be important for continuing to share a playful state (Palagi et al., 2016; Lampe et al., 2019). If so, to elucidate how play escalates into overt conflict, it is important to clarify the relationship between the level of advantage held by each individual and their relative age and rank. Indeed, in some species, dominant individuals are more offensive than subordinate ones during social play (dogs: Bauer and Smuts, 2007), and the degree of play asymmetry is greater in mixed-age dyads than in same-age dyads (wolves: Essler et al., 2016). According to the data used for *Prediction 3* ($N = 14$), six escalations occurred in same-age dyads and eight in mixed-age dyads. Due to this small sample size, we did not perform further statistical analysis to clarify the relationship between the level of advantage and each individual's relative age/rank. Future studies with larger sample sizes are needed to address these issues.

Even if it is true that unfairness causes the breakdown of play, it is difficult to determine based on our data whether the aggressor or victim directly triggered the escalation. It is hard to imagine that the benefits, if any, of turning play into overt conflict would outweigh the costs. Hence, it is unlikely that the aggressor willingly assumes the risk of escalation. Rather, it may be that a victim that reacts negatively to deviation from 50:50 fairness is the direct cause of the escalation. To address this question, it might be helpful to compare the level of advantage each individual maintains during escalated sessions with that in sessions that remain playful to the end.

The post-escalation behaviors of victims varied according to the dominance relationship with the aggressor. Victims with a higher rank than their aggressors were more likely to counterattack their partners immediately after escalation, whereas victims with a lower rank were more likely to evade their partners (Table 12; *Prediction 4* supported). In despotic species such as Japanese macaques, it may be especially inappropriate for lower-ranked individuals to provoke a negative response from higher-ranked ones. One can speculate that to reform and reverse this incorrect relationship, higher-ranked victims may retaliate. This study only focused on victim behavior within 5 s after the escalation to investigate whether a counterattack took place immediately after the play fighting turned into overt conflict. However, given that an individual's emotional state can persist for several minutes (e.g., Ioannou et al., 2014), play escalation may affect an individual's behavior beyond the 5-s time window. How play escalation affects subsequent long-term relationships between individuals is an interesting topic for future studies.

The main limitation of our study was the small sample size. As we treated dyads as independent and the same individuals contributed to multiple dyads, a risk of pseudoreplication and possible type I error should be considered. Accordingly, although we found support for *Predictions 1* to *4*, the results should be treated with caution. As many studies have indicated (Palagi and Cordoni 2012; Cordoni et al. 2018; Beltrán Francés et al. 2020), play fighting rarely escalates. Therefore, small sample size is an inevitable limitation when studying play escalation based on observational data from wild animals. In addition, as this study included a sample from a single group, our results should not be generalized too hastily to all Japanese macaques.

It would be interesting to determine whether play fighting is more likely to escalate in dyads that play infrequently than in dyads that play frequently. Several species preferentially choose same-age/size and same-sex partners for play (e.g., Boulton, 1991; Thompson, 1996). In long-tailed macaques, whereas the offspring of high-absolute-rank mothers preferentially play with one another, the offspring of low-absolute-rank mothers do not exhibit such rank preferences (Fady, 1976). To examine the effect of partner preferences on play escalation, the frequency with which each individual chooses specific partners should be recorded. As we did not use focal sampling, we were unable to collect data on partner preferences. More detailed studies are needed to address this.

Although this study did not focus on this particular topic, it is also possible that how the play begins can influence the outcome (i.e., whether and how it escalates). There are several patterns in which Japanese macaques begin play fighting (Iki and Hasegawa, 2020, 2021). One pattern involves a single play initiator. In this case, play is initiated by one individual making a surprise attack from behind on a partner. In other cases, there is no clear initiator of play, such as when both individuals form a face-to-face configuration and then begin to play together or when individuals continuously transition from other types of social interactions (e.g., grooming and mounting) to play. When there is a single play initiator, it would be interesting to find out whether the initiator is more likely to become an aggressor in play escalation than its partner. In Japanese macaque play fighting, cases with a single initiator are rarer than cases without one (Iki and Hasegawa, 2021). In the dataset used for *Prediction 3*, there were only four cases with a clear play initiator. Because of this small sample size, we did not examine whether play initiators were more likely to be aggressors.

In conclusion, this study highlighted the escalation of play fighting into overt conflict as an incidence of self–other dissociation. Our results suggest that the dissociation of playful states may follow inter-individual differences determined by the dominance rank and development. To understand how and why play fighting escalates and how animals prevent this from happening, future studies should compare escalated sessions and sessions that remain playful from the beginning to the end. We hope that the results of this study will provide a foundation for such a comparison.

Chapter 5: General discussion

5.1. Overview of the studies

Individuals identify with or are differentiated from others through state matching/mismatching. Although classical studies assumed that state matching is no more than a reflex response (Provine, 1986; Hatfield et al., 1993), recent studies have found that state matching is modulated by social factors and emotional connectedness (de Waal, 2008; Palagi et al., 2009). In this thesis, I extended the framework of the study of self–other matching (Fig. 10; cf. Fig. 1) by showing the social biases in the contagion of negatively valenced behavior (Chapter 2), signal use that contributes to sustaining state matching (Chapter 3), and social factors affecting the failure of self–other matching (Chapter 4).

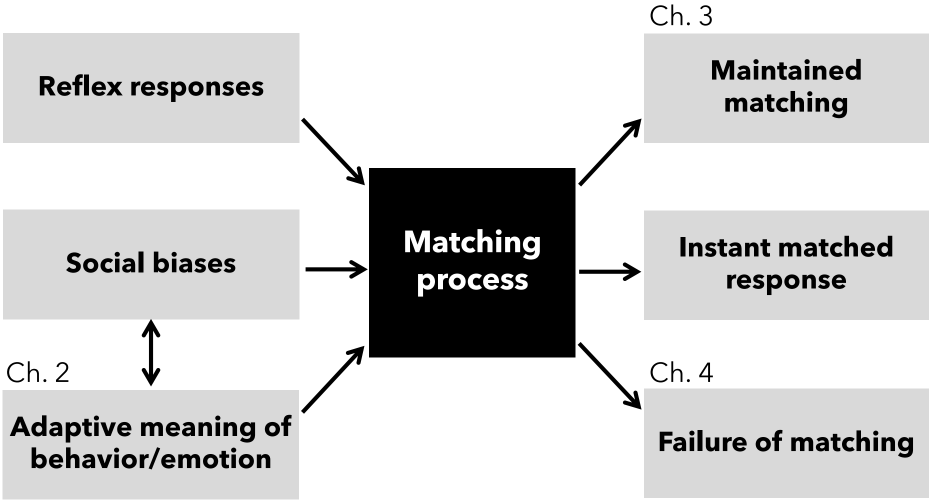

Fig. 10 Mechanisms of self–other matching proposed in this thesis.

Previous studies indicate that social bonds enhance contagious state matching (see Chapter 1). However, the study in Chapter 2 found no kinship bias in vigilance contagion in Japanese macaques that form strikingly strong social bonds between related individuals (Chapais et al., 1997). The study also found that although there are strong social bonds between Japanese macaque mothers and offspring, vigilance contagion was unidirectional from offspring to mother. These results imply that there is no social bond bias in vigilance contagion. When kin individuals are nearby, it may be more adaptive for Japanese macaques to decrease their vigilance than to match their vigilance with kin, as I showed in another paper (Iki and Kutsukake, 2021). Social bias may not affect all types of contagious matching in the same way, but rather contagious matching is affected by the interplay of the adaptive meaning of behavior and social biases.

The study in Chapter 3 focused on play fighting and examined the relationship between the maintenance of shared playful state and facial signal (i.e., play face). The study not only shows the relationship between the facial signals and the maintenance of the play state but also implies a possible mechanism by which facial signals can prolong state matching. The results indicate that play face may function to advertise toward partners the expresser's motivation for subsequent interactions and a receptive and tolerant stance. Emotional expressions such as laughter and play signals can make the expresser's mental states publicly observable (Gallagher, 2008). This type of signal would allow the observer to perceive the mental state of the expresser without employing cognitive and inferential attribution of mental states (i.e., Theory of Mind; Gallagher and Zahavi, 2012) and would provide cues for state matching and its maintenance. The result also indicates that playful interaction is prolonged not only when both interactants express play face but also when one of the interactants perceives the other’s play face. Consistent with the above interpretation, this suggests that the facial expression does not only correlate with its expresser’s mental state but also serves a communicative function of providing the perceiver with cues for state matching and sharing.

As mentioned in Chapter 1, self–other matching failures have received much less attention than successful state matching between individuals. The study in Chapter 4 shows that inter-individual differences determined by dominance relationships and developmental stages affect how self–other matching breaks down. Based on the results, it can be speculated that inter-individual differences may have led to asymmetries in play interactions, and these asymmetries may have caused the failure of maintenance of shared playful states. Also, the adaptive meaning of behavior may not only affect self–other matching, as discussed in Chapter 2, but may also affect self-other dissociation. Even if an interaction is playful in the beginning, the meaning of the interaction may change from playful to distressing once the interaction becomes excessively asymmetrical. This change in the adaptive meaning for the participants may have led to self-other dissociation.

In conclusion, this thesis suggests that self–other matching should be viewed as a more complex process than has been assumed by previous studies. Prior studies have focused primarily only on whether instant state matching occurs, with little attention to the adaptive meaning that varies from behavior to behavior and the time range of matching. The overlap between oneself and others is not simply determined by emotional closeness and social contexts. Instead, the overlap will depend on which behavioral and emotional states the researcher focuses on, each with a different adaptive meaning. Also, the self–other overlap can change over time: interactants manage their state matching with signals, and sometimes state dissociation occurs. In addition, ecological and social conditions, which vary from species to species, may affect self–other matching. A comparative study that takes into account the complex nature of self–other matching suggested by this thesis is expected to shed further light on the evolutionary background of basic social cognitive skills.

5.2. Future directions

In addition to the comparative study described in the last section, there are several other possible directions for future research. As mentioned in Chapter 1, self–other matching occurs across different domains, such as emotion, behavior, physiology, neural systems, and cognition. Studying the interaction between these different domains is essential to clarify the mechanisms underpinning self–other matching. The relationship between behavioral contagion and emotional contagion is an important cognitive science topic for understanding the causal relationship between the synchrony of externally expressed physical responses and the sharing of internal mental states. The behaviors I focused on in this thesis are emotional ones: vigilance is associated with negative emotions such as fear and anxiety, and play is associated with positive, playful emotions. However, I analyzed these behaviors without clearly distinguishing between behaviors and emotions. To separate emotions from behaviors, some experimental intervention would be needed. One of the possible interventions is to induce a negative or positive emotion in an individual. Through this intervention, we may be able to examine if the individual who has negative emotions in advance would be more susceptible to behaviors associated with negative emotions like vigilance, and individuals with positive emotions would be less susceptible to them.

Another interesting topic is the effect of social structure on state matching. Many studies, including this thesis, have focused on social relationships between two individuals (i.e., mother-offspring relationship, kinship, relative dominance, etc.) but not on the structure of the whole society. Meanwhile, psychiatry studies have found that mood disorders such as depression “spread” along social networks and are likely to occur on the periphery of social networks (Rosenquist et al., 2011). By using social network analysis and examining whether the “contagion network” of behaviors and emotions reflects the social position of individuals and the structure of the whole society, researchers may be able to find unknown social factors in contagious matching. Furthermore, comparisons between humans and other species from this perspective may enable us to explore the specific characteristics and evolutionary backgrounds of empathic phenomena in humans which have a particularly large and complex social network among group-living animals.

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