Animal Behavior and Cognition
ABC 2025, 12(3):300-329
DOI: https://doi.org/10.26451/abc.12.03.01.2025

Affective Responses and Behavioral Strategies to Social Fusion Events in Zoo-Housed Bonobos

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Citation – Laméris, D. W., Verspeek, J., Marina, S., Garcia-Co, C., Eens, M., & Stevens, J. M. G. (2025). Affective responses and behavioral strategies to social fusion events in zoo-housed bonobos. *Animal Behavior and Cognition, 12*(3), 300-329. https://doi.org/10.26451/abc.12.03.01.2025

Abstract – Species with fission-fusion dynamics may face heightened social tension during fusion events due to relationship insecurity and competition over resources. Affective consequences of such events are important determinants for behavioral responses, yet remain poorly understood. To evaluate the affective consequences of fusion events, we studied cognitive bias responses and changes in the behavior of zoo-housed bonobos following managed fission-fusion dynamics. Eight bonobos completed a response slowing task on touchscreens, in which individuals with negative affect show longer reaction times to targets when a mildly threatening stimulus is displayed. We tested the bonobos on days before, during, and after fusion events and simultaneously observed their behavior. Agonistic and socio-sexual behaviors increased during fusions. The bonobos also showed response slowing during trials with mildly threatening stimuli during fusion events, suggesting a shift towards negative affect. Response slowing effects were short and returned to baseline levels on days after the fusion events. Post hoc analyses furthermore showed arousal-related response speeding during control trials. Independent of testing condition, response slowing was negatively associated with socio-sexual behavior, and positively associated with social play behavior, highlighting affective correlates of these behaviors. Our findings provide insights into the affective responses to fusion events in bonobos, suggesting brief shifts towards negative affect. Nonetheless, changes in behavioral patterns, and cognitive correlates of affective states, presumably function to limit the escalation of conflict and facilitate successful fusions.

Keywords – Affect, Cognitive bias, Great ape, Sex, Social play, Touchscreen

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Species with fission-fusion dynamics are characterized by a social system in which individuals temporarily disperse into smaller subparties (fission) and later reunite to larger groups (fusion). This phenomenon is observed in a wide range of animals, including primates (Aureli et al., 2008), cetaceans (Parra et al., 2011), ungulates (Carter et al., 2013), bats (Patriquin et al., 2016), and birds (Silk et al., 2014), and enables reduced food competition (Ramos-Fernández et al., 2006) and optimized information exchange (Fishlock & Lee, 2013). However, the frequency and patterns of spatial and temporal separations in societies with high degrees of fission-fusion dynamics may also lead to uncertainty in social relationships upon fusion (Aureli & Schaffner, 2007; Barrett et al., 2003; East et al., 1993) and trigger competition over resources or conflicts over coordinated activities (Aureli et al., 2008). Members of fission-fusion societies must therefore adapt strategies to evaluate and re-establish relationships and resolve uncertainties to avoid escalation of social tension into conflict. This spans from elaborate displays during reunions in societies where fissions are less common, to more simple behaviors in societies with higher rates of fission events

(Aureli et al., 2008). In primates, for example, greeting behaviors have been observed upon fusions and are thought to reassure, appease or assess the partner when tension may arise (Okamoto et al., 2001; Schaffner & Aureli, 2005; Smuts & Watanabe, 1990).

Social interactions, including reunions, are accompanied by affective states (Aureli & Schaffner, 2002; Aureli & Whiten, 2003; de Waal, 2011), and affective experiences play a strong role in social group living by improving bonds, cooperation, and communication (de Waal, 2008; Špinka, 2012; Spoor & Kelly, 2004). Objectively assessing affective states in animals, however, is challenging as commonly used behavioral or physiological measures are species/individual/context-specific (Paul et al., 2005). Many of these indicators furthermore measure emotional arousal, but do not necessarily distinguish between emotional valence, i.e., whether the affective state is positive/pleasant/rewarding or negative/unpleasant/aversive (hereafter positive and negative, respectively). Cognitive biases, i.e., changes in cognitive processing modulated by underlying affective states, are a promising measure for changes in affective valence (Harding et al., 2004). Cognitive biases can be adaptive in that they promote memory storage and/or reconsolidation of relevant events (Cahill & McGaugh, 1998), flexible behavioral responses when met with risk or uncertainty (Bateson, 2016), or by promoting attention for relevant stimuli (Anderson, 2005; Pourtois et al., 2013; Schupp et al., 2003). Studying cognitive components of affective correlates during social events and behaviors is therefore a promising step in understanding the proximate mechanisms and motivations of social interactions.

Only few studies investigated the relationships between cognitive measures of affective states and social behaviors. Receiving more grooming, for example, is linked with heightened optimism-like states in tufted capuchins (*Sapajus* sp.) during a judgement bias task (Schino et al., 2016). In bottlenose dolphins (*Tursiops truncatus*) synchronous swimming, an important affiliative behavior, is associated with more optimistic judgements for ambiguous cues (Clegg et al., 2017). These studies focused on biases in decision-making during ambiguous situations, whereas attention bias is another class of cognitive biases which is especially relevant in social interactions. Attention, as a limited cognitive resource, selectively processes information which facilitates enhanced attention for relevant stimuli while ignoring irrelevant distractors (Compton, 2003). Affect-driven attention bias has been studied only in a few animal species using a limited number of paradigms (reviewed by Crump et al., 2018). Bethell et al. (2016) introduced a response-slowing paradigm to evaluate changes in social information processing that are modulated by affective states in rhesus macaques (*Macaca mulatta*). This paradigm is based on human psychological research on the freeze response. Whereas the freeze response is adaptive to threats (LeDoux, 2012), and facilitates processing of the threat through enhanced attention to the stimulus (Bradley, 2009), this response is typically altered in individuals with negative affect (Buss et al., 2004; Kalin et al., 1998). Individuals with negative affect exhibit subtle cognitive freezing in situations when presented with non-threat or ambiguous stimuli with potential threatening loading (Bar-Haim et al., 2007; Mogg & Bradley, 2016). While cognitive freezing in such non-threat or ambiguous events may be costly, as cognitive resources are allocated to stimuli that do not immediately require attention, it may also reflect the adaptive nature of affective states (except in psychopathological cases (Yiend, 2010)). If a negative affective state arises from previous negative experiences, adopting a more cautious attention scope may be beneficial to avoid further negative experiences (Faustino et al., 2015). The response-slowing paradigm, as introduced by Bethell et al. (2016), assesses shifts in affective responses towards negative valence. It accomplishes this by investigating the cognitive freeze response in individuals when confronted with mildly threatening, or ambiguous social cues, such as a direct gaze from unfamiliar individuals, in comparison to relatively neutral social cues, like an averted gaze. Depending on an individual's affective state, these ambiguous social cues can be interpreted as either negative or positive, where a negative interpretation typically results in a subtle cognitive freeze, quantified by delayed reaction times. This is referred to as ‘response slowing’. This paradigm has been applied in a number of non-human primate studies, identifying changes in affective states in response to husbandry and veterinary routines in captivity (Bethell et al., 2016; McGuire & Vonk, 2020) as well as external factors such as anthropogenic noises (Cronin et al., 2018). However, it has not yet been explored in the context of social interactions or events. Given that affect-driven attention biases play an integral role in shaping social interactions (Bethell et al., 2012; Yiend, 2010), and allow for behavioral flexibility (Aureli

& Whiten, 2003), furthering our understanding of the relationship between affect, attention and behavioral strategies in the context of social events is crucial to better understand animal behavior.

In the current study we investigated the behavioral and cognitive affective responses to social fusion events in a highly social primate species, the bonobo (*Pan paniscus*). In the wild, bonobos live in multi-male/multi-female communities of 10 to 63 individuals (Furuichi et al., 2008; Kano, 1992; Stevens, 2020) with a high degree of fission-fusion dynamics (Hohmann & Fruth, 2002). Aggregation patterns of bonobos are distinct, yet fluid, and vary considerably among bonobo populations and communities (Samuni et al., 2022). Rates of fission-fusion events differ among populations (Fruth, 1995; Furuichi, 1989; Hohmann & Fruth, 2002; Kano, 1992) making intra-community relationships highly flexible and complex in nature.

One study on the behavioral and physiological responses in female zoo-housed bonobos found that social fusions were relatively peaceful with little agonistic interactions, and increased levels of sexual solicitations (Moscovice et al., 2015). Socio-sexual behaviors, such as non-copulatory mounts and genital contact (de Waal, 1987), play an important role in regulating bonobo social dynamics, including reducing tension during feeding competition (Hohmann & Fruth, 2000; Paoli et al., 2007; Parish, 1994), reconciliation and consolation after conflict (Clay & De Waal, 2015; Hohmann & Fruth, 2000), and social bonding (Moscovice et al., 2019; Parish, 1994; Wrangham, 1993). While socio-sexual behavior has received most attention in bonobos, other behavioral mechanisms may also be important to regulate tensions associated with fusions. Social play has been suggested to be a mechanism for bonobos to reduce tension, and adult-adult play may be a mechanism to cope with tension and re-evaluate relationships also during fusion events (Palagi et al., 2006; Pellis & Iwaniuk, 2000). Grooming is an important mechanism among many primate species to (re-)establish social relationships (de Waal, 2000), including bonobos (Girard-Buttoz et al., 2020; Torfs et al., 2023). However, where chimpanzees might use short grooming bouts as greeting or appeasement mechanisms during encounters (Nakamura, 2003), this seems less frequent in bonobos (Kuroda, 1980), perhaps because bonobos form more stable groups with less fission-fusion events than chimpanzees (Sakamaki, 2013). In line with this, Moscovice et al. (2015) also found no increase in grooming during fusion events in zoo-housed female bonobos. While there is ample evidence that these previously mentioned behaviors may function to reduce social tension, it is currently unknown how these behaviors relate to cognitive correlates of affective states.

The first aim of this study was to compare behavior as coping mechanisms during intra-community fusion events. Based on theoretical and empirical evidence, suggesting that fusion events can create tension (Aureli et al., 2008; Aureli & Schaffner, 2007; Barrett et al., 2003; East et al., 1993), we had the following predictions. If fusion events present situations of increased social insecurity and tension, (1) we expected an increase in aggressive behaviors during fusions compared to baseline conditions. Additionally, by means of mitigating such social tension, (2) we expected to find an increase of socio-sexual behavior, (3) and an increase in play interactions compared to baseline condition, (4) but no changes in grooming activities.

The second aim was to evaluate changes in the cognitive components of affective states during fusion events, using touchscreen computers to test the response slowing paradigm (Bethell et al., 2016). If fusions induce social tension, (5) we predicted to find response slowing towards mildly threatening social stimuli (i.e., direct gaze stimuli) compared to neutral social stimuli (i.e., averted gaze stimuli) during fusions, which could indicate relative shifts towards negative affective states of the bonobos. We further (6) predicted to find differences in the responses between females and males as they take different positions within the social dynamics of bonobos (Stevens et al., 2007; Surbeck & Hohmann, 2013).

Our last aim was to investigate the correlations between the cognitive correlates of affective states and behavioral patterns during fusion events. If the behavioral changes under the first aim result from increases in social tension on days with fusion events, (7) we expected to find a positive association between aggressive behaviors and response slowing. Furthermore, if socio-sexual and play behaviors are coping mechanisms to reduce tension, (8) we expected to find a negative correlation between the response slowing effect and socio-sexual behavior during fusion days, but not during baseline days, and (9) similarly for social play behavior. Lastly, (10) we expected no clear correlation between grooming and response slowing.

Methods

Ethics Statement

All touchscreen training and testing sessions were conducted using positive reinforcement training and conform to the guidelines of the Ex-situ Program (EEP), formulated by the European Association of Zoos and Aquaria (EAZA), and complied with the ASAB guidelines (ASAB, 2020). Participation in these sessions by the bonobos was completely voluntary, and the bonobos were never separated from group members for the purpose of this study. This study was furthermore approved by the Ethics Committee of the Royal Zoological Society of Antwerp (EC-2/SGZ(10-12-19)) and conformed to the American Society of Primatologists Principles for the Ethical Treatment of Non-Human Primates.

Subjects and Housing Conditions

Eight bonobos (three females and five males; mean age = 15.8 years, range = 7-27 years), at Zoo Planckendael (Belgium) participated in the current study (Table 1). The bonobos were housed in an indoor enclosure (total area: 422 m^2) consisting of ten enclosures of which four main enclosures were visible for zoo visitors and six off-exhibit enclosures. When temperatures allowed (>13° C), the bonobos had access to an outdoor enclosure (3000 m^2). Fresh vegetables, fruits, browse, and primate chow was provided four times per day and the bonobos had access to water *ad libitum*.

The full bonobo group in Zoo Planckendael consisted of 20 individuals (13 females and 7 males) of varying ages (range: 0 – 43 years) and was managed in two subgroups. All individuals had been housed together prior to the study. The two subgroups could not physically interact with each other, but had limited visual contact in some parts of the building and could vocally communicate. The EAZA Best Practice Guidelines recommend simulated fission-fusion dynamics to mimic natural patterns and facilitate the maintenance of social relationships between subgroup members (Stevens, 2020). In practice, this means that typically one or multiple family units (i.e., females with their dependent offspring or independent sons) were transferred between the subgroups. Between February and July 2021, seven managed fission-fusion events took place (average = 1.4 per month, range = 1-2 per month) (Figure ESM1). These transfers were furthermore informed by the breeding program, based on within-subgroup tension, or to facilitate the maintenance of social relationships. As such, fusion events were not always predictable nor were they done following a systematic schedule. Changes in the group compositions were made in the morning after which we tested the bonobos. Due to time constraints, we only focused on the individuals who completed training for the touchscreen task, and who were directly or indirectly involved in transfers between groups. Here, we made a distinction between individuals who transferred (i.e., transferees) between groups, and individuals in the group to which other bonobos transferred (i.e., residents).

Considering the STRANGE framework for animal research (Webster & Rutz, 2020), the Zoo Planckendael group is relatively large compared to other captive groups in zoos (Stevens, 2020), but on the smaller end compared to wild bonobo groups, yet still within the natural range (Furuichi & Thompson, 2008; Kano, 1992). Group composition mimics that of their wild counterparts with a multi-male/multi-female structure and individuals of all age classes. All individuals participating in the touchscreen sessions were captive-born and mother-raised in social groups. Four individuals had previous experience working on touchscreens with limited exposure to social stimuli (Laméris, Verspeek, Eens, et al., 2022; Laméris, Verspeek, Salas, et al., 2022).

Table 1

Subject Information

Subject	Sex	Age	Parents	Previous touchscreen experience	Number of times transferred
Busira	Female	16.9	Birogu x Eja	Yes	2
Habari	Male	15.0	Vifijo x Djanoa	Yes	1
Kianga	Female	15.5	Diwani x Kombote	No	4
Kikongo	Male	6.9	Bolombo x Hortense	No	1
Mokonzi	Male	7.9	Luo x Banya	Yes	0
Nayembi	Female	14.8	Mobikisi x Liboso	No	3
Vifijo	Male	26.5	Kidogo II x Hortense	No	1
Zamba	Male	22.8	Kidogo II x Hortense	Yes	1

Behavioral Observations

An integrated camera system continuously recorded, and saved, footage of the bonobos. The four main enclosures were each permanently equipped with two cameras located in the top corners of the enclosure. The remaining six off-sight enclosures were each equipped with a single camera in a similar fashion. Using recordings from these cameras, we coded the behavior of the participating animals on days of cognitive testing. Behavioral coding was performed by one researcher (CG-C) after extensive training on our ethogram and reaching sufficient inter-rater reliability (κ = .78). By means of 30 min continuous focal sampling (Altmann, 1974), we recorded all agonistic, socio-sexual and affiliative interactions given or received by the focal using a standardized ethogram (Stevens et al., 2023) in The Observer (Noldus version XT 10, the Netherlands). Timing of the behavioral observations was determined by the onset of the fusion events, and were completed before cognitive testing commenced. Observations during the post-fusion started at matched times to those of the fusion condition. To avoid that pre-fusion observations overlapped with husbandry procedures (e.g., cleaning or feeding), these observations started during the average starting times of the fusion and post-fusion condition observations.

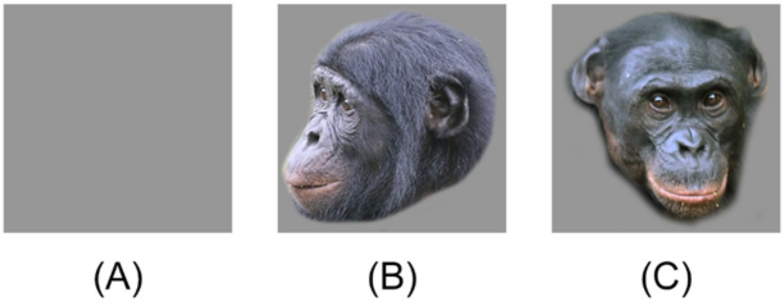
Touchscreen Setup

Touchscreen sessions were conducted on a 22’’ Viewsonic TD2220 touch-sensitive monitor (1920 x 1080 resolution). The researcher (DWL) controlled the sessions on a computer connected to the touchscreen and a second monitor enabled the researcher to view the subject’s responses in real-time. The touchscreen setup was mounted on an adjustable cart, placed outside one of the six off-exhibit enclosures. The touchscreen was placed parallel to the enclosure mesh, allowing the bonobos to work on the touchscreen through the mesh. Training and testing tasks were designed using *OpenSesame* (Mathôt et al., 2012).

Training and control stimuli consisted of grey rectangular frames (RGB 151, 151, 151) measuring 254 mm x 254 mm. Social content for the stimulus either comprised images of a profile view face picture with a neutral expression (i.e., an averted gaze), or a frontal face picture with a neutral expression (i.e., a direct gaze), see Figure 1. Here, the averted stimulus serves as a social control, whereas the direct stimulus serves as a mildly threatening stimulus. Stimuli collected from a personal photo library (JMGS) and only included images of adult bonobos who were unknown to the participants of this study. We collected a total of 26 direct and 26 averted gaze pictures and trimmed these images so that only the bonobo’s face was visible. These were then superimposed on the grey rectangular frame, and checked for luminosity and contrast values (Table ESM2). Stimulus preparation was done in Adobe Photoshop version 21.2.2.

Figure 1

Examples of (A) Control, (B) Averted, and (C) Direct Stimuli

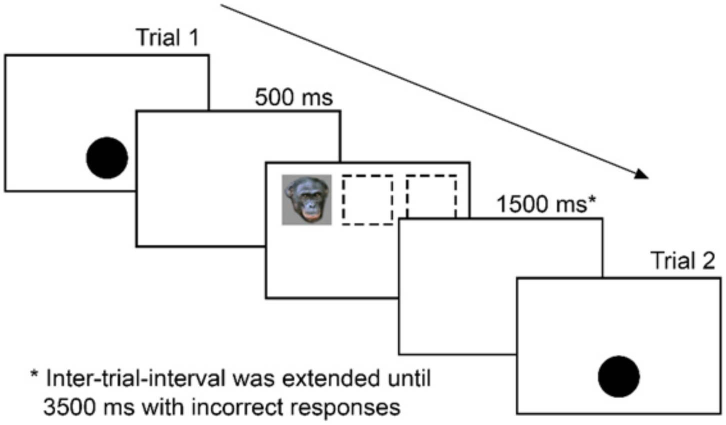


Procedure

We trained the bonobos on the response-slowing task between December 2020 and February 2021. Four of the bonobos had previous experience working on a touchscreen (Laméris, Verspeek, Eens, et al., 2022), and the remaining four bonobos were first trained to touch a small target when it appeared on the screen. Participation in these touchscreen sessions were conducted in social groups between 12:00 and 15:00, four to five times per week. Training and testing sessions were always voluntary, meaning that individuals were not separated from group members for this study. We invited the individuals by calling their name when they were not involved in social interactions, and participants were previously trained to complete touchscreen sessions individually. Sessions were paused if other bonobos distracted the subject. The bonobos who participate in touchscreen sessions are accustomed to gestures by the researcher (DWL) that signal to the animal that their session was finished, facilitating the transition to testing another individual.

Figure 2

Trial Outline of the Response-Slowing Paradigm



Note. The dashed squares indicate the other possible target locations

We employed the response-slowing task, designed by Bethell et al. (2016), but made a slight adaptation by including an initiation button (Figure 2). This was done to ensure that the bonobos were attending to the screen. On each trial, bonobos were presented with an initiation button, which was located at the lower center of the screen. Once this initiation button was touched, a 500 ms delay followed, after which the stimulus became visible at one of three locations (upper left, center or right). The stimulus remained on the screen until the bonobo touched it. Each response was followed by a 1500 ms inter-trial interval (ITI). In case the bonobo made an incorrect response (i.e., the bonobos did not accurately touch the target), no reinforcement was provided, and the trial was followed by an extended ITI of 3500 ms in total. The apes were rewarded on correct responses with automatic delivery of a DK Zoological Trainings Biscuit (small) triggered by a custom-made pellet dispenser. A secondary reinforcing tone was played via two speakers behind the touchscreen. Primary and secondary reinforcers were delivered with every correct response (i.e., a 100% fixed reinforcement ratio). Additionally, we manually provided a raisin through a PVC tube on every fifth correct response to maintain the bonobo's interest. If an individual finished all trials within a session, the animal received three peanuts.

During the training phase, the stimuli consisted solely of the grey squares. During test sessions, the trial types included a control stimulus (grey square), averted gaze stimulus, or direct gaze stimulus. Each session consisted of 33 trials and started with 3 practice trials in which the control stimuli were presented once at each of the three locations. Then, the bonobos were presented with 30 test trials: 12 averted gaze trials, 12 direct gaze trials and 6 control trials. The order of the trial type was randomized and the location of the target was counterbalanced. We made ten different versions to avoid order-effects.

We tested the bonobos on the response-slowing paradigm during three conditions: a pre-fusion condition; during days with fusion events; and a post-fusion condition. Pre-fusion cognitive data were collected during periods when the group composition remained stable for at least three weeks and collection was completed once an individual finished 10 sessions. For the majority of the subjects, this took place between January and February 2021, and subjects completed this between two and eight days. For two additional subjects we completed the pre-fusion data collection in March and July 2021. Preferably, we collected pre-fusion data on the day prior to fission-fusion events but it was not always predictable which individuals would switch between subgroups, neither was the day of this event. Fusion cognitive data were collected on days during which group composition changed, within two hours after the fusion event to allow the bonobos to interact with each other. Post-fusion data were collected on the subsequent day after the fusion events at matched times. On days with fusion events, and post-fusion days, each bonobo was limited to two sessions in order to collect cognitive data from all involved subjects.

We video recorded all of the test sessions using a Canon Legria HF R88. These recordings were later coded to exclude invalid trials e.g., when a bonobo other than the subject touched the screen, the participant did not attend the screen, the screen did not immediately register the response, or the participant missed the target. Such trials represent erroneous data or do not reflect 'true' reaction times and should therefore be excluded.

Statistical Analyses

All analyses were done in RStudio version 1.3.1073 (R Core Team, 2020). For the behavioral analyses, we created six behavioral variables (Table 2). We calculated frequencies as events per minute for the different behavioral variables for each 30 min observation point while correcting for time spent out of sight. We then tested the difference in frequency for each variable among the conditions, using generalized linear mixed models with a negative binomial distribution, using the package '*glmmTMB*' (Brooks et al., 2017). Behavioral events were included as dependent variable and observation time as offset. Condition was included as independent variable and subject ID as random intercept.

Table 2

List of Behavioral Variables and Included Behaviors

Behavioral Variables	Individual Behaviors
Grooming given	Grooming given
Grooming received	Grooming received
Social play	Calm and rough social play
Socio-sexual	Copulation, non-copulatory mount
Aggression given	Long/short charge given, aggressive intention given, directed display given
Agonistic response	Long/short charge received, aggressive intention received, directed display received, flee, flinch, displace, grin

Prior to the analyses of the cognitive testing, we removed invalid trials resulting in the removal of 1769 trials out of 6306 collected in total. We furthermore filtered our data on reaction times < 250 ms, as they likely represent anticipatory responses (Whelan, 2008) and detected slow reaction times, which might reflect low motivation or distraction, based on 2.5 standard deviations from the individual's mean (Berger & Kiefer, 2021), while controlling for target location and subject. This removed an additional 106 trials. Given that human studies typically find that high arousal, negative affective states result in a combination of arousal-related response speeding across conditions (Aston-Jones & Cohen, 2005; Fox et al., 2001), and valence-related response slowing for mildly threatening stimuli (Bar-Haim et al., 2007; Mogg & Bradley, 2016), we followed the human literature and calculated arousal-controlled response ratio scores (Bradley et al., 1998; Ly et al., 2014; McKenna & Sharma, 2004). This was done by dividing the mean of direct/averted trials by the mean of the control trials per testing day for each individual, while controlling for target location. Values greater than 1 reveal slowing of responses relative to the control trials, whereas values lower than 1 reveal response speeding. Hence, the response ratio scores represent an arousal-controlled measure for response slowing while simultaneously controlling for inter-individual variation in reaction times.

We fitted linear mixed models to examine the response ratio scores for direct and averted trials. The initial model included the predictors stimulus type (levels: averted, direct), condition (levels: pre-fusion, fusion, post-fusion), sex (levels: female, male) and a three-way interaction, and we included target location (levels: left, central, right) as a control variable. The model included a random intercept for subject ID with a random slope for condition and a random intercept for stimulus ID. Post-hoc analyses were performed using the *emmeans* package (Lenth, 2023) using a Tukey correction for multiple comparisons.

We used a linear mixed model using the package '*lme4'* (Bates et al., 2015) to analyze how behavioral variables, along with their interaction with condition, are associated with daily response ratio scores for direct stimuli in the response slowing task. We included a control variable for target location and a random intercept for subject ID.

Additionally, we post-hoc tested the absolute reaction time data to check whether response speeding, typical for stress-related arousal, occurred. As such, we fitted a generalized linear mixed model with a Gamma distribution and log link function to assess whether the absolute reaction times of the bonobos were influenced by stimulus type and depending on the condition. Fixed factors included an interaction term between stimulus type (levels: control, averted, direct), condition (levels: pre-fusion, fusion, post-fusion), and a control variable for target location (levels: left, central, right). Our model included a random intercept for subject ID with a random slope for condition and a random intercept for stimulus ID. Post-hoc analyses were performed using the *multcomp* package (Hothorn et al., 2008) using a Tukey correction for multiple comparisons.

We selected our models by comparing our full models to null models based on the Chi-square test. If models with higher-order interactions were not significantly better than the null model, we examined lower-order interactions by comparing their model fit to the null model. Diagnostic plots (residuals vs fitted and QQ plots) were used to examine assumptions of normality and homogeneity of variances and we additionally tested uniformity and dispersion of the residuals using the *DHARMa* package (Hartig, 2020).

Results

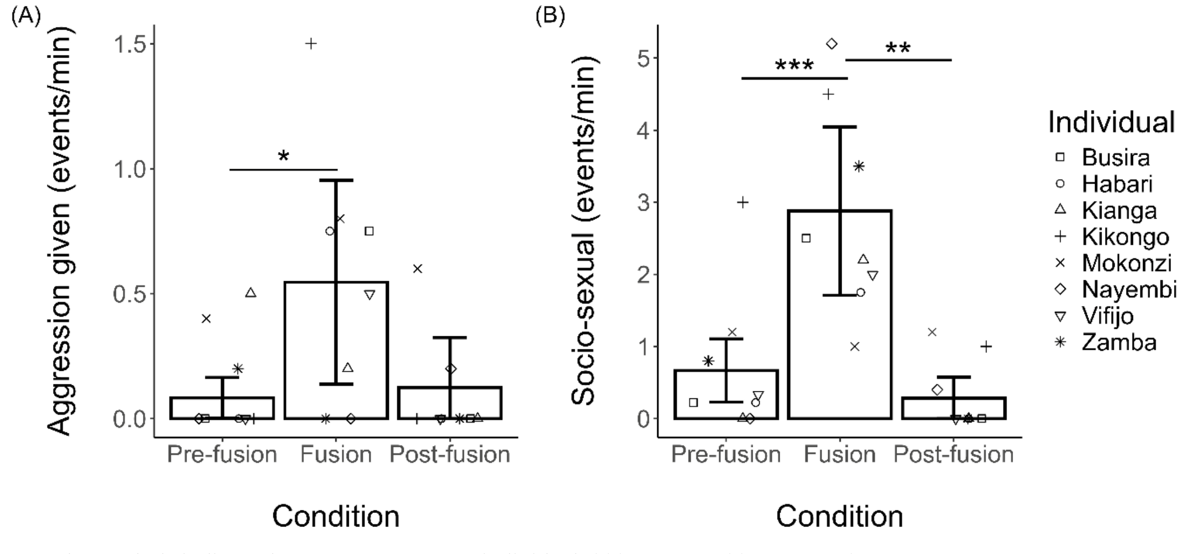
Between February and July 2021, seven fission-fusion events occurred, of which six were followed-up with cognitive testing (Table ESM3, Figure ESM1). Behavioral data were collected across 33 days. Between the eight participating bonobos, this resulted in 113 datapoints in total, of which 48 in the pre-fusion condition, 33 in the fusion condition, and 33 in the post-fusion condition. Subgroups consisted of a mean of 10 individuals (SD = 1.63) and social units that transferred between subgroups typically consisted of 3-4 (M = 3.6, SD = 1.44) transferees. The eight bonobos participating in this study completed a combined total of 4429 trials that were included in the analysis (range: 296-738 trials per individual), of which 1635 trials during the pre-fusion condition (range: 154-258 trials per individual), 1177 trials during the fusion condition (range: 44-245 trials per individual), and 1228 trials during the post-fusion condition (range: 35-235 trials per individual).

Behavioral Patterns Across Conditions

We tested for differences in the six behavioral variables of interest among the three testing conditions. Full-null model comparisons revealed that including condition as a fixed effect improved the model fit for aggression given $\chi^2(2) = 6.965$, $p = .031$ and socio-sexual behavior $\chi^2(2) = 24.131$, $p < .001$ (Table ESM4) The frequencies of aggression given (Figure 3A; $\chi^2(2) = 6.826$, $p = .033$) and socio-sexual behavior (Figure 3B; $\chi^2(2) = 20.327$, $p < .001$) differed between conditions (Table ESM5). Namely, aggression given was more frequent during the fusion condition compared to the pre-fusion (ratio = 5.670, $z = 2.434$, $p = .039$), but not compared to the post-fusion condition (ratio = 3.650, $z = 1.707$, $p = .203$). Socio-sexual behavior was also more frequent during the fusion condition compared to the pre-fusion (ratio = 2.539, $z = 3.023$, $p = .007$) and post-fusion (ratio = 8.208, $z = 3.934$, $p < .001$). The full models testing the other behavioral variables (grooming given/received, social play and agonistic response) did not show a better fit than the null models (Table ESM4).

Figure 3

Average Rates (Events/Minute) (± 95% Confidence Intervals) gor (A) Aggression Given, (B) Socio-Sexual Behavior in the Three Testing Conditions



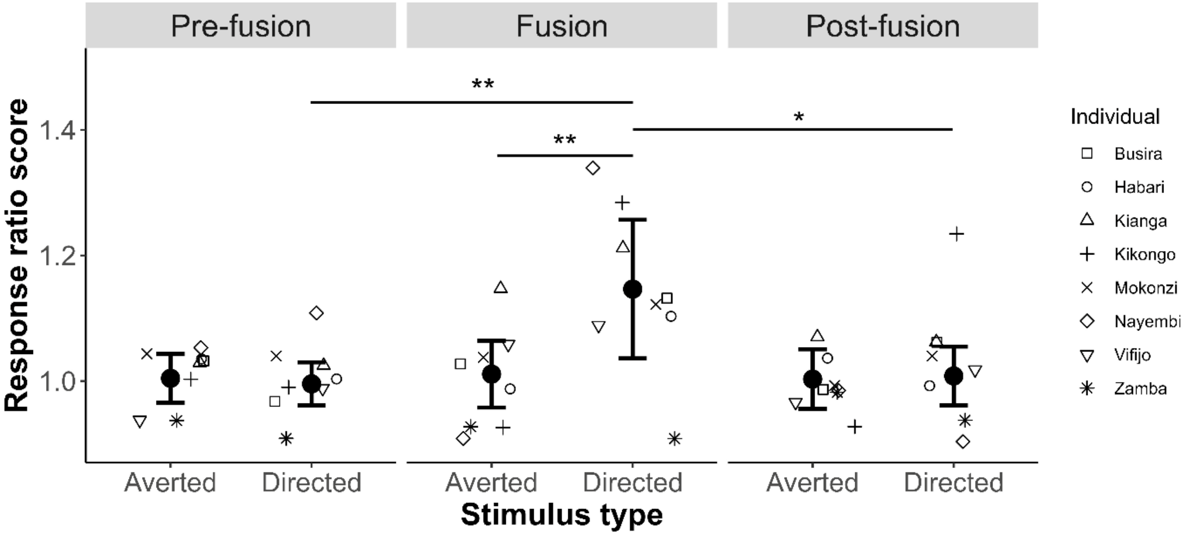
Note. The symbols indicate the average scores per individual. *** $p < .001$, ** $p < .010$, * $p < .05$.

Response Slowing

Based on the analyses of the response ratio scores, the model including the three-way interaction between stimulus type, condition, and sex significantly reduced the model fit ($\chi^2(11) = 20.112$, $p = .044$). The updated model with the underlying two-way interactions did improve the model fit ($\chi^2(9) = 18.953$, $p = .026$). This model revealed a significant interaction between condition and stimulus type (Figure 4; $\chi^2 = 7.035$, df = 2, $p = .029$). Pairwise comparison, using condition as contrast, indicated that the bonobos showed longer response latencies for direct trials compared to averted trials during the fusion condition ($t_{559} = 3.162$, $p = .002$), but not during the pre-fusion ($t_{559} = -0.150$, $p = .881$) or post-fusion condition ($t_{562} = 0.145$, $p = .885$). Between conditions, the bonobos also took longer to respond in direct trials during the fusion condition compared to the pre-fusion ($t_{19.6} = 3.330$, $p = .009$) and post-fusion condition ($t_{17.7} = 3.231$, $p = .012$). Responses for the averted trials did not differ between conditions (all $p > .05$, see Table ESM6).

Figure 4

Average Response Ratio Scores (± 95% Confidence Intervals) for the Different Stimulus Types Depending on Testing Conditions



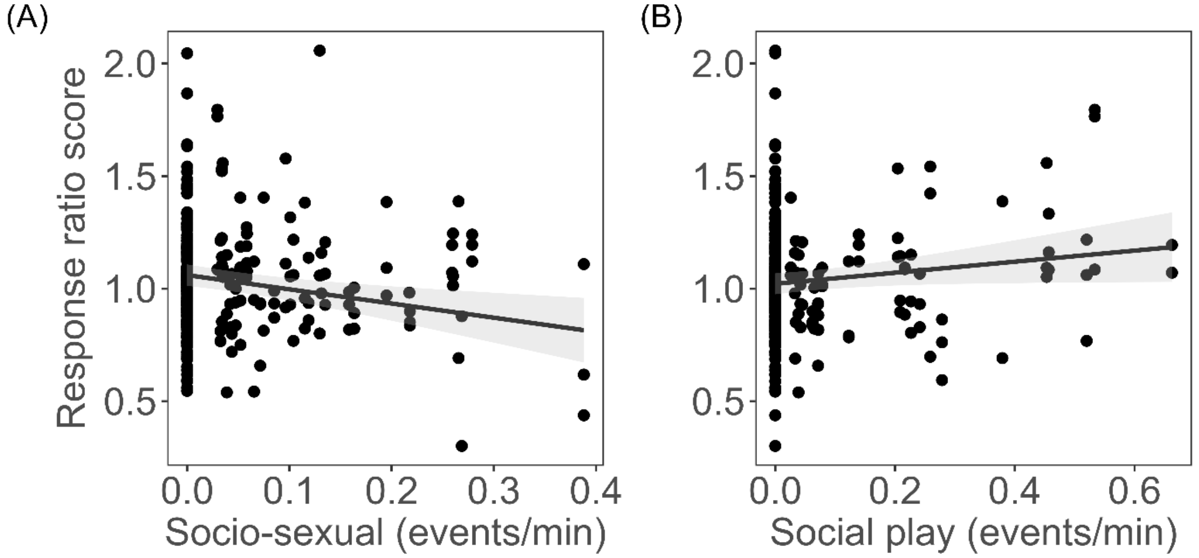
Note. The symbols indicate the average scores per individual bonobo. $^{**}p < .010$, $^{*}p < .050$.

Behavioral Associations with Response Slowing

We found no interaction effects between condition and any of the behavioral variables on response slowing. However, we did find that daily response ratio scores for direct stimuli were significantly correlated with frequencies of socio-sexual behavior (Figure 5A; $\chi^2 = 9.880$, df = 1, $p = .002$) and social play behavior (Figure 5B; $\chi^2 = 3.93$, df = 1, $p = .047$). On days when bonobos engaged more in socio-sexual interactions, they showed lower ratio scores ($\beta = -0.630$, SE = 0.201, $p = .002$). Contrary, when bonobos engaged more frequently in social play interactions, they had higher ratio scores on those days ($\beta = 0.246$, SE = 0.124, $p = .049$). Other behavioral measures were not significantly correlated with the ratio scores (see Table ESM7).

Figure 5

Daily Ratio Scores for Direct Trials, Controlled for Stimulus Location, as Function of (A) Socio Sexual Rates, and (B) Play Rates



Note. Ratio scores greater than one indicate response slowing.

Post-hoc Test: Arousal Related Response Speeding

The model including the two-way interactions significantly improved the model fit ($\chi^2(15)$ = 54.821, $p < .001$) and revealed a significant interaction effect between condition and stimulus type ($\chi^2(4)$ = 14.294, $p = .006$, Figure ESM2). Pairwise comparison, using stimulus type as contrast, revealed that reaction times for control trials were faster during fusion days compared to pre-fusion days ($z = -2.956$, $p = 0.020$) and to the post-fusion days ($z = -2.380$, $p = .046$). The bonobos were also faster to touch the averted gaze trials during fusion days compared to pre-fusion days ($z = -3.504$, $p = .001$), but not compared to post-fusion days ($z = -2.111$, $p = .088$). Additionally, using condition as contrast, pairwise comparison indicated that response times were slower on fusion days during trials showing directed gaze stimuli compared to control trials ($z = 3.534$, $p = .001$), and to averted gaze trials ($z = 3.709$, $p < .001$). Reaction times did not differ among stimulus types during pre- and post-fusion days (all $p > .050$, see Table ESM8).

Discussion

This study aimed to evaluate changes in the behavioral and cognitive components of affective states in zoo-housed bonobos in response to managed social fusion events. We found that both agonistic and socio-sexual behavior increased during fusions, but not grooming or social play. On days with fusions, the bonobos showed a response slowing effect for direct gaze stimuli compared to averted gaze stimuli, suggesting a shift towards more negative affect. On days after these events, this response slowing effect was no longer present, indicating that the effect was short lasting. Response slowing was negatively associated with socio-sexual behavior, and positively associated with social play behavior.

Following the prediction that fusion events can induce social tension, we indeed observed that aggression was more frequent during fusions than during pre-fusion days. The observed increase in aggression and socio-sexual behavior is similar to that reported in a previous study with female bonobos (Moscovice et al., 2015). The lack of an increase in grooming may be due to the less specialized function of grooming during encounters in bonobos compared to chimpanzees (Nakamura, 2003; Sakamaki, 2013). The increase in socio-sexual behavior appears to fit the hypothesized function that this behavior reduces social tension in bonobos (de Waal, 1987, 1990; Furuichi, 1989; Hohmann & Fruth, 2000). The simultaneous increase in aggressive behaviors could alternatively suggest that (part of) the increase in socio-sexual interactions were a response to the aggression, and functioned to facilitate reconciliation (Clay & De Waal, 2015). We additionally observed that the increase in socio-sexual behaviors returned to pre-fusion levels the day after the fusion event, while rates of aggression given retained similar levels to days with fusion events. Socio-sexual behavior is typically a short-term conflict resolution in bonobos (Hohmann & Fruth, 2000), whereas aggression may reflect the settling of new dominance patterns which spans over longer periods (Vervaecke et al., 2000).

Our results from the response-slowing task revealed changes in cognitive processing linked to negative affect, regardless of the bonobos' sex. These findings align with previous studies showing response slowing during stressful events (Bethell et al., 2016; Cronin et al., 2018). Notably, while response slowing occurred in the fusion condition with ambiguous stimuli, post-hoc analyses also revealed response speeding for control and non-threatening social control trials. This response speeding, often associated with stress-related arousal (Aston-Jones & Cohen, 2005; Fox et al., 2001), was similarly reported by Bethell et al. (2016). Using response ratio scores helped isolate individual arousal effects, indicating that the response slowing during fusion events more likely reflects a shift in affective valence. Importantly, the absence of response speeding for direct gaze stimuli in the fusion condition suggests arousal alone cannot explain the effects. Additionally, the lack of arousal-controlled response slowing in pre- and post-fusion conditions points to the fusion condition as the cause of the observed response slowing. Nonetheless, the observed response speeding for control trials should be acknowledged and is necessary to fully understand changes in both valence and arousal. Together, these findings suggest that the within-condition response slowing for mildly threatening stimuli reflects changes in valence, while the between-condition response speeding for control trials indicates arousal. Finally, the return to baseline cognitive performance in the post-fusion condition indicates that these effects were short-term.

While previous studies have linked affiliative behaviors to heightened positive affect in bottlenose dolphins (Clegg et al., 2017) and tufted capuchins (Schino et al., 2016), the affective correlates to socio-sexual behaviors have not yet been studied and our results can likely be explained by bonobo socio-ecology. Supporting our predictions regarding potential affective correlates of behavioral patterns, we found that heightened rates of socio-sexual behavior were associated with reduced negative affect. This suggests that affective correlates of socio-sexual behavior are general across these contexts, and could hint at a common stress-alleviating effect. While many studies suggest that socio-sexual behavior is used to alleviate social tension in bonobos, no previous studies actually report on possible cognitive correlates of this behavior. Other studies examining physiological associations with socio-sexual behaviors found inconclusive relationships. Cortisol, both salivary and urinary levels, were not linked to the frequency of socio-sexual interactions (Hohmann et al., 2009; Moscovice et al., 2015), whereas a positive link has been found between bonobo female same-sex interactions and urinary oxytocin (Moscovice et al., 2019), a neuropeptide that is thought to, amongst other things, play an anxiolytic role in the stress response in social contexts (Kumsta & Heinrichs, 2013). However, how peripheral levels of oxytocin approximate central levels is currently debated (Crockford et al., 2014; Valstad et al., 2017) which limits further extrapolations to our findings.

While frequencies of play did not differ significantly between fusion days and baselines, we did find that social play behavior showed a positive association with response slowing, independent of the testing condition. This contradicts our prediction where we expected to find a negative relation between play and response slowing. Play is often linked with positive affective states (Boissy et al., 2007; Held & Špinka, 2011), for which most compelling evidence exists that sub-optimal conditions, that are thought to cause negative affect, suppress play (Oliveira et al., 2010) and some studies have reported links between situations associated with positive affect and increases in play (Ahloy-Dallaire et al., 2018). However, the relationship between play and affect is not as straightforward as proposed, and may depend on the species, sub-type of play and age (Ahloy-Dallaire et al., 2018; Marley et al., 2022; Palagi, 2023). For example, play behavior in adult animals has been suggested to have an affiliative function to promote social bonds (Enomoto, 1990; Palagi & Paoli, 2007), or to reduce tension during food competition (Asensio et al., 2022; Norscia & Palagi, 2011; Palagi et al., 2006; Yamanashi et al., 2018), social insecurity (Antonacci et al., 2010) or social crowding (Crast et al., 2015; Tacconi & Palagi, 2009), and therefore facilitate social tolerance (Palagi, 2023). Others have suggested that play behavior can occur as displacement during stressful events (Kortmulder, 1998) or function as a coping mechanisms after stressful events (Francesconi et al., 2024; Hausberger et al., 2012).

Adult social play has a prominent role in some species to regulate tension and social assessment tool, especially in species with a high degree of fission-fusion dynamics like bonobos (Pellis & Iwaniuk, 2000), and may fulfil a role similar to socio-sexual behavior in mitigating social tension. Interestingly, we found an opposite association between affect with play and socio-sexual behavior, which suggests different affective correlates. One major disparity, which could potentially explain differences in the affective correlates reported in this study, is that play as means of tension regulation or social assessment can also include competitive components (Palagi, 2006; Rooney et al., 2000). Successful playful interactions involve a balance between cooperative and competitive components (e.g., play fighting) and different variations of play are likely to have different affective correlates. Specific communicative signals can indicate benign intent and maintain a playful nature of the interaction (Demuru et al., 2015), whereas other playful interactions may escalate into aggression (Palagi et al., 2016). While we did not observe play escalation, more fine-grained behavioral coding would be needed to identify additional markers of the positive nature of the play sessions. Additionally, while we coded calm play separately from rough play, we pooled these behaviors for analysis for statistical reasons. Many theories have been proposed to explain the function of play, and depending on different variables, the affective experience of such interactions may either be positive or negative (Cordoni & Norscia, 2024). Importantly, for the behavioral associations with the response slowing effect, we cannot disentangle correlation from causation. Hence, it is at this point unclear if the changes in affective states were a result of the behavioral patterns, or vice versa. The correlations between our cognitive and behavioral measures were an attempt to better understand the affective correlates during such social interactions, but the results suggest that this relationship may be more ambiguous than previously thought, and further research across different contexts is needed to better understand the affective consequences of social interactions.

We encountered several (potential) limitations. First, it is currently unclear how bonobos interpret a direct gaze in others. It has been described that bonobos use a direct stare, in combination with other facial actions such as a tense mouth, in aggressive or competitive contexts (de Waal, 1988). Bonobos additionally pay relatively more attention to the eye region compared to chimpanzees (Kano et al., 2015; Mulholland et al., 2020), although the underlying motivational systems are unclear. Hence, although it remains unclear whether a direct gaze is interpreted as mildly threatening by bonobos, our results suggest that it becomes a more salient social cue during social tension. We visually selected our stimuli in this study for neutrality, but, ideally, we should have coded our stimuli using the Facial Action Coding System (FACS) to rule out the presence of other facial cues. However, at the time of this study there was no bonobo-specific FACS fully developed (but see Gaspar (1999, 2006)). Nonetheless, if a direct gaze would alter attentional processing we would expect to find a difference in reaction times for the stimuli in baseline conditions, for which we found no evidence.

Only during the fusion events did we observe changes in attentional processing of the direct gaze, suggesting that the stimuli of the response slowing paradigm are suitable to detect changes in the bonobos' attentional processing mediated by potential affective events. Second, as the participation of the bonobos in the touchscreen sessions was completely voluntary, we could not control whether individuals chose to join or not. It is therefore possible that individuals with certain personality traits, which may influence both their willingness to participate (Herrelko et al., 2012) and their responses to the fusion events, were under- or overrepresented, potentially biasing our results. Third, we should acknowledge the temporal discrepancy between our behavioral and cognitive data. We aimed to collect the cognitive data as soon as possible after the fusion events, without disrupting the social interactions of the bonobos, which was typically within two hours after fusions. Yet, our behavioral data was collected within the first 30 minutes after fusion events. Hence, it is possible that in the meantime other events occurred that could have influenced the cognitive data. Fourth, whereas wild bonobos initiate and coordinate social fusion events (Schamberg et al., 2016), in our study zoo staff decided which social units changed between the subgroups. Objective criteria exist to decide who transfers between subgroups (Stevens, 2020), but ultimately this decision remains partly based on subjective factors. Generalizations of results from captive studies to wild populations should therefore be made with care. Additionally, it is likely that individual variables of our participating bonobos, such as inter-individual relations, ontogeny or affective styles, shaped their affective experiences, which draws further caution against generalizations and requires further investigation. Hence, although we report on one specific group of bonobos, the results from the current study provide a unique perspective on the affective consequences of fusion events and behavioral correlates in bonobos.

Finally, our results can have implications for animal welfare and the management of bonobos under human care. Although we found evidence that fusion events were associated with shifts towards negative affect, these were only temporary. An increase in aggression was observed, but limited to mild, non-contact aggression, and the increase in socio-sexual behavior might suggest that the bonobos were able to mitigate the social tension (Moscovice et al., 2015). If zoo-housed bonobo groups are not able to naturally fission and fusion, mimicking natural fission-fusion dynamics is advised for managed populations (Stevens, 2020) and can benefit the bonobos' social dynamics (Classen et al., 2016). The impact on the welfare of the bonobos of the social tension associated with fusion events would be limited if the bonobos are able to cope adaptively with the situation (Englund & Cronin, 2023). In the current study, this appeared to be the case, but requires case-by-case evaluation.

Conclusion

We observed temporary shifts towards negative affective states in the bonobos during social fusions. During fusion events the bonobos showed increased rates of mild aggressive and socio-sexual behavior. The lack of severe contact aggression could indicate a role of socio-sexual behavior in mitigating this tension. Additionally, the negative association between socio-sexual behavior and cognitive response slowing could further hint at tension reducing mechanisms. The positive association between response slowing and adult-adult social play, however, raises questions about the affective experience of such playful interactions. However, it is important to note that our study does not investigate the causal relationship between these behaviors and affective states, but we demonstrate that socio-sexual behavior and social play either induced certain affective states in the bonobos, and/or were induced by them. Further research will enhance our understanding of the affective consequences of social events and the mechanisms and motivations of behavioral strategies.

Author Contributions: Conceptualization: D.W.L. and J.M.G.S.; Methodology: D.W.L., M.E., J.M.G.S.; Formal analysis: D.W.L. and J.V.; Investigation: D.W.L. and C.G-C; Writing - Original Draft: D.W.L. and J.M.G.S.; Writing - Review & Editing: D.W.L., J.V., M.S., C.G-C., M.E., J.M.G.S.

Funding: This research was funded by Research Foundation Flanders (FWO 11G3220N to DWL and FWO 1173823N to CG-C), and the Antwerp Zoo Centre for Research and Conservation which is structurally funded by the Flemish government.

Conflict of Interest: The authors declare no competing interests.

Data Availability: All data and code used in the analyses are available on Zenodo (Laméris et al., 2025)

Acknowledgements

We are grateful to the staff of the Royal Zoological Society of Antwerp (RZSA) for their support in this study. Special thanks go to the bonobo keepers of Zoo Planckendael and Marjolein Osieck for their assistance throughout the study. We are grateful to two anonymous referees for their valuable comments on earlier drafts of the manuscript.

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Supplementary Material

Table S1

Ethogram Used in this Study

Behavior	State/Event	Description
Grooming	State	Subject manipulates Receiver's body surface and hair with lips, fingers…
Calm social play	State	Subject and Receiver play socially in a calm way, with play face, exaggerated movements and (occasionally) with laughing sounds.
Rough social play	State	Subject and Receiver play socially in a rough way, with play face, exaggerated movements and (occasionally) with laughing sounds.
Copulation	State	Heterosexual mount accompanied by pelvic thrusts and intromission between two sexually mature partners.
Non-copulatory mount	State	Subject mounts Receiver without intromission of the penis in the vagina, or without thrusting of the pelvis; or any sexual contact between 2 individuals of the same sex; or sexual contact involving immature individuals. Includes GG rubbing between females. Various positions are possible.
Long charge	Event	Subject shows tensed running towards Receiver over a longer distance (more than five steps). Modifiers: hit, kick, bite, wrestle, nothing.
Short charge	Event	Subject shows tensed running towards Receiver over a few meters (or up to five steps). Modifiers: hit, kick, bite, wrestle, nothing.
Aggressive intention	Event	Subject directs a sudden tense hand or body movement in the direction of the Receiver in a non-playful context or hitting, kicking etc. without locomotion. Modifiers: hit, kick, bite, wrestle, nothing.
Directed display	Event	Subject runs tensed in the direction of, parallel to or closely passing by Receiver, often while pushing an object. This can end in a collision or other contact. There is often a clear phase where the display is built up (body swaying). Modifiers: hit, kick, bite, wrestle, nothing.
Flee	Event	Subject moves away after a quick aggressive approach or charge without indication of play, and the fleeing lasts at least until the aggression stops
Flinch	Event	This may vary from a slightly ducking of the head, via more intense withdrawal movements of the upper part of the body to short momentary actual retreat movements, in that Subject takes one or more steps backwards. The retreat may be performed by crouching backwards.
Displace	Event	Subject approaches to within arm's reach of the Receiver, or moves in direction of receiver with attention focused on receiver and Receiver retreats spatially or yields within 30 seconds
Grin	Event	Retraction of the lips resulting in partial or complete exposure of the gums and teeth with the face directed to the partner [a]

Note. [a] Based on de Waal (1988)

Figure S1

Overview of the Cognitive Testing and Behavioral Observation Timeline

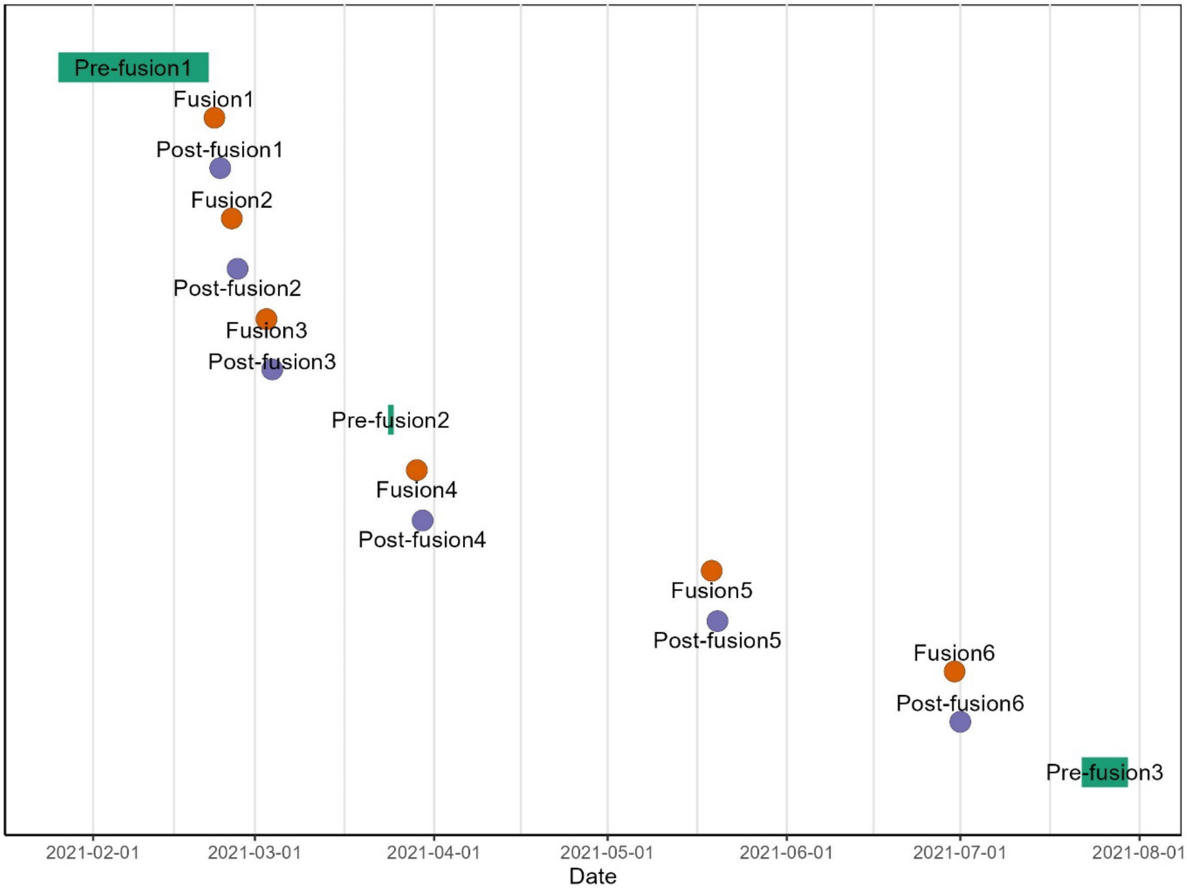


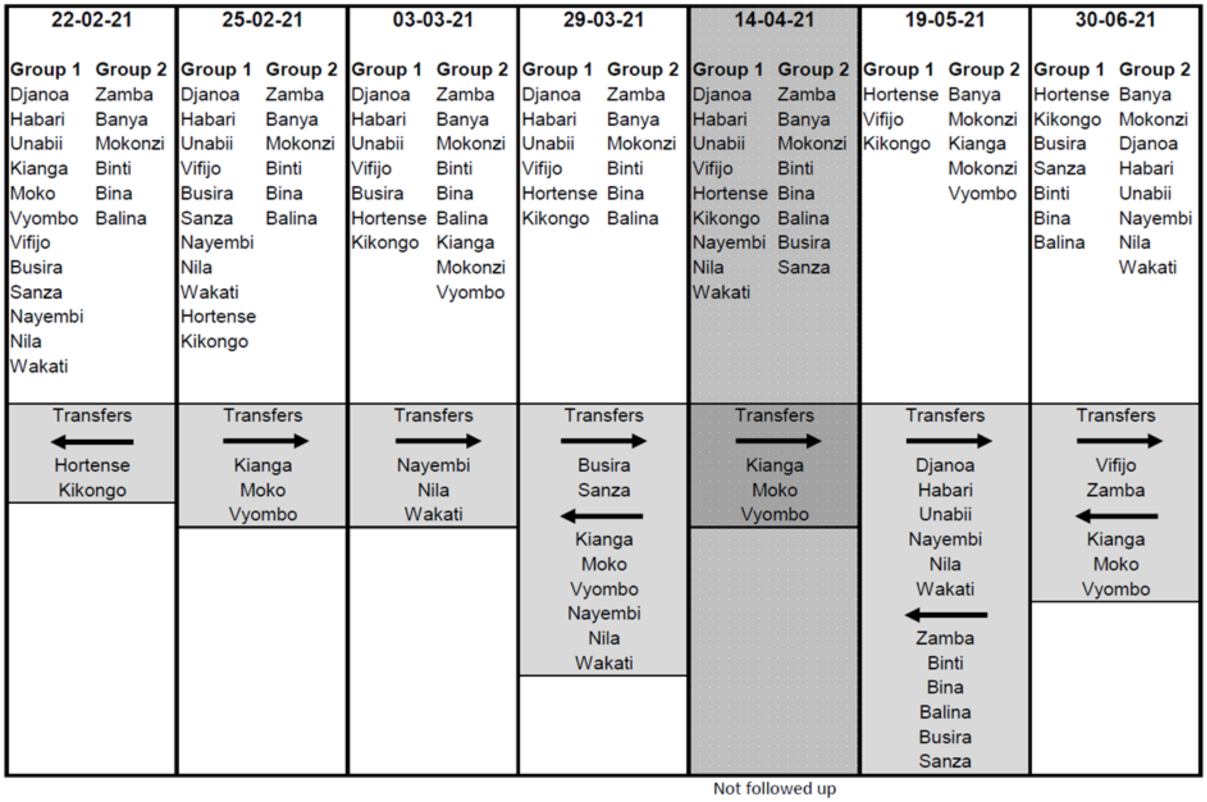
Table S2

Mean Luminance and Contrast Values for the Different Stimuli Used

	Luminance		Contrast	
	Mean	SD	Mean	SD
Direct	0.477	0.008	0.167	0.022
Averted	0.479	0.011	0.169	0.015
Anova statistics	$F(1, 50) = 0.633, p = .430$		$F(1, 50) = 0.137, p = .713$	

Table S3

Group Compositions and Social Units that Transferred Between Groups Throughout the Study Period



22-02-21		25-02-21		03-03-21		29-03-21		14-04-21		19-05-21		30-06-21	
Group 1	**Group 2**	**Group 1**	**Group 2**	**Group 1**	**Group 2**	**Group 1**	**Group 2**	**Group 1**	**Group 2**	**Group 1**	**Group 2**	**Group 1**	**Group 2**
Djanoa	Zamba	Djanoa	Zamba	Djanoa	Zamba	Djanoa	Zamba	Djanoa	Zamba	Hortense	Banya	Hortense	Banya
Habari	Banya	Habari	Banya	Habari	Banya	Habari	Banya	Habari	Banya	Vifijo	Mokonzi	Kikongo	Mokonzi
Unabii	Mokonzi	Unabii	Mokonzi	Unabii	Mokonzi	Unabii	Mokonzi	Unabii	Mokonzi	Kikongo	Kianga	Busira	Djanoa
Kianga	Binti	Vifijo	Binti	Vifijo	Binti	Vifijo	Binti	Vifijo	Binti		Mokonzi	Sanza	Habari
Moko	Bina	Busira	Bina	Busira	Bina	Hortense	Bina	Hortense	Bina		Vyombo	Binti	Unabii
Vyombo	Balina	Sanza	Balina	Hortense	Balina	Kikongo	Balina	Kikongo	Balina			Bina	Nayembi
Vifijo		Nayembi		Kikongo	Kianga			Nayembi	Busira			Balina	Nila
Busira		Nila			Mokonzi			Nila	Sanza				Wakati
Sanza		Wakati			Vyombo			Wakati					
Nayembi		Hortense											
Nila		Kikongo											
Wakati													
Transfers ← Hortense Kikongo		Transfers → Kianga Moko Vyombo		Transfers → Nayembi Nila Wakati		Transfers → Busira Sanza ← Kianga Moko Vyombo Nayembi Nila Wakati		Transfers → Kianga Moko Vyombo		Transfers → Djanoa Habari Unabii Nayembi Nila Wakati ← Zamba Binti Bina Balina Busira Sanza		Transfers → Vifijo Zamba ← Kianga Moko Vyombo	
								Not followed up					

Note. One fusion event (on 14-04-2021) was not followed up due to logistical reasons.

Table S4

Full-Null Model Comparison of Models Testing the Effect of Condition on the Different Behavioral Categories

	Chisq	df	*p*
Grooming given	2.877	2	.237
Grooming received	2.382	2	.304
Social play	3.882	2	.144
Agonistic response	1.043	2	.594
Socio-sexual	24.131	2	<.001
Aggression given	6.965	2	.031

Table S5

Model Outputs Testing the Effect of Condition on the Behavioral Categories of Which the Full Model was Better than the Null Model

Socio-sexual ~ Condition		Chisq	Df	*p*
	Condition	20.327	2	< .001
Fixed factor	Ratio	SE	z-value	p
Pre-fusion – Fusion	2.539	0.783	3.023	.007
Post-fusion – Fusion	8.208	4.392	3.934	< .001
Pre-fusion – Post-fusion	0.309	0.172	-2.114	.087
Aggression given ~ Condition		Chisq	Df	*p*
	Condition	6.826	2	.033
Fixed factor	Ratio	SE	z-value	*p*
Pre-fusion – Fusion	5.670	4.040	2.434	.039
Post-fusion – Fusion	3.650	2.770	1.707	.203
Pre-fusion – Post-fusion	1.550	1.320	0.519	.862

Table S6

Final Model Outputs Testing the Effects of Stimulus Type, Condition, and Sex on the Response Ratio Scores

Response ratio score ~ Stimulus type*Condition + Sex + Target location			Chisq	Df	*p*
		Stimulus type	2.783	1	.095
		Condition	6.881	2	.032
		Sex	1.464	1	.226
		Target location	2.173	2	.337
		Stimulus * Condition	7.035	2	.029
		Stimulus * Sex	0.082	1	.775
		Condition * Sex	1.721	2	.423
Contrast = Stimulus type	Estimate	SE	Df	t-ratio	*p*
Averted					
Fusion / Pre-fusion	0.003	0.044	19.8	0.077	.997
Fusion / Post-fusion	0.012	0.045	18.6	0.273	.960
Post-fusion / Pre-fusion	-0.009	0.043	21.3	-0.205	.977
Direct					
Fusion / Pre-fusion	0.146	0.044	19.6	3.330	.009
Fusion / Post-fusion	0.143	0.044	17.7	3.231	.012
Post-fusion / Pre-fusion	0.003	0.043	20.5	0.076	.997
Contrast = Condition	Estimate	SE	Df	t-ratio	*p*
Pre-fusion					
Averted / Direct	0.006	0.040	559	0.150	.881
Fusion					
Averted / Direct	-0.136	0.043	559	-3.162	.002
Post-fusion					
Averted / Direct	-0.006	0.043	562	-0.145	.885

Table S7

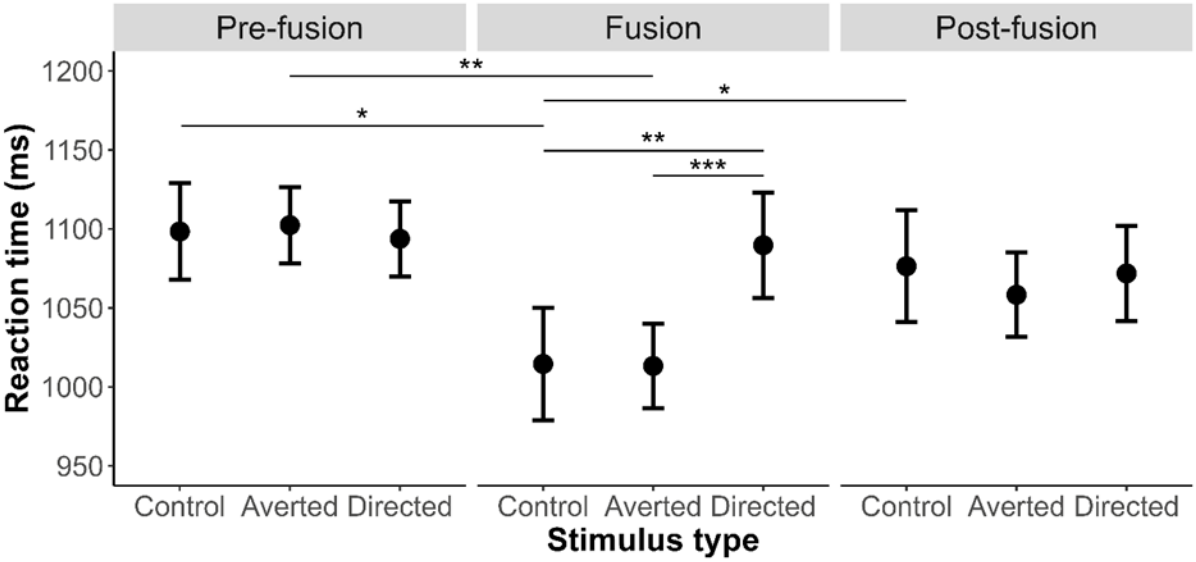
Final Model Outputs Testing the Effect of Condition and Behavior on Response Ratio Scores

	Chisq	df	*p*
Grooming given	0.600	1	.454
Grooming received	1.260	1	.262
Socio-sexual	9.880	1	.002
Social play	3.930	1	.047
Aggression given	2.342	1	.126
Agonistic response	0.085	1	.771
Condition	16.516	2	<.001
Target location	6.483	2	.039

Note. The final model was: ration score (Direct) ~ Grooming given + Grooming received + Socio-sexual + Social play + Aggression given + Agonistic response + Condition + Target location

Figure S2

Average Reaction Times (± 95% Confidence Intervals) for the Different Stimulus Types Depending on Testing Conditions



Note. ***p < .001, **p < .001, *p < .050.

Table S8

Final Model Outputs Post-Hoc Testing the Effects of Stimulus Type and Condition on the Reaction Times to Check for Arousal-Related Response Speeding

Reaction time ~ Stimulus type * Condition + Target location + Sex				
		Chisq	Df	*p*
	Stimulus type	5.242	2	.073
	Condition	7.583	2	.023
	Sex	0.000	1	.990
	Target location	34.633	2	<.001
	Stimulus type * Condition	14.294	4	.006
	Stimulus type * Sex	5.604	2	.061
	Condition * Sex	0.469	2	.791
Contrast = Stimulus type	Ratio	SE	z-ratio	*p*
Control				
Fusion / Post-fusion	0.941	0.024	-2.380	.046
Fusion / Pre-fusion	0.942	0.021	-2.665	.021
Post-fusion / Pre-fusion	1.001	0.023	0.047	.999
Averted				
Fusion / Post-fusion	0.951	0.022	-2.111	.088
Fusion / Pre-fusion	0.931	0.019	-3.504	.001
Post-fusion / Pre-fusion	0.979	0.020	-1.037	.553
Direct				
Fusion / Post-fusion	1.012	0.023	0.530	.857
Fusion / Pre-fusion	1.005	0.020	0.268	.961
Post-fusion / Pre-fusion	0.993	0.020	-0.336	.940
Contrast = Condition	Ratio	SE	z-ratio	*p*
Pre-fusion				
Control / Averted	0.987	0.017	-0.793	.708
Control / Direct	0.996	0.017	-0.259	.964
Averted / Direct	1.009	0.016	0.578	.832
Fusion				
Control / Averted	0.997	0.020	-0.128	.991
Control / Direct	0.932	0.019	-3.534	.001
Averted / Direct	0.935	0.017	-3.709	<.001
Post-fusion				
Control / Averted	1.009	0.020	0.456	.892
Control / Direct	1.004	0.020	0.180	.982
Averted / Direct	0.995	0.018	-0.302	.951