Short report

Chimpanzees communicate to coordinate a cultural practice

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Abstract

Human culture is considered to differ from animal culture due to its interactive nature built on shared intentionality and cognitive flexibility. Here, we investigated whether chimpanzees use communication to engage in cultural practices by analyzing grooming handclasp (GHC) interactions – a socio-cultural behavior requiring coordination. Previous accounts attributed GHC imitations to behavioral shaping whereby the initiator physically molds the partner's arm into the GHC posture. Using frame-by-frame analysis and matched-control methodology, we find that chimpanzees use gestural communication to initiate GHC, which requires an active and synchronized response from the partner. This showcases a behavioral expression of joint commitment to engage in this shared cultural practice. Moreover, we show that GHC initiators used various initiation strategies, attesting to situation-contingent interactional flexibility. We conclude chimpanzees can be jointly committed to a cultural practice, which suggests that culture predicated on shared intentionality and flexible communication may not be unique to the human species.

Introduction

Culture – the inheritance of behavioral phenotypes through social learning (Laland and Janik, 2006) – lies at the heart of the biological success of the human species (Henrich, 2016). It is thought to qualitatively differ from culture in non-human animals (henceforth 'animals') by its communicative nature reflecting both shared intentionality and cognitive flexibility (Enfield and Levinson, 2006; Tomasello, 2019). Shared intentionality is present in collaborative interactions in which participants share psychological states with one another (Tomasello and Carpenter, 2007). It facilitates mutual engagement and commitment from the collaborators by synchronizing their attention and attuning their actions into adequate and complementary action-response sequences. In human culture, two individuals may thus enter a state of shared commitment to engage in a cultural ritual together (e.g., shaking hands when meeting each other (Oxlund, 2020)), which allows for the coordination of the required actions to pursue and complete the shared ritual (Bratman 1992; Enfield and Levinson 2006).

According to an influential view in developmental psychology, animals lack the prerequisites for shared intentionality (Tomasello, 2019; Tomasello et al., 2012; Tomasello and Carpenter, 2007; Tomasello and Moll, 2010). Series of experiments showed that chimpanzees (*Pan troglodytes*) are equivalent to humans when it comes to cognitive skills for dealing with the physical world (e.g., space, causal reasoning), but lag behind substantially in the social realm (e.g., high-fidelity imitative learning, cooperative communication; Herrmann et al. 2007; Tomasello and Moll 2010). In turn, it has been suggested that these reduced socio-cultural capacities preclude chimpanzees from understanding the roles of joint activities and sharing joint goals, the prerequisites for shared intentionality (see (Tomasello and Moll, 2010)).

Recent work, however, has challenged this view and proposed to seek for evolutionary precursors of human shared intentionality not with experimental designs but

58 within naturally occurring contexts of interacting animals (Genty et al., 2020; Heesen et al.,
59 2020, 2017). From an interactional perspective, correlates of shared intentionality could
60 manifest in the establishment of joint attention, joint commitment and joint actions, given
61 their requisite functions for sharing psychological states (Enfield and Levinson, 2006; Genty
62 et al., 2020). Bonobos, for example, have been observed to use communication to facilitate
63 re-engagement of the partner during social games (Pika and Zuberbühler, 2008), and
64 naturally occurring interactions (Heesen et al., 2020), which attests to their commitment to
65 joint activities (Genty et al., 2020). Given the interactional nature of human culture (Enfield
66 and Levinson, 2006; Tomasello, 2019) and the quest for what makes human culture unique
67 (Boyd et al., 2011; Ramsey, 2013; Richerson and Boyd, 2005), an important outstanding
68 question is whether great apes similarly display (correlates of) shared intentionality during
69 the execution of their joint cultural practices.

70 Here, we investigate whether chimpanzees communicate their desire to engage
71 partners in a joint cultural practice requiring the coordination of actions – the grooming
72 handclasp (McGrew and Tutin, 1978). The grooming handclasp (henceforth "GHC") is a
73 cultural social-grooming variant defined as a symmetrical postural configuration in which
74 two partners simultaneously extend one of their arms overhead and clasp each other's
75 extended hand at the palm, wrist or forearm, while grooming each other with the other arm
76 (McGrew and Tutin, 1978; Nakamura and Uehara, 2004; van Leeuwen et al., 2012). While
77 the cultural nature of GHC has been firmly established (McGrew et al., 2001; Nakamura,
78 2002; van Leeuwen et al., 2017, 2012; Wrangham et al., 2016), little is known about the ways
79 in which chimpanzees (or bonobos: (Fruth et al., 2006)) coordinate the execution of the GHC,
80 other than one individual (i.e., the initiator) physically shaping the body of the envisioned
81 partner into the GHC posture (De Waal and Seres, 1997). To learn more about this
82 coordination process, we studied the onset of GHCs with frame-by-frame analysis and

compared the observed behaviors with matched-control windows (i.e., social grooming events of the same partners without GHC) (*sensu* De Waal and Yoshihara 1983). Furthermore, we examined whether chimpanzees initiated GHCs flexibly or in ritualized sequences to shed light on their interactional versatility. Lastly, we inspected whether chimpanzees showed signs of determination/goal-directedness to perform this joint action together with their allocated partner, by identifying the use of persistence and/or elaboration of initial initiation strategies when the desired response (i.e., the partner's commitment to GHC) remained absent. In conjunction, these investigations may illuminate if great apes have the capacity and motivation to engage in socio-cultural practices by means of (correlates of) shared intentionality.

Results

GHC initiations

We examined GHC initiations in a group of 52 semi-wild chimpanzees (Table S1). To determine the mechanisms underlying GHC initiation, we investigated the occurrences of ten selected chimpanzee behaviors (Table S2 and Table S3) in a comparison between *i*) GHC initiations and initiations of regular grooming bouts, and *ii*) pre-handclasp (PH) periods and their matched-control (MC) windows (see Methods and Figure 1). Four behaviors ("head touch", "nosewipe", "self-scratch" and "torso") occurred both during GHC initiations and initiations of regular grooming bouts (>15% of the bouts; see Table S3), and were thus not considered unique to GHC initiations. Six behaviors were observed infrequently during initiations of regular grooming bouts (<15%) and more frequently in the PH compared to the MC context (Wilcoxon signed-rank: all $p<0.04$, Holm-corrected; $n_{\text{ph-mc}}=94$; $n_{\text{ind}}=33$; see Table S4). These behaviors were thus considered specific to GHC initiations. Two of these behaviors ("elbow hold" and "hand grab") corresponded to the practice of shaping (De Waal and Seres 1997; e.g., Video S11), while the remaining behaviors ("elbow touch", "hand touch", "head move", and "hold") did not involve any/prolonged physical contact with the partner. These latter behaviors were considered to be potentially communicative, i.e., in the form of gestures (Liebal and Call 2012; e.g., Video S12).

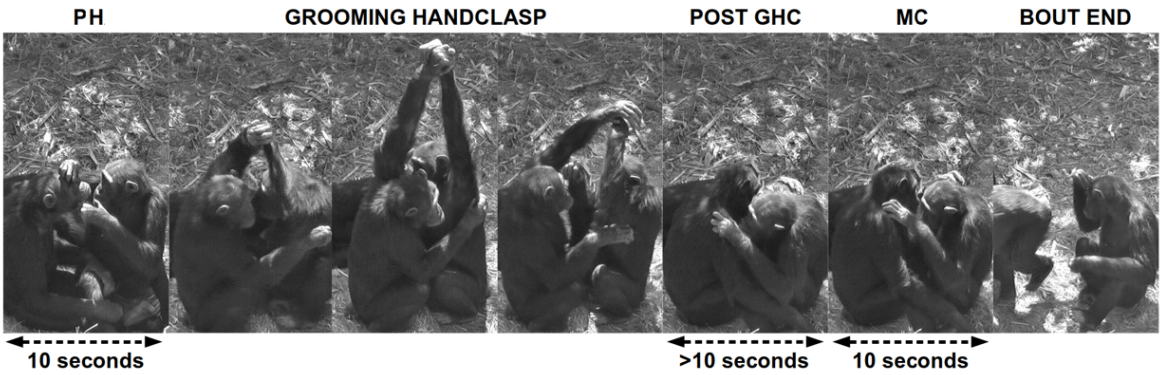

Figure 1. GHC bout including the identified pre-handclasp (PH) and matched-control period (MC). The PHs and MCs were chosen to exactly match in terms of individuals, bodily positioning and activities (grooming) in order to identify mechanisms specific to the initiation of GHC.

Gestures are defined as bodily actions that are mechanically ineffective and recipient-directed, and result in a voluntary response from the recipient (Pika, 2008; Liebal and Call 2012). The four potentially communicative GHC-initiation behaviors followed this definition – they were mechanically ineffective bodily actions resulting in voluntary GHC responses. Only for "head move" we could envision partly non-intentional co-variation with other behaviors like changing grooming posture or redirecting attention. "Elbow touch" and "hand touch" involved targeted physical contact from actor to recipient and were thus recipient-directed, and during "hold" and "head move" signalers faced their recipient in 100% of observed instances (n=31 and n=18, respectively). These gestures were produced flexibly, with 14 of 15 individuals with more than one GHC initiation showing variation in the start behavior (only counting the 6 GHC-specific behaviors determined above) of their initiation sequences (Binomial test: $p<0.001$; also see Figure 2 and associated R-code). The gestures were also produced in a goal-directed way, as indicated by the occurrence of *elaboration* (i.e., the use of additional behavior: Leavens et al., 2005) in 31% of the cases where an initial gesture failed to initiate a GHC (n=10 out of the 32 instances where gestures were used as an initiation strategy, see Figure 2 and details below). Elaboration occurred after an average

132 response waiting time of 0.5s and took the form of another gesture (*n*=4), a shaping behavior
133 (*n*=2), or a combination of both another gesture and a shaping behavior (*n*=4) before the
134 GHC finally commenced. Taken together, these observations show that chimpanzees are
135 flexibly capable and determined to (re-)transmit their motivation to engage in GHC when
136 needed.

137 In general, of the 94 PH/MC comparison bouts, 21 (22%) contained either or both
138 shaping behaviors ("elbow hold", "hand grab"), 32 (34%) contained one or more of the four
139 communicative gestures ("elbow touch", "hand touch", "hold", "head move") and no
140 shaping, and 41 (44%) contained neither shaping nor potentially communicative behaviors.
141 We labeled the third type of GHC initiation as "synchronous", as the individuals appeared to
142 commit to the GHC near-simultaneously. Moreover, if any behavior was scored during the
143 PH window in the synchronous GHCs aside from the raising of the arms (which by definition
144 occurs before every GHC), these were behaviors common to the initiation of regular
145 grooming bouts ("head touch", "nosewipe", "self-scratch", "torso", see Table S3).

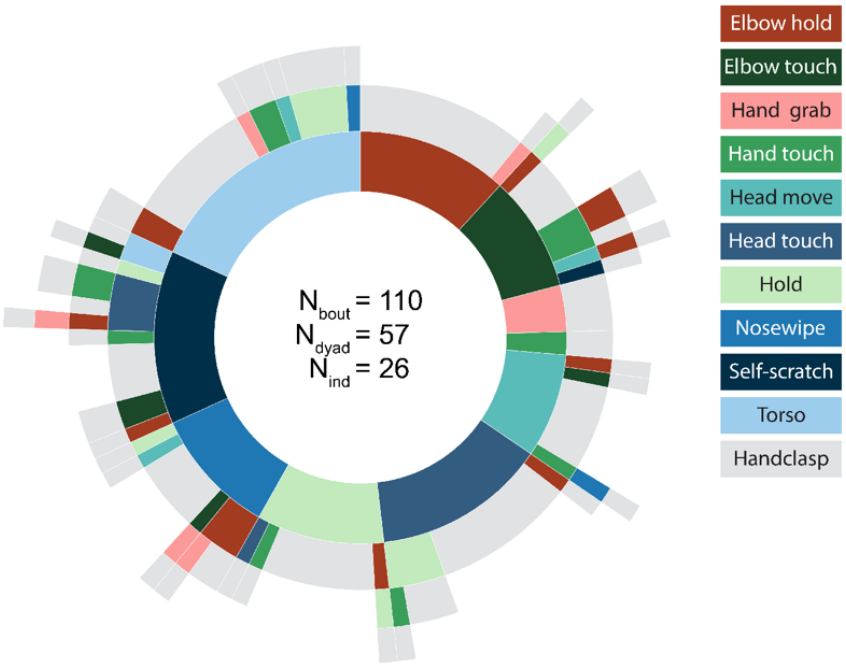

Figure 2*. Behavioral sequences by the initiator leading to GHC (*n*=110). Starting behaviors are depicted in the inner colored circle, with the grey outer circle being the endpoint of the sequence (i.e., GHC). In order to consider the full flexibility of all types of GHC initiations, we included the four "synchrony" behaviors that are also common to the initiation of regular grooming bouts ("head touch", "nosewipe", "self-scratch", and "torso"). * Interactive version available as Figure S13.

Discussion

Our findings show that chimpanzees communicate to engage in one of their most enigmatic socio-cultural practices, the grooming handclasp (McGrew and Tutin, 1978). To date, the mechanism underlying the emergence and stability of the GHC culture in chimpanzees has been described in terms of physical shaping (De Waal and Seres, 1997). By applying matched-control methodologies (De Waal and Yoshihara, 1983) and following established criteria in the field of communication (Leavens et al., 2005; Liebal and Call, 2012; Pika, 2008), we identify flexible and goal-directed gestural communication as an additional mechanism by which chimpanzees initiate and coordinate their grooming handclasps.

The grooming handclasp is a cooperative activity that requires coordination for successful execution. Chimpanzees cooperate (Mitani, 2009), but not much is known about the ways in which they coordinate their joint efforts. In experimental settings, some chimpanzees used location enhancing behaviors (e.g., bodily positioning, touching, peering) (Melis and Tomasello, 2019), or generic gestures (e.g., arm fling, clapping, banging on panels; Voinov et al. 2020) to entice their conspecific partners into a joint action. In natural contexts, chimpanzees and bonobos communicate to coordinate joint actions like joint travel (Fröhlich et al., 2016) and social play (Heesen et al., 2017; Hobaiter and Byrne, 2014), yet "… the degree to which these actions are joint in terms of whether or not partners aim to achieve shared goals together, or whether partners have shared intentions, remains unknown." (Genty et al., 2020). Moreover, none of these examples pertain to cultural practices, while joint and shared intentionality (Koreň, 2016; Tomasello and Carpenter, 2007) conducive to joint action are so central to human accounts of culture (Enfield and Levinson, 2006; Tomasello, 2019).

Our findings identify chimpanzees to use gestural communication in a natural context to overcome a coordination challenge in the socio-cultural domain (McGrew and Tutin, 1978;

178 Nakamura and Uehara, 2004; van Leeuwen et al., 2012). The socio-cultural interaction was
179 not just shaped by one invested individual (De Waal and Seres, 1997), but when the initiator
180 communicated its desire to engage in the GHC (e.g., by holding out its flexed arm at face
181 level in front of the desired partner), an active commitment in the form of a complementary
182 action by the partner was required to accomplish the interaction. As such, when
183 communicated, the cultural GHC practice appeared to ensue with a degree of joint
184 commitment regulating the coordination of the required actions, similar to the handshake
185 example in humans. We conclude that chimpanzees synchronize their attention to a joint
186 cultural action to which they are both committed, which suggests that chimpanzee social
187 culture, like human culture, may be founded on (correlates of) shared intentionality (cf.
188 (Tomasello et al., 2012; Tomasello and Carpenter, 2007; Tomasello and Moll, 2010)).
189 Reflecting on these findings, we posit that also for animals the socio-cultural context
190 *i*) facilitates and shapes mechanisms conducive to coordinating joint actions (also see (Genty
191 et al., 2020)), and *ii*) provides the adequate breeding ground for the transformation of
192 individualistic to collaborative predispositions and capacities – a transformation thought to be
193 unique to the evolution of the human species (Tomasello and Carpenter, 2007). Regarding *i*),
194 the socio-cultural property of the GHC (McGrew et al., 2001; Nakamura, 2002; van Leeuwen
195 et al., 2012) entails a group-level engagement which spurs in individuals both the motivation
196 to instigate and be susceptible to requests for interaction and, in the case of initiating GHC,
197 solve a coordination challenge. Whereas at first this context may produce overzealous
198 individuals who physically shape their naïve partners into GHC (De Waal and Seres, 1997),
199 in a later stage, the shared readiness to coordinate this joint cultural practice may catalyze the
200 transformation of one-sided shaping (only one actor) into two-sided communication (two
201 committed actors). This hypothesis would *a*) explain why communication for coordination
202 purposes has not been readily observed in chimpanzees (i.e., cultural contexts have been

overlooked) (Duguid et al., 2020a, 2020b), and *b*) predict more communication and seamless coordination in more experienced dyads as focus for future research. Regarding *ii*), it has been posited that humans are unique in their cooperative engagement owing to their capacities for shared intentionality (Tomasello, 2019). Humans are thought to transform individualistic activities into joint, collaborative activities during ontogeny and especially throughout socio-cultural immersion – a process presumably absent in chimpanzees (Tomasello and Carpenter, 2007). It may thus be no coincidence that exactly in this socio-cultural GHC-context we observed capacities for joint attention and commitment in chimpanzees, similar to the ones ascribed to young children engaging in joint activities (Tomasello, 2019). The ontogeny of chimpanzees' cultural engagement with a specific focus on elements of shared intentionality may provide exciting insights for theories on the evolution of human thinking (Heyes, 2018; Tomasello, 2019).

Methods

Subjects

Subject were 52 chimpanzees (Table S1) at the Chimfunshi Wildlife Orphanage, Zambia. GHC has been a customary behavior in the group for over 15 years, and 39 individuals (including all 32 adults) were observed to GHC at least once. The study was approved by the Chimfunshi Research Advisory Board (permit: CWOT_ 2019C039), and conformed to the nationwide legal requirements. Chimfunshi is accredited by PASA and adheres to the rules and regulations with respect to animal care and management as stipulated by the Zambia Wildlife Authority.

Collection & Coding

Data were collected by ZG from 23-03-2019 to 04-06-2019 between 8am-4pm with handheld digital video cameras (Panasonic HDC-HS100). To capture GHC initiations, filming commenced as soon as two individuals approached one another. Filming continued if the individuals started social grooming and lasted until they (a) had stopped grooming for over 30 seconds, (b) started grooming another individual, or (c) physically separated. A grooming bout was defined as running from the start of grooming until the moment one of the aforementioned ending conditions was met. A bout was considered a GHC-bout if it contained one or multiple GHCs, and a regular grooming bout if no GHCs occurred.

GHC-bouts had either a *side* or *back* view and were analyzed for initiation behaviors if a 10 sec pre-handclasp (PH) social grooming window was available before the first GHC in the bout. We only analyzed the initiation of the first GHC in GHC-bouts, because previous GHCs could possibly function as signals for subsequent GHCs. The start of a GHC was defined as the instance of handclasp above face level; the end as the instance that physical

240 contact of the palms/wrists was broken. Moreover, a Matched-Control (MC) period was
241 recorded to enable comparison of individual initiation behaviors across conditions (De Waal
242 and Yoshihara, 1983). The MC-period was defined as a 10sec-window minimally 10sec after
243 the last GHC occurrence in the GHC bout, in which the individuals had to be positioned in
244 the same relative positions as during the GHC, while still engaging in social grooming
245 (Figure 1). Additionally, initiations of regular, non-GHC-bouts were opportunistically
246 recorded ($n_{side\ and\ back}$=23, Table S3) to identify behaviors used in the initiation of regular
247 grooming bouts.

248 Videos were scored in ELAN (Wittenburg et al., 2006), behaviors were coded based
249 on preliminary screening of the videos and established chimpanzee ethograms (Nishida et al.,
250 1999) (see Table S2 and SI videos). An individual was considered the initiator of a GHC bout
251 when they were either a) the first one to produce a GHC-specific initiation behavior or b) in
252 the absence of these behaviors, the first to raise their arm for the GHC. A subset of 20% of
253 the data was coded by two further observers to establish IRR. Mean dyadic agreement was
254 0.833 for coding behaviors (range 0.81-0.89), and 0.973 for identifying the initiating
255 individual (range 0.89-1; see SI for details).

256

257 ***Analyses***

258 Analyses were done in R 3.6.1. Non-parametric statistics were applied, including Bonferroni-
259 Holm corrections for multiple testing (Holm, 1979). For the PH-MC comparison, we
260 analyzed those behaviors that *i*) occurred ≥5 times in GHC-bouts, and *ii*) did not also
261 frequently (>15% of bouts) occur during initiations of regular grooming bouts (see Table S3).
262 Given that social grooming occurred in both PH and MC windows by definition (see Figure 1
263 and "Collection & Coding"), we did not consider the grooming behaviours (see Table S3) as

possible signals for GHC initiation. We only used GHC-bouts with a *side*-view (optimal vantage point) and a Matched Control period (n=94). Auxiliary analysis including also *back*-view observations (n_{total}=133) supported our main analyses (all 6 behaviors p<0.02, Holm corrected; see Tables S3 & S4). When assessing flexibility and elaboration in GHC initiations (Figure 2), we used all *side*-view bouts regardless of the presence of MCs (n=110).

Data availability statement

The code and data used for analyses are available via http://doi.org/10.5281/zenodo.4616274.

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Competing interests

The authors declare to have no competing interests.

Compliance with Ethical Standards

The authors declare no conflict of interests to exist. The research on chimpanzees was strictly non-invasive/observational and adhered to the ethical guidelines provided by the Chimfunshi

Research Advisory Board. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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Supplementary Information captions

SI_1. Supplementary information and tables, including subject demographics, the behavioral ethogram, frequency table of behavior, outcomes of the Wilcoxon-signed rank tests, and details on the inter-rater reliability calculation.

Video S1. Elbow hold.

Video S2. Elbow touch.

Video S3. Hand grab.

Video S4. Hand touch.

Video S5. Head move.

Video S6. Head touch.

Video S7. Hold.

Video S8. Nosewipe.

Video S9. Self-scratch.

Video S10. Torso.

Video S11. Video example of a grooming handclasp initiated with shaping behavior.

Video S12. Video example of a grooming handclasp initiated with gestural communication.

Interactive Figure S13. Interactive version of Figure 2.

Supplementary Information

Chimpanzees communicate to coordinate a cultural practice

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Table S1. Subject demography of Group 2 at Chimfunshi Wildlife Orphanage on 01-07-2019.

	Male	Female	Total
Adult (> 12 years)	8	24	32
Juvenile (3-11 years)	7	5	12
Infant (< 3 years)	3	5	8

Table S2. Ethogram of behavior, with reference to supplementary videos of behaviors.

Behavior	Video	Definition
Elbow Hold	S1	Places own hand on elbow or arm of other, maintaining physical contact as arm of other moves
Elbow Touch	S2	Briefly touches elbow or arm of other with own hand
Hand Grab	S3	Grabs hand of other with own hand, maintaining contact as arm or hand of other moves
Hand Touch	S4	Briefly touches hand of other with own hand
Head Move	S5	Tilts head up or downwards
Head Touch	S6	Touches (side of) head of other with hand, brief or prolonged contact
Hold	S7	Holds arm up in the air at peak of arm-raise movement, i.e., the raising of the upper arm with some flexion in the elbow
Nosewipe	S8	Swipes hand across or underneath nose in quick motion
Self-scratch	S9	Drags hand across body in long rough strokes
Torso	S10	Turns torso towards or away from other

Table S3. Occurrence of all ethogram behaviors in pre-handclasp (PH) and matched-control (MC) periods, as well as initiation of regular grooming bouts (IRG). Reported is the total number of instances and between brackets the number of instances divided by the number of bouts.

	Side view			Side and back view		
Behavior	**PH (n = 94)**	**MC (n = 94)**	**IRG (n = 17)**	**PH (n = 133)**	**MC (n = 133)**	**IRG (n = 23)**
Elbow hold	18 (0.19)	1 (0.01)	0 (0)	25 (0.19)	1 (0.01)	0 (0)
Elbow touch	14 (0.15)	0 (0)	0 (0)	16 (0.12)	0 (0)	0 (0)
Groom face	29 (0.31)	44 (0.47)	7 (0.41)	41 (0.31)	63 (0.47)	8 (0.35)
Groom hand/arm	24 (0.26)	25 (0.27)	5 (0.29)	28 (0.21)	32 (0.24)	6 (0.26)
Groom other	53 (0.56)	70 (0.74)	8 (0.47)	79 (0.59)	95 (0.71)	14 (0.61)
Hand grab	5 (0.05)	0 (0)	0 (0)	8 (0.06)	0 (0)	0 (0)
Hand touch	6 (0.06)	0 (0)	0 (0)	6 (0.05)	0 (0)	0 (0)
Head move	11 (0.12)	1 (0.01)	0 (0)	17 (0.12)	1 (0.01)	1 (0.04)
Head touch	14 (0.15)	3 (0.03)	3 (0.18)	18 (0.14)	3 (0.03)	4 (0.17)
Hold	14 (0.15)	1 (0.01)	1 (0.06)	16 (0.12)	1 (0.01)	1 (0.04)
Nosewipe	12 (0.13)	2 (0.02)	6 (0.35)	16 (0.12)	2 (0.02)	7 (0.30)
Self-scratch	25 (0.27)	9 (0.10)	3 (0.18)	31 (0.23)	13 (0.10)	5 (0.22)
Torso	30 (0.32)	0 (0)	10 (0.59)	44 (0.33)	0 (0)	11 (0.48)

Table S4. Results of the paired Wilcoxon signed rank test of behavior frequency between the PH and MC periods.

	Side view (n = 94)			Side and back view (n = 133)		
Behavior	**V**	**P-value (raw)**	**P -value (adjusted Holm)**	**V**	**P-value (raw)**	**P -value (adjusted Holm)**
Elbow hold**	10	<0.001	0.001	13.5	<0.001	<0.001
Elbow touch*	0	<0.001	0.001	0	<0.001	<0.001
Hand grab*	0	0.037	0.039	0	0.006	0.012
Hand touch*	0	0.020	0.039	0	0.020	0.020
Head move**	6.5	0.004	0.013	8.5	<0.001	0.001
Hold**	0	<0.001	0.001	0	<0.001	<0.001

* indicates $p < 0.05$, ** indicates $p < 0.01$

Inter-rater reliability assessment

To establish inter-rater reliability, two additional coders (JB and AM) analyzed the PHs and MCs of 20% (N = 19) of the GHC bouts. Additionally, ZG coded this subset for a second time to compare to her first coding one year prior.

Due to the continuous nature of the behavioral scoring and the importance of observers not only agreeing on the presence of (often rare) behaviors but also the order in which they occurred, the usual Cohen's Kappa approach was not feasible. We calculated inter-rater reliability as follows (see also attached data for each rater's coding and an overview):

If raters both scored the same behavior in the same order at the same time (within 1 second) it was noted as an "agree", if either of the raters scored a behavior the other one did not score it was a "disagree". As an informed estimation for the total amount of behaviors per video we used the sum of the instances of agree and disagree. To correct for the probability of two raters agreeing on a behavior by chance, we multiplied the probability of scoring a particular behavior (1/11, the amount of different behaviors) by the probability of scoring it for a certain individual (0.5).

The final calculation of the reliability score combined this probability of agreement based on chance (POA) with the relative observer agreement (ROA, defined as agreed behaviors/total amount of behaviors), in the form of $\frac{ROA-POA}{1-POA}$. For instance, 50 agrees out of 70 total behaviors leads to a reliability score of $\frac{(\frac{50}{70})-(0.5*\frac{1}{11})}{1-(0.5*\frac{1}{11})}$ = 0.70. For this study, all dyads showed inter-rater reliability scores above 0.80 (ZG_2-ZG_1 = 0.89; JB-ZG_1 = 0.81; AM-ZG_1 = 0.82; JB-AM = 0.81). Furthermore, each rater also coded who they thought initiated the bout, and inter-rater reliability on initiator was calculated in a similar manner (with POA being 0.5) and was above 0.90 for all raters (JB-ZG_1 = 0.89; all other dyads = 1).