Face-to-face opening phase in Japanese macaques' social play enhances and sustains participants' engagement in subsequent play interaction

Sakumi Iki [1,2] · **Toshikazu Hasegawa** [2]

[1] Department of Evolutionary Studies of Biosystems, School of Advanced Sciences, SOKENDAI (The Graduate University for Advanced Studies), Hayama, Kanagawa 240-0193, Japan
[2] Department of Life Sciences, Graduate School of Arts and Sciences, The University of Tokyo, Meguro, Tokyo, Japan
* Sakumi Iki sakumi.iki@gmail.com

Abstract

A face-to-face "opening phase" in human interaction serves as a platform for the interactants to initiate and manage their interaction collaboratively. This study investigated whether, as is the case in humans, a face-to-face opening phase in animal interaction serves to manage a subsequent interaction and establish interactants' engagement. We compared the dyadic play fighting of Japanese macaques (*Macaca fuscata*) initiated with and without a face-to-face opening phase. Our observations showed that play sessions with a face-to-face opening phase lasted longer than did sessions without one. Furthermore, our results indicate that facing toward playmates was a sign of interactants' engagement. In sessions with a face-to-face opening phase, both players were likely to gain an advantage over their playmates, whereas in sessions without such an opening phase, only an individual who unidirectionally faced toward another individual who looked away when play began was likely to maintain an advantage over a long period. Our findings demonstrate that a face-to-face opening phase has a socio-cognitive function to establish and sustain interactants' social engagement during subsequent interaction not only in humans but also in Japanese macaques.

Keywords

Face-to-face interaction · Social cognition · Communication · Social play · Play fighting · *Macaca fuscata*

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Introduction

Sequences of some social interactions can be divided into macro-level phases of opening, main body, and closing (Heesen et al. 2017). In daily interactions, such as conversations, humans collaboratively initiate their interaction through a specific opening phase (Schegloff 1968; Pillet-Shore 2018). This opening phase is followed by the main-body phase during which the actual interaction unfolds (e.g., exchanges of utterances in conversation). The present study focuses on the influence of the opening phase with the main-body phase in animal interaction. The influences have been well studied in humans. The opening phase serves as a platform for human interactants to sequence the subsequent main-body phase successfully (Schegloff 1968) by constituting and confirming interactants' relationship (Schegloff 1968). During the opening phase, human interactants exchange communicative signals (Goffman 1981) to establish and communicate their engagement in subsequent interaction (Robinson 1998). These signals have socio-cognitive functions to establish the nature of the subsequent main-body phase that will follow (Pillet-Shore 2018), as they specify the roles that interactants will take and clarify the meaning of the actions they will perform (Goffman 1967). Among such communicative signals, mutual gazes, or face-to-face configurations, play a crucial role for human interactants (Cary 1978). However, attention should be paid to the fact that there are cross-cultural differences in how face-to-face configurations are used in daily interactions (e.g., Akhtar and Gernsbacher 2008) and that a large portion of studies examining the practice of face-to-face communication were performed in Western, educated, industrialized, rich, and democratic (WEIRD) populations (Henrich et al. 2010). Several studies that have sampled WEIRD populations have reported that a face-to-face opening phase identifies an interactive partner (Goodwin 1981), constructs a situation in which the interactants are mutually attentive and responsive (Cary 1978; Robinson 1998), and demonstrates the participants' availability for future interaction (Goodwin 1981; Kendon 1990). Furthermore, human interactants continue to coordinate their engagement after entering into the main-body phase (Heesen et al. 2017). For example, it has been reported that during the main-body phase, interactants sustain dyadic engagement through turn-taking in emotional expression (e.g., turn-taking of smiles and laughs; Trevarthen 1979) and mirroring of emotional valence (e.g., expressing the same emotion by different behaviors, such as vocalization and facial expression; Stern 1985), and they re-engage a reluctant partner to interact again after an interruption (Warneken et al. 2006).

Coordination of social engagement in non-human animals (hereafter, animals) in the course of interaction has been well studied in the main-body phase of play fighting. Play fighting is a widespread social interaction in mammalian species (Burghardt 2005; Brownell 2011). In general, play fighting involves behavioral patterns that are also used in serious aggression, such as biting, grabbing, and wrestling (Burghardt 2005; Bauer and Smuts 2007; Palagi et al. 2016). Although these behavioral patterns are applied gently to avoid causing injury to their opponents, play fighting can be misleading and sometimes escalates into serious aggression (Palagi et al. 2016). As one of the defining criteria of play, play fighting must be spontaneous and voluntary (Burghardt 2005, 2010). As play is often endogenously motivated and is performed for its own sake (Held and Špinka 2011), it cannot be initiated or maintained unless individuals are in a playful mood and participate spontaneously. Therefore, to maintain a play session and avoid misunderstanding, animals need to deal with socio-cognitive work of indicating and understanding that they are spontaneously engaged in play. Indeed, in the main-body phase of play fighting, during which the pseudo-aggressive behavioral patterns are exchanged, the states

of the interactants' engagement are coordinated by play signals. Previous studies have demonstrated that play sessions with (mirroring of) play signals last longer (chimpanzees, *Pan troglodytes*: Davila-Ross et al. 2011; geladas, *Theropithecus gelada*: Mancini et al. 2013; Tonkean macaques, *Macaca tonkeana*: Scopa and Palagi 2016; domestic dogs, *Canis lupus familiaris*: Palagi et al. 2015; Hanuman langurs, *Semnopithecus entellus*: Špinka et al. 2016; South American sea lions, *Otaria flavescens*: Llamazares-Martín et al. 2017) and become rougher (western gorillas, *Gorilla gorilla gorilla*: Palagi et al. 2007; geladas: Palagi and Mancini 2011; Barbary macaques, *Macaca sylvanus*, long-tailed macaques, *Macaca fascicularis*, lion-tailed macaques, *Macaca silenus*, Tonkean macaques: Preuschoft 1992, 1995) than sessions without such signals.

In terms of the opening phase of play fighting, many studies have reported that animals have several ways of initiating play interactions (Heesen et al. 2017). For example, African great apes gaze at each other (chimpanzees: Fröhlich et al. 2016; gorillas: Yamagiwa 1992) and use visual and audible gestures (chimpanzees: Fröhlich et al. 2016; gorillas: Yamagiwa 1992; Tanner 2004) immediately before a play session begins. Orangutans (*Pongo pygmaeus*) make a "stiff approach" or "loutish approach" toward their playmates before they engage play (Rijksen 1978). Canids (domestic dogs, wolves, *Canis lupus*, coyotes, *Canis latrans*) bow down to partners to initiate play interactions (Bekoff 1974, 1995; Byosiere et al. 2016). Kakas (*Nestor meridionalis*) and keas (*Nestor notabilis*) initiate play with head cocks or hopping approaches or by rolling over (Diamond and Bond 2003). Researchers regard these behaviors as solicitations or invitations to play, as they are used during situations where players are in a face-to-face configuration and/or are making direct eye contact (Yamagiwa 1992; Bekoff 1974; Fröhlich et al. 2016; Rijksen 1978; Byosiere et al. 2016). By establishing a context in which animal interactants are mutually attentive, a face-to-face opening phase may serve as a platform for animals to successfully sequence the subsequent main-body phase of play.

Although it has attracted less research attention (but see Heesen et al. 2017), play initiation is not always characterized by specific opening phases. Play can be initiated in situations in which individuals are not facing each other, as when one individual performs a surprise attack from behind an inattentive other. This allows us to compare play sessions having two types of initiation (i.e., play sessions initiated with and without a face-to-face opening phase) and thereby clarify the socio-cognitive function of a face-to-face opening phase. If the face-to-face opening phase serves to sequence the subsequent main-body phase of play appropriately and establish interactants' engagement in play, as is the case in some human populations, we would expect that play sessions with such openings would be successfully managed for long stretches of time and characterized by interactants' active engagement in play. Using dyadic play-fighting data from free-ranging Japanese macaques, we tested this idea by comparing play sessions with an opening phase in which players were in a face-to-face configuration (FF-initiated play) with play sessions initiated without any specific opening phase (non-FF-initiated play). We tested the following four predictions:

Prediction 1 Several studies have demonstrated that play signals emitted in the main-body phase of play by animals to fine-tune playful interactions prolong the interactions (Davila-Ross et al. 2011; Mancini et al. 2013; Scopa and Palagi 2016; Palagi et al. 2015). Likewise, if a face-to-face opening phase successfully contributed to the management of the subsequent main-body phase of play, we expected that FF-initiated play would last longer than non-FF-initiated play.

Prediction 2 Studies have shown that players displaying emotional engagement signals

behave more actively and roughly (Palagi et al. 2007; Palagi and Mancini 2011; Preuschoft 1992, 1995). In play fighting, players compete for an advantage over their partners (Aldis 1975; Reinhart et al. 2010; Himmler et al. 2013). We classified states of play into four categories based on which player, if either, gained an advantage (see "Methods"). We expected that transitions in play states would frequently occur in FF-initiated play if face-to-face opening phases establish both players' active engagement to gain an advantage. Hence, we predicted a higher rate of state transitions in FF-initiated play than in non-FF-initiated play.

Prediction 3 If facing toward playmates is itself a sign of interactants' engagement in play, then both individuals would be expected to play vigorously in FF-initiated play. In some situations of play fighting, both players mutually attack each other (i.e., symmetric attack; see "Methods"). In such situations, each player has a chance to gain an advantage over the other player. We investigated the likelihood that an individual (i.e., S-player; see "Methods") who played less vigorously and maintained an advantage for a shorter period from the beginning of play would gain an advantage over the other individual immediately after a symmetric attack. We predicted that an S-player would be more likely to gain an advantage immediately after a symmetric attack in FF-initiated play than in non-FF-initiated play.

Prediction 4 Consistent with Prediction 3, we predicted that a play initiator who unilaterally faced toward his partner when non-FF-initiated play began would play more vigorously than the player who looked away at the beginning of play. Hence, we predicted that the play initiator of non-FF play would be more likely than the other player to gain an advantage for a longer duration.

Methods

Study sites and subjects

This study of a free-ranging provisioned group of Japanese macaques was conducted in Shiga-Heights, Nagano Prefecture, Japan. Demographic records have been kept since 1962, and all individuals are identifiable. Group size changed from 213 to 211 individuals due to deaths. In January 2017, there were 14 adult males (5 year and older), 93 adult females (4 year and older), 30 juvenile males (1–4 year), 38 juvenile females (1–3 year), 18 infant males, and 20 infant females. The group was fed barley, soybeans, and apples four times daily (09:00, 12:00, 15:00, and 16:30) by the staff of Jigokudani Monkey Park. For a detailed description of the research site, see Wada and Ichiki (1980). To exclude the effects of sex and age differences between players, we focused on play bouts between two individuals of the same sex and same age. Our study subjects were 0- to 2-year-old males participating in play fighting (0 year old: infants; 1 and 2 years old: small juveniles). We chose immature males for efficient data collection because they play more frequently than immature females (Eaton et al. 1986) and prefer to play with partners of the same sex (Glick et al. 1986). As all infants were born in the period between April 2016 and June 2016, they were 7–9 months old at the beginning of our observation and had begun to feed themselves, but they were not fully weaned. In our subject groups, there were 18, 11, and 13 male individuals, aged 0, 1, and 2 years old, respectively.

Data collection

The first author conducted behavioral observations from January 2017 to March 2017 (40 days). The observer stood at specific places from which the study group individuals could be observed and recorded all bouts of visible play fighting on video. To avoid observation bias, the observer

regularly changed standing locations. When several play bouts occurred simultaneously, we focused on the pairs within the target age group with the least number of observations. Video recording was conducted from 09:00 to 16:30 using a digital video camera (HDR-TD10; Sony Corporation, Tokyo, Japan). We did not observe animals 30 min before or after feeding times, and maintained a distance of more than 1.5 m from subjects at all times. As it was likely that age differences between interactants might affect which player gained an advantage over the other and might influence the degree to which they were engaged in play, we included only interactions between two individuals of the same age in our analysis. In addition, all play bouts fulfilled the following requirements (Reinhart et al. 2010): the entire interaction, from initiation to conclusion, occurred on relatively flat ground but not in a three-dimensional environment, such as in trees or on fences; at least one bite was involved but no behavioral components to denote serious fighting were demonstrated (e.g., screaming or bared teeth); and no objects, such as leaves or rocks, were used. We excluded play bouts preceded by grooming, contact-sitting, mounting, or play chasing within the ten frames (about 0.333 s) immediately before the first playful attack because these behaviors might have influenced interactants' engagement in play. Therefore, we analyzed only FF- and non-FF-initiated play bouts. During the course of this study, we collected approximately 117 h of video data that recorded the play fighting of a total of 31 dyads of 0-year-old males, 20 dyads of 1-year-old males, and 15 dyads of 2-year-old males.

Video coding

We conducted frame-by-frame (30 fps) video analyses using Behavioral Observation Research Interactive Software (BORIS; Friard and Gamba 2016). We defined play bout initiation as the moment when an individual directed any playful attack at his partner (i.e., biting, grabbing, pushing, slapping, wrestling). Play bouts ended when partners ceased play for at least 10 s. The beginning of each play fight was classified as FF or non-FF. We considered a bout to be FF-initiated play when individuals faced one another within ten frames (about 0.333 s) immediately before the first playful attack. We considered a bout to be non-FF-initiated play when one individual oriented his face toward his partner while his partner was looking away and initiated play from behind the partner. Every ten frames (about 0.333 s), we determined which player, if any, gained an advantage. We considered a player to have the advantage if he unidirectionally attacked his partner (Pellis and Pellis 1987, 1997) or pinned down his partner (Biben 1986; Bauer and Smuts 2007). An attack was considered unidirectional when the attacker's face or belly faced his partner while his partner's whole body was oriented away from him. Pinning down was defined as when a player in a standing or sitting position had weight on his partner, leading his partner to lie down in a prone, supine, or lateral position. Every 10 frames, we classified each player within each pair as an L-player or S-player according to the player's cumulative duration of maintaining an advantage since the beginning of a bout. The L-player was the one with an advantage for a longer duration than his partner, whereas an S-player had the advantage for a shorter duration. States of play interaction were coded every ten frames (about 0.333 s) and divided into the following four categories:

Symmetric attack	Both players attacked each other and neither gained an advantage
No attack	Neither player delivered any attacks
L-player's attack	An L-player had an advantage over his partner
S-player's attack	An S-player had an advantage over his partner

If the state of the current ten frames was the same as the state of the previous ten frames, it was considered to have continued. According to this procedure, the sequences of play fighting

can be described as transitions among the above four states. Examples of the coded play sequences are shown in Fig. 1. Twenty randomly chosen bouts (i.e., 10.8% of all play sessions) were coded by a separate researcher to assess inter-observer reliability. The resulting Cohen's kappa coefficient values were 0.765 for the type of play initiation and 0.825 for the type of play state.

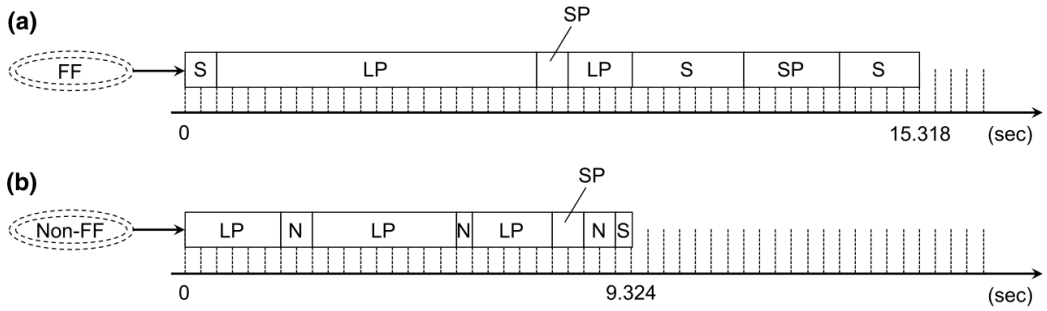


Fig. 1 Examples of the coded play sequences. a A sequence of FF-initiated play bout. b A sequence of non-FF-initiated play bout. S, LP, SP, and N in rectangles indicate symmetric attack, L-player's attack, S-player's attack, and no attack, respectively. Each division on the horizontal scale indicates 0.333 s (i.e., 10 frames)

Statistical analyses

We used generalized linear mixed models (GLMMs) by R v. 3.4.2 and SAS v. 9.4. In all GLMM analyses, we included play dyad as a random effect because there were multiple samples from the same dyad. We included player age as a fixed variable to control confounding effects. We set our alpha level at 0.05. To test the significance of the predictors, we compared the full models with the null models including only the control factor (i.e., age) and the random effect (i.e., play dyad) using the likelihood ratio test. The datasets analyzed in the present study can be accessed at: https://osf.io/tgqkz.

Play duration and the rate of state transition (Predictions 1 and 2)

To examine whether a face-to-face opening phase influenced the duration of play bouts (Prediction 1), we used a GLMM with a gamma error structure and log link function. Similarly, we examined the rate of state transition (Prediction 2) using GLMMs with a Poisson error structure and log link function. We calculated the rate of state transition as the number of state transitions per second. Type of play initiation (FF or non-FF) was a fixed variable in each model. In the analyses of the rate of state transitions, the duration of the play bout (ln transformed) was controlled as an offset variable.

Factors affecting the rates of transitions from a symmetric attack to an L-player's attack and from a symmetric attack to an S-player's attack (Prediction 3)

To test Prediction 3, we applied a GLMM with a multinomial error function and a generalized logit link function. Multinomial logistic regression analyses the effects of fixed variables on odds of response categories relative to a reference category. To investigate the extent to which a face-to-face opening phase influenced the probability of each player's gaining an advantage immediately after a symmetric attack, we focused on the L-player's attack as a response category and the S-player's attack as a reference category. Although the multinomial GLMM analyzed the effects on odds of other response categories (i.e., no attack and end state) to the reference category, we did not report these effects as they were irrelevant to our purpose. We included the

following as fixed variables.

Type of play initiation (FF or non-FF)	We predicted that an S-player in FF-initiated play was more likely to gain an advantage immediately after a symmetric attack than was a player in non-FF-initiated play.
Elapsed time from start of play	We tested the possibility that states of interactants' engagement changed with progress of an interaction. We expected that an initially unengaged individual would become more strongly engaged as time passed following the initiation of a bout. If this was true, we predicted a corresponding increase in the probability that an S-player would gain an advantage immediately after a symmetric attack.
The last state preceding a symmetric attack	This variable included four levels: L-player's attack S-player's attack, no attack, and start state. We examined the possibility of turn-taking in gaining an advantage by choosing the S-player's attack as a reference category. This allowed us to compare transitions from symmetric attacks preceded by the S-player's attacks to symmetric attacks preceded by other states (i.e., the L-player's attack, no attack, or start state). If turn-taking in gaining an advantage occurred, it was predicted that symmetric attacks preceded by an L-player's attack or no attack would be more likely to transition into an S-player's attack.
Two-way interaction between type of play initiation and elapsed time	It was expected that the temporal change in states of engagement would vary according to the type of play initiation. In FF-initiated play, both players would be engaged from the start of play. On the other hand, in non-FF-initiated play, only one player (i.e., the L-player) would be engaged from the start of play, whereas the S-player would initially be unengaged and then gradually begin to play vigorously as the interaction progressed. Therefore, we predicted that a temporal increase in the probability that an S-player would gain an advantage immediately after a symmetric attack was more likely in non-FF-initiated play than in FF-initiated play.

The player who maintained a duration in non-FF-initiated play (Prediction 4)

To examine Prediction 4 (whether an initiator of non-FF-initiated play was more likely than his partner to gain an advantage for a longer duration in a play session), we applied a generalized linear mixed model (GLMM) with a binomial error function and a logit link function. The initiator (0) and the other player (1) were the response variables in this GLMM, which was based on which player gained an advantage for the longest duration. We included only an intercept term as a fixed variable. We expected that the rate of play bouts in which an initiator gained an advantage for a longer duration would be higher than the rate of those in which the other player gained an advantage for a longer duration. Specifically, we predicted that our analysis would yield an intercept term that deviated from 1:1 (i.e., deviated from zero in the logit-transformed scale) with a bias toward initiators. The key predictor in this analysis was the intercept term. Therefore, in a likelihood ratio test, we compared the full model with the null model lacking the intercept term but consisting of the control factor and the random effect.

Results

A total of 185 play bouts met the requirements described in "Methods" (71, 46, and 68 bouts for 0-, 1-, and 2-year-old subjects, respectively). The duration of play bouts ranged from 1.33 to

172.16 s, with a mean duration of 21.05 s (SD: 25.22). The mean durations of play bouts involving 0-, 1-, and 2-year-old subjects were 17.23, 22.93, and 23.78 s, respectively (SD: 24.62, 22.34, and 27.43).

For the duration of play bout and the rate of state transitions, the full models accounted for significantly more variance than the null models (play duration: $\chi^2 = 9.17$, df = 1, $p < 0.01$; rate of state transition: $\chi^2 = 4.62$, df = 1, $p < 0.05$). Play bout duration was influenced by the type of play initiation, with FF-initiated play lasting significantly longer than non-FF-initiated play (Table 1, Fig. 2a). This result is consistent with Prediction 1. However, contrary to Prediction 2, the rate of state transitions in non-FF-initiated play was higher than that in FF-initiated play (Table 1, Fig. 2b).

For the rates of transitions from a symmetric attack, the full model accounted for significantly more variance than the null model ($\chi^2 = 126.22$, df = 7, $p < 0.001$). Regarding Prediction 3, we found a significant two-way interaction between elapsed time and the type of play initiation (Table 2). Post hoc comparisons between FF-initiated play and non-FF-initiated play at every 0.5 value of ln-transformed elapsed time (i.e., ln(elapsed time + 1) = 0.5, 1.0, 1.5, 2.0, 2.5, and 3.0) showed that the probability of each player's gaining an advantage was significantly different between FF-initiated play and non-FF-initiated play before the 2.0 time point (Table 3). This result suggests that an S-player in FF-initiated play was more likely to gain an advantage than an S-player in non-FF-initiated play (Fig. 3). After this time window, the probability was not significantly different between FF-initiated play and non-FF-initiated play. These results indicate that S-players in FF-initiated play were actively engaged from the beginning of play. By contrast, S-players in non-FF-initiated play were initially unengaged and gradually became more vigorously engaged in play to gain an advantage as time passed. The probability of each player's gaining advantage was influenced by the last state preceding a symmetric attack (Table 2). This result showed that a symmetric attack preceded by no attack was more likely to transition into an L-player's attack than into an S-player's attack. Although it was not significant, a symmetric attack preceded by an L-player's attack tended to transition into an L-player's attack. These results indicated that turn-taking in a form that a player with a longer advantage (i.e., an L-player) allows his partner (i.e., an S-player) to gain an advantage is an unlikely outcome within each bout between these dyad members of the same age.

For the player who maintained a duration advantage in non-FF-initiated play, the full model accounted for significantly more variance than the null model ($\chi^2 = 21.34$, df = 1, $p < 0.001$). The test of Prediction 4 showed that the intercept term deviated significantly from zero (1:1; Table 1), indicating that, as expected, initiators of non-FF-initiated play were significantly more likely than the other player to maintain an advantage for a longer duration (the number of play bouts in which an initiator and the other player maintained an advantage for a longer duration in a bout was 34 and 1, respectively).

Table 1 Factors affecting the duration of play bouts, rate of state transitions, and identity of the player who maintained a duration advantage in non-FF-initiated play

Model	Estimate	SE	χ^2	p value
Duration				
Intercept	2.27	0.20		
Age	0.07	0.13	0.52	0.605
Type of initiation (FF)	0.59	0.19	3.17	0.002

Rate of state transitions				
Intercept	− 0.56	0.09		
Age	− 0.03	0.06	− 0.41	0.679
Type of initiation (FF)	− 0.19	0.09	− 2.18	0.029
Player who maintained a duration advantage in non-FF-initiated play				
Intercept	4.02	1.57	2.56	0.011
Age	–0.62	1.21	− 0.51	0.607

Identity of play dyad was included as a random effect. Sample size: n = 185 for duration and rate of state transitions; n = 35 for the player who maintained a duration advantage in non-FF-initiated play

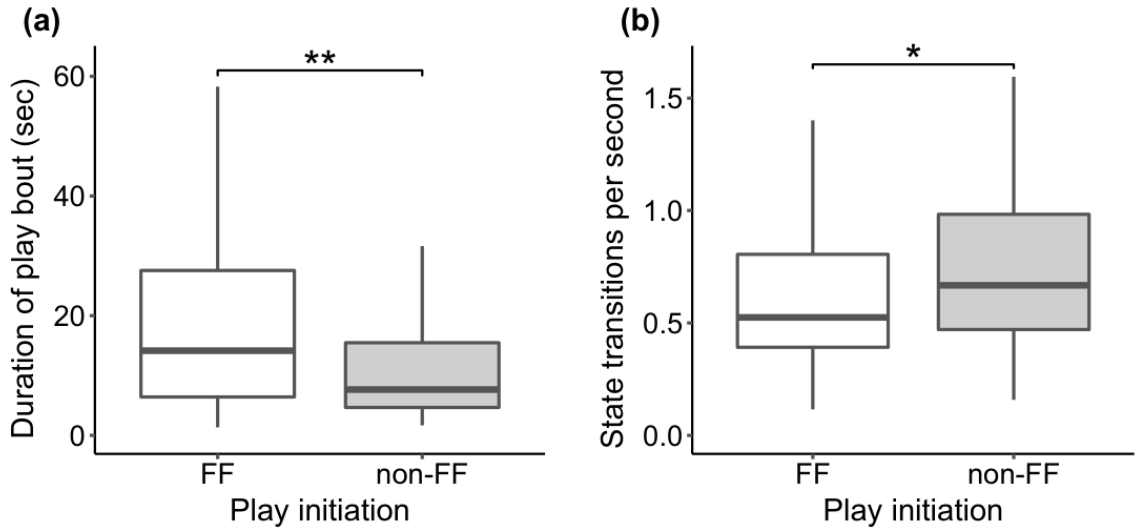


Fig. 2 Boxplots of a duration of play bout and b state transition rate per second in FF- and non-FF-initiated play (*p < 0.05, **p < 0.01)

Table 2 Factors affecting the rates of transitions from a symmetric attack to an L-player's attack and from a symmetric attack to an S-player's attack

Model	Estimate	SE	DF	t value	p value
Intercept	5.09	2.13			
Age	− 0.21	0.14	610	− 1.55	0.121
ln(elapsed time + 1)	− 1.58	0.74	610	− 2.15	0.032
Type of initiation (FF)	− 4.84	2.15	610	− 2.26	0.024
Last state (reference category: S-player's attack)					
L-player's attack	0.51	0.28	610	1.84	0.067
No attack	0.87	0.32	610	2.74	0.006
Start state	12.29	56.46	610	0.22	0.828
ln(elapsed time + 1): Type of initiation (FF)	1.57	0.74	610	2.11	0.035

Elapsed time was ln transformed. Identity of play dyad was included as a random effect. Total sample size: n = 739

Table 3 Results of post hoc comparisons between the odds of transitioning in FF-initiated play and non-FF-initiated play at every 0.5 value of ln-transformed elapsed time (i.e., ln(elapsed time + 1) = 0.5, 1.0, 1.5, 2.0, 2.5, and 3.0)

	Estimate	SE	t value	p value
FF vs. non-FF at ln(elapsed time + 1) = 0.5	− 4.06	1.79	− 2.27	0.024
FF vs. non-FF at ln(elapsed time + 1) = 1.0	− 3.27	1.44	− 2.28	0.023
FF vs. non-FF at ln(elapsed time + 1) = 1.5	− 2.48	1.10	− 2.26	0.024
FF vs. non-FF at ln(elapsed time + 1) = 2.0	− 1.70	0.79	− 2.14	0.033
FF vs. non-FF at ln(elapsed time + 1) = 2.5	− 0.91	0.57	− 1.59	0.112
FF vs. non-FF at ln(elapsed time + 1) = 3.0	− 0.13	0.55	− 0.23	0.818

For both types of play, we calculated the odds of transitioning from a symmetric attack to an L-player's attack relative to transitioning from a symmetric attack to an S-player's attack. We applied Bonferroni's post hoc comparison using ESTIMATE statement in the GLIMMIX procedure in SAS software

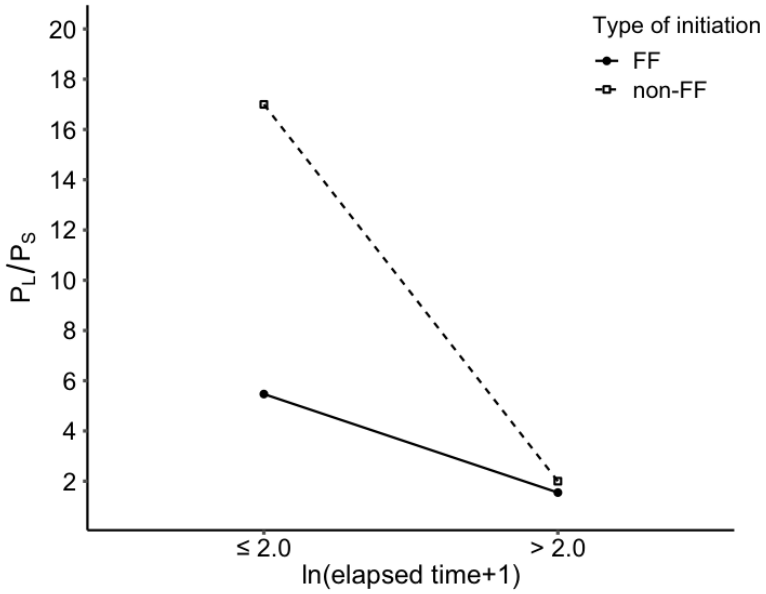


Fig. 3 The odds of transitioning from a symmetric attack to an L-player's attack relative to transitioning from a symmetric attack to an S-player's attack. PL and PS indicate the transition probability from a symmetric attack to an L-player's attack and from a symmetric attack to an S-player's attack, respectively. In this figure, the odds of the transition occurring in less than and greater than the 2.0 value of the ln-transformed elapsed time (i.e., ln(elapsed time + 1) = 2.0) are shown separately. The solid and dotted lines represent the odds of FF- and non-FF-initiated play, respectively

Discussion

Human daily interaction has a specific opening phase (Schegloff 1968; Pillet-Shore 2018). Human interactants' mutual gaze or face-to-face configuration in this opening phase has socio-cognitive functions to indicate the parties' social engagement and to manage the subsequent main-body phase of interaction successfully, at least in some WEIRD populations (Schegloff 1968; Cary 1978; Robinson 1998; Akhtar and Gernsbacher 2008). Our results indicate that this is not a trait that appears only in some human populations. A face-to-face opening phase in Japanese macaques' play fighting prolonged the subsequent main-body phase of play (Fig. 2a; Prediction 1 was supported). In the opening phase of human interaction, interactants display a positive and friendly stance toward their partner (Pillet-Shore 2018) and confirm the intimacy of the relationship (Goffman 1967; Schegloff 1968). In a parallel way, it is likely that animals engage in socio-cognitive work of assessing whether their partners are hostile or friendly to them

before the main-body phase of play begins. This kind of assessment may be indispensable for successfully managing a playful session for a long stretch of time because play fighting contains behavioral patterns that are also used in serious aggression (e.g., biting or grabbing) and can, therefore, be misleading. These observations raise the question of whether Japanese macaques do or do not intentionally make a face-to-face opening phase. To answer this question, it is necessary to examine whether Japanese macaques change their body positions and/or orientations to face each other immediately before a play session begins.

Our results indicate that facing toward playmates is itself a sign of interactants' engagement in play. Indeed, even an S-player was likely to gain an advantage in FF-initiated play compared with non-FF-initiated play (Fig. 3; Prediction 3 was supported). In contrast, in most cases of non-FF-initiated play, the initiator, who unidirectionally oriented his face toward the other individual when play began, was more likely than the other player, who had initially looked away, to maintain an advantage for a longer duration in a given session (Prediction 4 was supported). However, the rate of state transitions in a play session with a face-to-face opening phase was lower than that in a play session without one (Fig. 2b; Prediction 2 was not supported). This may have been because players in FF-initiated play attacked their partner for a longer duration than did players in non-FF-initiated play (Iki and Hasegawa, in preparation).

These results do not necessarily imply that players' attitudes toward play were fully determined before the main-body phase of play fighting began. In contrast, even in non-FF-initiated play, an S-player became gradually more aggressive and more likely to gain an advantage as time passed following the start of play (Fig. 3). As Špinka et al. (2016) suggested, interactants' engagement in play may be fragile at the very beginning of a play session. This may be the reason that an S-player in non-FF-initiated play was initially unengaged in play and that a symmetric attack performed immediately after play initiation was unlikely to transition to an S-player's attack. Moreover, a large body of literature has shown that players actively coordinate and promote their engagement during an ongoing main-body phase of play. Animals emit specific play signals (e.g., the play bow in canids: Bekoff 1995; the open mouth play face in primates: van Hooff 1967; the ultrasonic vocalization in rats: Kisko et al. 2015). These signals contribute to prolonging playful interaction (e.g., Waller and Dunbar 2005; Mancini et al. 2013), clarifying the meaning of subsequent aggressive but playful behavior (Bekoff 1975), and reducing the risk that play fighting will escalate into serious fighting (Palagi 2008). Interestingly, human laughter also has emotional and cognitive functions to encourage playmates to continue the playful interaction (Rothbart 1973) and to clarify the meaning of the preceding behavior (Vettin and Todt 2004). In general, an opening phase characterized by a face-to-face configuration may not always be sufficient to manage the subsequent interaction; therefore, interactants must coordinate and reinforce their engagement by exchanging communicative signals during the main-body phase.

Nevertheless, these findings should be interpreted with caution. As we focused on play interactions to examine the function of face-to-face opening phases in animals, we cannot exclude the possibility that such phases in other kinds of social interactions work differently from play interactions. However, there have been a number of previous descriptions suggesting that face-to-face configurations in primates serve as introductions to reconciliation (chimpanzees: De Waal and Yoshihara 1983) and copulation (bonobos, *Pan paniscus*: Savage and Bakeman 1978). Hence, it is expected that face-to-face opening phases have the same functions as suggested by the present study, at least in non-hostile and/or affiliative interactions engaged in by some

primates. In addition, given that the data in our study were based only on immature males aged 0–2 years, we cannot verify how sex and life stage may affect the function of face-to-face opening phases.

Although we did not focus on it in the present study, an opening phase can involve several specific play signals (e.g., laughter and/or smiles in humans: Smith and Boulton 1990; the play bow in canids: Bekoff 1977; visual and audible gestures in chimpanzees: Fröhlich et al. 2016). While some studies have reported that play signals are used to maintain a play session rather than to initiate one and that an opening phase is not always accompanied by play signals (geladas: Palagi and Mancini 2011; Tibetan macaques, *Macaca thibetana*: Wright et al. 2018), it is expected that players' behavior in subsequent interactions would be affected by whether face-to-face opening phases were characterized by play signals. Consistent with previous studies showing that play signals expressed in main-body phases prolong interactions and enhance players' active attitude toward play, we expected that players engaging in play sessions preceded by a face-to-face opening phase involving play faces or other play signals would play for longer and more vigorously than would players engaged in sessions not characterized by play signals. More detailed studies are needed to test this hypothesis.

In addition, although not examined in this study, it is expected that the influences of face-to-face opening phase on play fighting may be affected by social factors, such as social bonds, dominance relationships, and kinships between playmates. Indeed, several studies have suggested that there are relationships between face-to-face configurations and these social factors. For example, Emery (2000) suggested that some primates, including humans, use face-to-face configurations to strengthen the affiliative bond. In humans and non-human primates, dominance relationships are established in face-to-face encounters (i.e., a dominant individual's stare is followed by a submissive individual's gaze aversion) (Mazur and Booth 1998; Terburg et al. 2011). Specifically, given the great variety of social styles from despotic to egalitarian systems across the genus *Macaca* (Thierry 2000), comparison between despotic species (e.g., Japanese macaques) and egalitarian species (e.g., Tonkean macaques) in terms of the function of a face-to-face opening phase will be an interesting area of future research. With regard to kinships, baboons emit play faces toward kin more frequently than toward non-kin (Palagi and Mancini 2011). More detailed studies are needed to investigate the effects of social bonds, kinship, and dominance relations.

Previous studies have suggested that, as is the case in some human populations, face-to-face animal interactions may play a key role in developing social skills (Dettmer et al. 2016), enhancing mimicry and synchrony (Mancini et al. 2013; Yu and Tomonaga 2015), and promoting social affiliations (Nishida 1970; Sclafani et al. 2015). Moreover, the present work indicates that a face-to-face opening phase provides a platform with which both humans and Japanese macaques collaboratively initiate their interactions and successfully sequence subsequent interactions. Overall, our results imply that face-to-face opening phases have socio-cognitive functions to establish and sustain interactants' social engagement in the main-body phase that follows, not only in humans but also in Japanese macaques.

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Compliance with ethical standards

Conflict of interest The authors declare no conflicts of interest.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. We conducted this study in accordance with the guidelines of the Animal Experiment Committee of the University of Tokyo. This study was approved by the Animal Experiment Committee of the University of Tokyo (Permission number 28-3).

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