1 Short report

2 Chimpanzees communicate to coordinate a cultural practice

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19 Abstract

20 Human culture is considered to differ from animal culture due to its interactive nature built 21 on shared intentionality and cognitive flexibility. Here, we investigated whether chimpanzees 22 use communication to engage in cultural practices by analyzing grooming handclasp (GHC) 23 interactions - a socio-cultural behavior requiring coordination. Previous accounts attributed 24 GHC imitations to behavioral shaping whereby the initiator physically molds the partner's 25 arm into the GHC posture. Using frame-by-frame analysis and matched-control methodology, 26 we find that chimpanzees use gestural communication to initiate GHC, which requires an 27 active and synchronized response from the partner. This showcases a behavioral expression 28 of joint commitment to engage in this shared cultural practice. Moreover, we show that GHC 29 initiators used various initiation strategies, attesting to situation-contingent interactional 30 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 31 32 be unique to the human species.

33 Introduction

34 Culture – the inheritance of behavioral phenotypes through social learning (Laland and Janik, 35 2006) – lies at the heart of the biological success of the human species (Henrich, 2016). It is 36 thought to qualitatively differ from culture in non-human animals (henceforth 'animals') by 37 its communicative nature reflecting both shared intentionality and cognitive flexibility 38 (Enfield and Levinson, 2006; Tomasello, 2019). Shared intentionality is present in 39 collaborative interactions in which participants share psychological states with one another 40 (Tomasello and Carpenter, 2007). It facilitates mutual engagement and commitment from the 41 collaborators by synchronizing their attention and attuning their actions into adequate and 42 complementary action-response sequences. In human culture, two individuals may thus enter 43 a state of shared commitment to engage in a cultural ritual together (e.g., shaking hands when 44 meeting each other (Oxlund, 2020)), which allows for the coordination of the required actions 45 to pursue and complete the shared ritual (Bratman 1992; Enfield and Levinson 2006). 46 According to an influential view in developmental psychology, animals lack the prerequisites for shared intentionality (Tomasello, 2019; Tomasello et al., 2012; Tomasello 47

48 and Carpenter, 2007; Tomasello and Moll, 2010). Series of experiments showed that 49 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 50 51 the social realm (e.g., high-fidelity imitative learning, cooperative communication; Herrmann 52 et al. 2007; Tomasello and Moll 2010). In turn, it has been suggested that these reduced 53 socio-cultural capacities preclude chimpanzees from understanding the roles of joint activities 54 and sharing joint goals, the prerequisites for shared intentionality (see (Tomasello and Moll, 2010)). 55

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 manifest in the establishment of joint attention, joint commitment and joint actions, given 60 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 re-engagement of the partner during social games (Pika and Zuberbühler, 2008), and 63 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

83 compared the observed behaviors with matched-control windows (i.e., social grooming 84 events of the same partners without GHC) (sensu De Waal and Yoshihara 1983). Furthermore, we examined whether chimpanzees initiated GHCs flexibly or in ritualized 85 86 sequences to shed light on their interactional versatility. Lastly, we inspected whether 87 chimpanzees showed signs of determination/goal-directedness to perform this joint action 88 together with their allocated partner, by identifying the use of persistence and/or elaboration 89 of initial initiation strategies when the desired response (i.e., the partner's commitment to 90 GHC) remained absent. In conjunction, these investigations may illuminate if great apes have 91 the capacity and motivation to engage in socio-cultural practices by means of (correlates of) 92 shared intentionality.

93 **Results**

94 GHC initiations

95 We examined GHC initiations in a group of 52 semi-wild chimpanzees (Table S1). To 96 determine the mechanisms underlying GHC initiation, we investigated the occurrences of ten 97 selected chimpanzee behaviors (Table S2 and Table S3) in a comparison between i) GHC 98 initiations and initiations of regular grooming bouts, and *ii*) pre-handclasp (PH) periods and 99 their matched-control (MC) windows (see Methods and Figure 1). Four behaviors ("head 100 touch", "nosewipe", "self-scratch" and "torso") occurred both during GHC initiations and 101 initiations of regular grooming bouts (>15% of the bouts; see Table S3), and were thus not 102 considered unique to GHC initiations. Six behaviors were observed infrequently during 103 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 104 105 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 106 107 and Seres 1997; e.g., Video S11), while the remaining behaviors ("elbow touch", "hand 108 touch", "head move", and "hold") did not involve any/prolonged physical contact with the 109 partner. These latter behaviors were considered to be potentially communicative, i.e., in the 110 form of gestures (Liebal and Call 2012; e.g., Video S12).

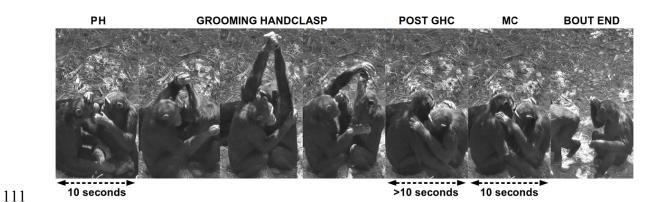


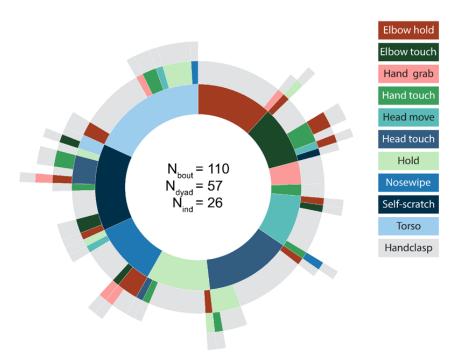
Figure 1. GHC bout including the identified pre-handclasp (PH) and matched-control period (MC).
The PHs and MCs were chosen to exactly match in terms of individuals, bodily positioning and
activities (grooming) in order to identify mechanisms specific to the initiation of GHC.

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116 Gestures are defined as bodily actions that are mechanically ineffective and recipient-117 directed, and result in a voluntary response from the recipient (Pika, 2008; Liebal and Call 118 2012). The four potentially communicative GHC-initiation behaviors followed this definition 119 - they were mechanically ineffective bodily actions resulting in voluntary GHC responses. 120 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 121 122 touch" involved targeted physical contact from actor to recipient and were thus recipient-123 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, 124 125 with 14 of 15 individuals with more than one GHC initiation showing variation in the start 126 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 127 128 were also produced in a goal-directed way, as indicated by the occurrence of *elaboration* (i.e., 129 the use of additional behavior: Leavens et al., 2005) in 31% of the cases where an initial 130 gesture failed to initiate a GHC (n=10 out of the 32 instances where gestures were used as an 131 initiation strategy, see Figure 2 and details below). Elaboration occurred after an average

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



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147 **Figure 2***. Behavioral sequences by the initiator leading to GHC (n=110). Starting behaviors are

148 depicted in the inner colored circle, with the grey outer circle being the endpoint of the sequence (i.e.,

149 GHC). In order to consider the full flexibility of all types of GHC initiations, we included the four

150 "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.

153 **Discussion**

154 Our findings show that chimpanzees communicate to engage in one of their most enigmatic 155 socio-cultural practices, the grooming handclasp (McGrew and Tutin, 1978). To date, the 156 mechanism underlying the emergence and stability of the GHC culture in chimpanzees has 157 been described in terms of physical shaping (De Waal and Seres, 1997). By applying 158 matched-control methodologies (De Waal and Yoshihara, 1983) and following established 159 criteria in the field of communication (Leavens et al., 2005; Liebal and Call, 2012; Pika, 160 2008), we identify flexible and goal-directed gestural communication as an additional 161 mechanism by which chimpanzees initiate and coordinate their grooming handclasps. 162 The grooming handclasp is a cooperative activity that requires coordination for 163 successful execution. Chimpanzees cooperate (Mitani, 2009), but not much is known about 164 the ways in which they coordinate their joint efforts. In experimental settings, some 165 chimpanzees used location enhancing behaviors (e.g., bodily positioning, touching, peering) 166 (Melis and Tomasello, 2019), or generic gestures (e.g., arm fling, clapping, banging on 167 panels; Voinov et al. 2020) to entice their conspecific partners into a joint action. In natural 168 contexts, chimpanzees and bonobos communicate to coordinate joint actions like joint travel 169 (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 170 171 achieve shared goals together, or whether partners have shared intentions, remains unknown." 172 (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 173 174 joint action are so central to human accounts of culture (Enfield and Levinson, 2006; 175 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 communicated its desire to engage in the GHC (e.g., by holding out its flexed arm at face 180 181 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),

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

203 overlooked) (Duguid et al., 2020a, 2020b), and b) predict more communication and seamless 204 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 205 206 capacities for shared intentionality (Tomasello, 2019). Humans are thought to transform 207 individualistic activities into joint, collaborative activities during ontogeny and especially 208 throughout socio-cultural immersion – a process presumably absent in chimpanzees 209 (Tomasello and Carpenter, 2007). It may thus be no coincidence that exactly in this socio-210 cultural GHC-context we observed capacities for joint attention and commitment in 211 chimpanzees, similar to the ones ascribed to young children engaging in joint activities 212 (Tomasello, 2019). The ontogeny of chimpanzees' cultural engagement with a specific focus 213 on elements of shared intentionality may provide exciting insights for theories on the 214 evolution of human thinking (Heyes, 2018; Tomasello, 2019).

216 Methods

217 Subjects

- 218 Subject were 52 chimpanzees (Table S1) at the Chimfunshi Wildlife Orphanage, Zambia.
- 219 GHC has been a customary behavior in the group for over 15 years, and 39 individuals
- 220 (including all 32 adults) were observed to GHC at least once. The study was approved by the
- 221 Chimfunshi Research Advisory Board (permit: CWOT_2019C039), and conformed to the
- 222 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
- 224 Wildlife Authority.

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226 Collection & Coding

227 Data were collected by ZG from 23-03-2019 to 04-06-2019 between 8am-4pm with handheld 228 digital video cameras (Panasonic HDC-HS100). To capture GHC initiations, filming 229 commenced as soon as two individuals approached one another. Filming continued if the 230 individuals started social grooming and lasted until they (a) had stopped grooming for over 231 30 seconds, (b) started grooming another individual, or (c) physically separated. A grooming 232 bout was defined as running from the start of grooming until the moment one of the 233 aforementioned ending conditions was met. A bout was considered a GHC-bout if it 234 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).

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257 Analyses

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258 Analyses were done in R 3.6.1. Non-parametric statistics were applied, including Bonferroni-
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Holm corrections for multiple testing (Holm, 1979). For the PH-MC comparison, we

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
- and "Collection & Coding"), we did not consider the grooming behaviours (see Table S3) as

264	possible signals for GHC initiation. We only used GHC-bouts with a side-view (optimal
265	vantage point) and a Matched Control period (n=94). Auxiliary analysis including also back-
266	view observations (n_{total} =133) supported our main analyses (all 6 behaviors p <0.02, Holm
267	corrected; see Tables S3 & S4). When assessing flexibility and elaboration in GHC initiations
268	(Figure 2), we used all <i>side</i> -view bouts regardless of the presence of MCs (<i>n</i> =110).
269	
270	Data availability statement
271	The code and data used for analyses are available via http://doi.org/10.5281/zenodo.4616274.
272	
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278	
279	Competing interests
280	The authors declare to have no competing interests.
281	
282	Compliance with Ethical Standards
283	The authors declare no conflict of interests to exist. The research on chimpanzees was strictly
284	non-invasive/observational and adhered to the ethical guidelines provided by the Chimfunshi

- 285 Research Advisory Board. All applicable international, national, and/or institutional
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287

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398 Supplementary Information captions

- 399 SI 1. Supplementary information and tables, including subject demographics, the behavioral
- 400 ethogram, frequency table of behavior, outcomes of the Wilcoxon-signed rank tests,
- 401 and details on the inter-rater reliability calculation.
- 402 Video S1. Elbow hold.
- 403 Video S2. Elbow touch.
- 404 Video S3. Hand grab.
- 405 Video S4. Hand touch.
- 406 Video S5. Head move.
- 407 Video S6. Head touch.
- 408 Video S7. Hold.
- 409 Video S8. Nosewipe.
- 410 Video S9. Self-scratch.
- 411 Video S10. Torso.
- 412 Video S11. Video example of a grooming handclasp initiated with shaping behavior.
- 413 Video S12. Video example of a grooming handclasp initiated with gestural communication.
- 414 Interactive Figure S13. Interactive version of Figure 2.

415 Supplementary Information

416 Chimpanzees communicate to coordinate a cultural practice

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- 422
- 423
- Table S1. Subject demography of Group 2 at Chimfunshi Wildlife Orphanage on 01-07 2019.
- 426

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

427 428

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

430

Behavior	Video	Definition			
Elbow Hold	S 1	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			

431 432

434 **Table S3.** Occurrence of all ethogram behaviors in pre-handclasp (PH) and matched-control

435 (MC) periods, as well as initiation of regular grooming bouts (IRG). Reported is the total

436 number of instances and between brackets the number of instances divided by the number of437 bouts.

438

		Side view		Side and back view			
Behavior	PH (n =	MC (n =	IRG (n =	PH (n =	MC (n =	IRG (n =	
	94)	94)	17)	133)	133)	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	24 (0.26)	25 (0.27)	5 (0.29)	28 (0.21)	32 (0.24)	6 (0.26)	
hand/arm							
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)	

439

440441 Table S4. Results of the paired Wilcoxon signed rank test of behavior frequency between the

442 PH and MC periods.

443

		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		

444 * indicates p < 0.05, ** indicates p < 0.01

445

447 Inter-rater reliability assessment

448 To establish inter-rater reliability, two additional coders (JB and AM) analyzed the PHs and 449 MCs of 20% (N = 19) of the GHC bouts. Additionally, ZG coded this subset for a second 450 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).

463 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 464 behaviors/total amount of behaviors), in the form of $\frac{ROA - POA}{1 - POA}$. For instance, 50 agrees out of 465 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 466 showed inter-rater reliability scores above 0.80 (ZG 2-ZG 1 = 0.89; JB-ZG 1 = 0.81; AM-467 468 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 469 470 being 0.5) and was above 0.90 for all raters (JB-ZG 1 = 0.89; all other dyads = 1).