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RESEARCH ARTICLE

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“Giving” and “responding” differences in gestural communication between nonhuman great ape mothers and infants

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Abstract

In the first comparative analysis of its kind, we investigated gesture behavior and response patterns in 25 captive ape mother–infant dyads (six bonobos, eight chimpanzees, three gorillas, and eight orangutans). We examined (i) how frequently mothers and infants gestured to each other and to other group members; and (ii) to what extent infants and mothers responded to the gestural attempts of others. Our findings confirmed the hypothesis that bonobo mothers were more proactive in their gesturing to their infants than the other species. Yet mothers (from all four species) often did not respond to the gestures of their infants and other group members. In contrast, infants “pervasively” responded to gestures they received from their mothers and other group members. We propose that infants’ *pervasive responsiveness* rather than the quality of mother investment and her responsiveness may be crucial to communication development in nonhuman great apes.

KEYWORDS

gesture, infant, mother, nonhuman great apes, responsiveness

1 | INTRODUCTION

Human children start gesturing early in infancy. Gestures, such as pointing with outstretched arms, hands, and fingers to effectively communicate with others, emerge before their first spoken words (toward the end of the 1st year of life; Bates, 1976; Bates, Benigni, Bretherton, Camaioni, & Volterra, 1979; Carpenter, Nagell, & Tomasello, 1998; Iverson & Thal, 1998; Masur, 1980), and play a facilitative role in language development itself (e.g., Iverson & Goldin-Meadow, 2005). We also know that the caregiver, for example, mother (as predominantly demonstrated in Western cultures), can play an important and active role in the development of their infants’ early communicative behavior (including gestures) by scaffolding and enhancing their potential (e.g., Bruner, 1983; Bullowa, 1979; Stern, 1977). By responding promptly, contingently and appropriately to their infants’ behavior, mothers positively affect communication skills

(e.g., Bornstein et al., 1992; Kärtner et al., 2008; Kärtner, Keller, & Yovsi, 2010; Masur, Flynn, & Eichorst, 2005; Nicely, Tamis-LeMonda, & Grolnick, 1999; Wu & Gros-Louis, 2014; see Ochs & Schieffelin, 1982 for alternative interactional patterns in non-Western cultures).

In contrast to humans, we know far less about the mother–infant communicative interactions in our closest living relatives. In this study, we aimed to address this gap in our knowledge by investigating the gestural “giving” (in terms of prevalence) and response behavior between mother and infant across the nonhuman great apes: bonobos, chimpanzees, gorillas, and orangutans. Systematically contrasting the communicative behavior across these species affords the opportunity to reveal the features that constitute the core of human communication as well as those that we share with other ape species. Moreover, these data are essential to make inferences about the features that may have already been present in ancestral species (Bard, 2005; Cheney & Seyfarth, 1990; Marler, 1976; Plooi, 1979).

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1.1 | Gesturing in nonhuman great apes

While the level and sophistication of vocal communication in nonhuman great apes (and other nonhuman primates) continues to be debated (e.g., Fischer, 2016; Seyfarth & Cheney, 2016; Townsend et al., 2016), there appears to be consensus that apes communicate via gestures in sophisticated ways. Through utilizing body, head, and limbs, apes produce intentional, flexibly used, and “meaningful” signals to communicate with others (e.g., Bard et al., 2014b; Call & Tomasello, 2007; Hobaiter & Byrne, 2011; Roberts, Vick, & Buchanan-Smith, 2013). Chimpanzees, for example, elaborate their gestures when previous communicative attempts fail (in wild populations: Roberts et al., 2013; and captive populations: Leavens, Russell, & Hopkins, 2005), and distinct gestures are judged to have specific meanings independent of the sender and context (Hobaiter & Byrne, 2014; Roberts, Vick, & Buchanan-Smith, 2012; cf., Scott-Phillips, 2015a,b for critical discussion about inferring meaning in nonhuman primate communication).

To date, comparative gesture research has mainly targeted humans’ phylogenetic closest living relatives, genus *Pan* (Prüfer et al., 2012), that is, bonobos and chimpanzees (Fröhlich et al., 2016a; Pollick & de Waal, 2007; cf., De Waal, 1988). Although these two species share a number of socio-behavioral characteristics (e.g., similar group organizational structures; Badrian & Badrian, 1984; Goodall, 1986); gestural repertoires (Schneider, Call, & Liebal, 2012b) and engage in complex gestural turn-taking sequences (in relation to travel “negotiations;” Fröhlich et al., 2016a), they differ in other important ways. Bonobos, for example, are more “elaborate” in their sexual behavior, tend to be less overtly aggressive and, generally, females attain a higher dominance rank than in chimpanzees (De Waal, 1988; Furuichi, 2011; Kano, 1992; Palagi, 2006; Wilson et al., 2014). Moreover, comparative experimental studies indicate bonobos show more tolerant and cooperative behaviors when accessing or distributing food (Hare, Melis, Woods, Hastings, & Wrangham, 2007; Wobber, Wrangham, & Hare, 2010), and are perhaps generally more “socially inclined.” Bonobos, for example, are more likely to look at the eyes and faces of conspecifics; indicating higher social “attentional and motivational levels” (Kano, Hirata, & Call, 2015). Specific to communication, bonobos are reported to pair gestures more flexibly and effectively in relation to facial expressions and vocalizations (Pollick & de Waal, 2007; see also Genty, Neumann, & Zuberbühler, 2015 who observed this in sexual-related signaling), are judged to use head movements in more sophisticated ways (Schneider, Call, & Liebal, 2010) and are more likely to initiate gestural interactions through gaze (Fröhlich et al., 2016a). In sum, while nonvocal communication repertoires in chimpanzees and bonobos are “fundamentally similar,” bonobos appear more “variable” and sophisticated in their communicative behavior (De Waal, 1988).

Apart from experimental studies (e.g., Liebal, Pika, Call, & Tomasello, 2004; Pelé, Thierry, Dufour, & Call, 2009; Tempelmann, Kaminski, & Liebal, 2011), few observational investigations have systematically compared naturally occurring gestural communication across various nonhuman great ape species (cf., Call & Tomasello, 2007). This is not surprising given that observational cross-species comparisons (in both wild and captive environments) are thwarted by logistical and practical challenges; making it difficult to apply

standardized observational data collection and analytical methods (Tomasello & Call, 2011). In the first, and to our knowledge only, systematic observational study considering the early gesture development of captive bonobos, chimpanzees, gorillas, and orangutans; first gestures emerged in African apes between 9 and 11 months of age—broadly resembling gesture onset in human infants—while orangutans, in line with their slow life history, began gesturing significantly later (Schneider, Call, & Liebal, 2012a; cf., Bard et al., 2014b, who reported gesture-specific onset ages as early as 3.5 months for nursery-reared chimpanzees).

1.2 | Ape infants and mothers’ “roles” in communicational development

Compared to the existing knowledge about the role that human mothers play in their infants’ communicational development, we still know very little about this issue in nonhuman great apes. Previous work demonstrates the ape mother–infant relationship to be the most stable social unit, with bonds lasting for several years (Plooij, 1978, 1984; Van Lawick-Goodall, 1967; Van Noordwijk et al., 2009). It is therefore not surprising that some of the richest repertoires of nuanced, subtle communication have been described between mothers and offspring (Bard, 1990, 1992; Van Lawick-Goodall, 1967, 1968). For example, Bard (1990) described how orangutans younger than 10 months use various goal-directed and “manipulative” begging actions to solicit food from their mothers (e.g., pulling on mothers body parts). Similarly, Van Lawick-Goodall (1967, 1968) highlighted the importance of “manipulative” tactile movement and signals between chimpanzee mothers and infants in the first few months of the infants’ life; for example, “hair pull” by the infant during suckling episodes or mother “pushes” to adjust position prior to or during breastfeeding.

As the infant increasingly moves away from the mother with age, visual signals (including overt gestures and facial expressions) gain importance (Van Lawick-Goodall, 1967). This is congruent with our observations (Schneider et al., 2012a) that advanced motility might be an important antecedent in gestural onset and development; as it encourages independence from the mother, and increases the likelihood of interactions with other group members (see Fröhlich, Wittig, & Pika, 2016 for similar findings in wild chimpanzees). In juxtaposition, we observed orangutans, who were the last to start gesturing, to be the last to gain independent locomotion, and that in African apes, visual signaling gained prominence over time as tactile signaling decreased and inter-conspecific distances increased (Schneider et al., 2012a).

In a systematic comparison of bonobos’ and chimpanzees’ mother–infant gesturing, we found gestural repertoires to be dissimilar (Schneider et al., 2012b); infants and mothers were more likely to share repertoires with same-age peers across species than they were with each other. These findings indicate a phylogenetic influence in the formation of early gestural repertoires, which are then likely to be further shaped through social encounters during development (Schneider et al., 2012b; see also Call and Tomasello, 2007). The current study aims to establish rudimentary communicative patterns in these early social encounters, through considering the

gestural prevalence and response behavior between mother and infant; relative to their communication to other group members. Studies incorporating the recipient (rather than sender) perspective have only relatively recently emerged (Slocombe, Waller, & Liebal, 2011) and, as of yet, have not incorporated different ape species or targeted the mother–infant dyad (Cartmill & Byrne, 2010; Hobaiter & Byrne, 2014; Luef & Liebal, 2012, 2013; Pollick & de Waal, 2007; Roberts et al., 2012; cf., Fröhlich et al., 2016a).

1.3 | The current study

The potential for human mothers to play a “giving,” “responding,” and “scaffolding” role in the development of their children’s communication is well established (e.g., Bullowa, 1979; Kaye, 1979; Keller, Lohaus, Völker, Cappenberg, & Chasiotis, 1999). To what extent nonhuman great ape mothers play a similar role in their infants’ communication development is largely unknown. We addressed this gap in our knowledge by investigating ape mothers gestural “giving” and “responding” behavior in interactions with their infants. In the first comparative study of its kind (incorporating bonobos, chimpanzees, gorillas, and orangutans) we analyzed the gesture frequency and response patterns in mother–infant dyads, along with their interactions with other group members. We observed 25 ape mother–infant dyads in order to: (i) identify the prevalence of mothers and infants’ gesturing to each other (as well as to other group members); and (ii) investigate the extent to which mothers and infants reacted to gestures both from inside and outside the dyad. In line with a growing body of evidence suggesting that bonobos are more socially “sophisticated” than other species, we predicted that bonobo mothers would be more proactive in their infant-directed gesturing (i.e., would gesture more frequently) than mothers of the other species. No other species or group membership differences were predicted.

2 | METHODS

Six bonobo, eight chimpanzee, three gorilla, and eight orangutan mother–infant dyads were observed during the offspring’s infancy (i.e., from 0 to 2.5 years of age). They were housed in social groups (of varied size and age distribution) in six European zoos. Dyads were followed for up to the first 20 months of the infants’ life with a minimum observation time of 4 months (see Online Supporting Information, Table S1 for detailed information on individuals, parity of mothers, group and zoo affiliation, observation times and protocols; see also Schneider et al., 2012a). All zoos shared similar animal husbandry protocols, and all enclosures contained climbing and resting structures, as well as foraging materials and other enrichment opportunities.

Using *focal animal sampling* (Altmann, 1974), the authors CS, JC, and research assistants videoed different mother–infant dyads over an 8-year period. Infant and mother social interactions were recorded for four sessions per month, each lasting 5 min (resulting in 20 min per month and per infant); this culminated in an average of 27 hr of video footage per species.

Following Call and Tomasello (2007), a gesture was defined as a motoric action directed to a particular recipient (by using head, limbs, or whole body), which served a functional purpose, and where the sender showed anticipation of the recipient’s reaction (e.g., gestures were accompanied by gazing and body orientation). For each gesture, we recorded: the sender, recipient, gesture modality (tactile: involving body contact with recipient, e.g., *hitting*; visual: signaling via body movement or posture over distance, e.g., *arm raising*; and auditory: signaling via the acoustic channel which was not produced by vocal chords, e.g., *chest beating*); specific gesture type (e.g., *arm on and gentle touch*; Online Supporting Information, Table S2); behavioral context (as judged by the available information that accompanied the signal, i.e., access, affiliation, agonism, ingestion, playing, sexual, and locomotion; Online Supporting Information, Table S2); and the reaction of recipient. Gesture modality, type, and behavioral context information was not considered in inferential statistics due to considerably reduced number of gestures which remained after individual ape scores were categorized by these codes.

We recorded both infant and mother gestures (directed to respective dyad member and other social group members), as well as their behavioral responses to gestures from others (i.e., respective dyad member and other group members). Moreover, gestures from other group members (referred to as “others”) directed to both infants and mothers were recorded. For both mothers and infants, we calculated gesture frequencies within the dyad per hour (note, where relevant for infants, individual gestural onset dates were taken as baseline; Online Supporting Information, Table S1; Schneider et al., 2012a). Gestures to “others” were summed for each dyad member and again production was subsequently calculated per hour (gestures from “others” were similarly summed for each dyad member). To ascertain whether the frequency of gestures mother and infant directed to “others” varied with group size in the four species (i.e., whether individuals living in bigger groups directed more gestures to others), we conducted Kendall’s tau (τ) correlations.

To study the reaction that followed a received gesture for both infants and mothers, we recorded whether a reaction occurred or not within 10 s. A *reaction* was either another gesture or a “non-communicative” action in relation to one of the behavioral contexts outlined above. *No reaction* was recorded if no visible behavioral change was observed after a gesture was received (e.g., individuals continued behavior evident before gesture was shown). For the analyses, gesture response cases were only incorporated when a “reaction” or “no reaction” distinction could be made; cases where this was not possible were referred to as *unknown* (e.g., visibility was hindered or another individual interfered before the receiver “could react”) and were excluded. We calculated a “response ratio” to determine the (proportional) responsiveness to gestures in mother and infant recipients (Martin & Bateson, 2007; Pollick & de Waal, 2007). For example, if an individual “reacted” to all gestures directed at them, they scored 1; if an individual never showed a reaction to any gestures directed at them, they scored 0. The resulting responsiveness scores were compared across species and contrasted between mother and infant.

We used nonparametric tests (i.e., Kruskal–Wallis, Mann–Whitney, and Wilcoxon test) and *p* values were two-tailed. If computations were possible, exact significances were reported; otherwise we referred to

Monte Carlo significances (Mehta & Patel, 2012). A null hypothesis was rejected at an alpha-level of 5%. Effect sizes were reported for the Wilcoxon and Mann-Whitney tests (using Pearson's correlation coefficient r ; Field, 2013). An effect size of 0.10 represented a small effect, 0.30 a medium effect, and greater than 0.50 a large effect (Cohen, 1988).

CS coded the video material. To ensure inter-observer reliability, 10% of data (randomly chosen across species) were coded by a second independent observer. The resulting Cohen's Kappa values of 0.89 ($p < 0.001$) for gesture type (incorporating gestures produced by mother, infant, and other group members) and of 0.8 ($p < 0.001$) for gestural response (for mother and infant recipients) indicate "good" to "very good" levels of agreement (Altman, 1991).

2.1 | Ethical Considerations

The research was purely observational and did not intrude on apes' daily routines. Our study fully adhered to the regulations and legal requirements for the involvement of animal subjects of the countries in which it was conducted. Moreover, collaborating zoos complied with the animal husbandry principles of the European Association of Zoos

and Aquaria (EAZA; 'EAZA Minimum Standards for the Accommodation and Care of Animals in Zoos and Aquaria').

3 | RESULTS

3.1 | Overview of gestures

Overall, we observed 1529 gestures. Infants produced 298 gestures (114 gestures were directed to mother and 184 to other group members), and mothers produced 529 gestures (303 gestures directed to the infant and 226 to other group members). Moreover, we recorded 370 gestures group members directed at the infant and 332 gestures they directed at the mother (Table 1).

3.2 | Bonobo mothers are more likely to gesture to infants

When contrasting the four species, we found frequency differences for the gestures mothers directed to their infants; Kruskal-Wallis test:

TABLE 1 Production of gestures in observed time frames for each dyad member and the number of gestures directed to infant and mother from other group members (referred to as "others")

Species (no. of dyads)	Dyad (infant-mother)	Infant to		Others to infant	Mother to		Others to mother
		Mother	Others		Infant	Others	
Bonobo ($n = 6$)	Habari-Djanao	1	26	11	8	6	1
	Hongo-Hortense	15	6	12	59	4	4
	Huenda-Hermien	2	4	26	5	1	14
	Kivu-Yala		10	24	37	26	29
	Luiza-Ulindi	6	2	3	36	11	6
	Nayembi-Liboso	7	5	16	13	2	
Chimpanzee ($n = 8$)	Gihneau-Gaby	11	24	22	10		9
	Kara-Fraukje	2	5	62	33	13	30
	Kofi-Ulla	3	19	36		17	29
	Lobo-Corry	2	16	30	5	28	17
	Lome-Corry	6	1	17	7	7	21
	Mora-Riet	2		6	11	15	14
	Nafia-Yola	2	7	15	32	6	47
	Tai-Riet	1	9	18	5	11	17
Gorilla ($n = 3$)	Kibara-Virginika	15	9	6	4	17	24
	Louna-Bebe	15	2	14	13	12	12
	Shaila-Shatilla		1	5	1	3	9
Orangutan ($n = 8$)	Dayang-Sandy	1	2	10	1	1	
	Güsa-Sabatini		1			12	2
	Ito-Temmy	5	1	5	7	2	10
	Kila-Dunja	1	7	2		6	13
	Maia-Dunja			3	4	4	6
	Merah-Radja	3	9	7		4	1
	Pagai-Dokana	14	7	11	6	17	15
	Raja-Pini		11	9	6	1	2
Total		114	184	370	303	226	332

$H(3) = 10.07$, $p = 0.009$, $N = 25$; but not for those gestures mothers directed to others, $H(3) = 0.29$, $p = 0.966$, $N = 25$. Bonobo mothers ($n = 6$) gestured significantly more to their infants than orangutans; Mann-Whitney test ($n = 8$): $U = 1$, $z = -2.98$, $p = 0.001$, $r = -0.80$, and gorillas ($n = 3$), $U = 1$, $z = -2.07$, $p = 0.048$, $r = -0.69$; but not chimpanzees ($n = 8$), $U = 12.5$, $z = -1.49$, $p = 0.151$, $r = -0.40$. Chimpanzee mothers ($n = 8$), however, did not differ in infant-directed gestures compared with orangutans ($n = 8$), $U = 18.5$, $z = -1.43$, $p = 0.166$, $r = -0.36$; and gorillas ($n = 3$), $U = 6$, $z = -1.23$, $p = 0.255$, $r = -0.37$ (Figure 1).

Bonobos, but not chimpanzees and orangutans, directed significantly more gestures to their infants than to other group members; Wilcoxon test: bonobo ($n = 6$), $z = -2.20$, $p = 0.031$, $r = -.64$; chimpanzee ($n = 8$), $z = -0.51$, $p = 0.688$, $r = -0.13$; orangutan ($n = 8$), $z = -1.57$, $p = 0.156$, $r = -0.39$. We did not include gorillas in this analysis as their small sample size ($n = 3$) was below the threshold for a Wilcoxon test to be statistically meaningful (Siegel, 1956); however, visual inspection of their data showed they directed less gestures to infants than to other group members (see below, for correlation analyses of “other” gesture frequency and group size).

For infants, the gestures directed to mothers did not significantly differ to those directed to other group members; Wilcoxon test: bonobo ($n = 6$), $z = -0.53$, $p = 0.688$, $r = -0.15$; chimpanzee ($n = 8$), $z = -1.40$, $p = 0.195$, $r = -0.35$; orangutan ($n = 7$), $z = -1.52$, $p = 0.141$, $r = -0.41$ (again gorillas were excluded

from this analysis, see above). Across species, we found no statistical differences in gesture frequency for both mother-directed gestures by infants, $H(3) = 0.2$, $p = 0.981$; $N = 24$; and for those gestures infants directed to other group members, $H(3) = 2.71$, $p = 0.457$, $N = 24$ (Figure 2).

Finally, to ascertain whether the gestures mother and infant directed to “others” varied with group size in the four species, we conducted Kendall's tau (τ) correlations. Chimpanzee mothers ($n = 6$) living in bigger groups were more likely to produce a greater number of gestures, $\tau = 0.79$, $p = 0.032$. We found no other significant relationships between group size and the gestures mothers (bonobo, $n = 6$: $\tau = -0.55$, $p = 0.165$; orangutan, $n = 7$: $\tau = -0.47$, $p = 0.174$), and infants (bonobos, $n = 6$: $\tau = 0.18$, $p = 0.643$; chimpanzees, $n = 6$: $\tau = 0.65$, $p = 0.079$; orangutans, $n = 7$: $\tau = 0.00$, $p = 1$) directed to others.

3.3 | Infants are more likely to “respond” to gestures than mothers

Overall, and across all species, we considered 1119 responses; 673 gestures were directed to infants and 446 gestures directed to mothers (Table 1; note, 121 responses directed to infants and 16 to mothers, coded as “unknown,” were not incorporated; see Section 2).

We calculated “response ratios” to determine the (proportional) responsiveness to gestures in mother and infant recipients. Across all

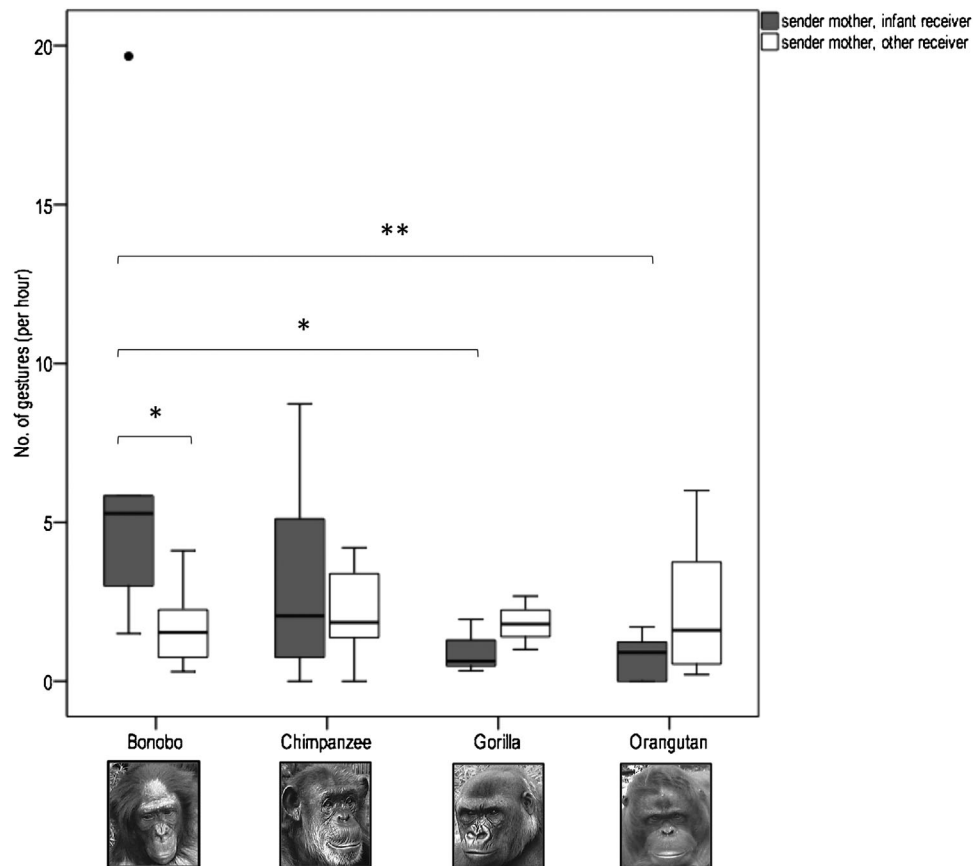


FIGURE 1 Boxplots showing the median number of gestures (per hour) mothers directed to their infants and other group members (referred to as “other”) across the four nonhuman great ape species (bonobos, $n = 6$; chimpanzees, $n = 8$; gorillas, $n = 3$; orangutans, $n = 8$; * $p < 0.05$; ** $p < 0.01$)

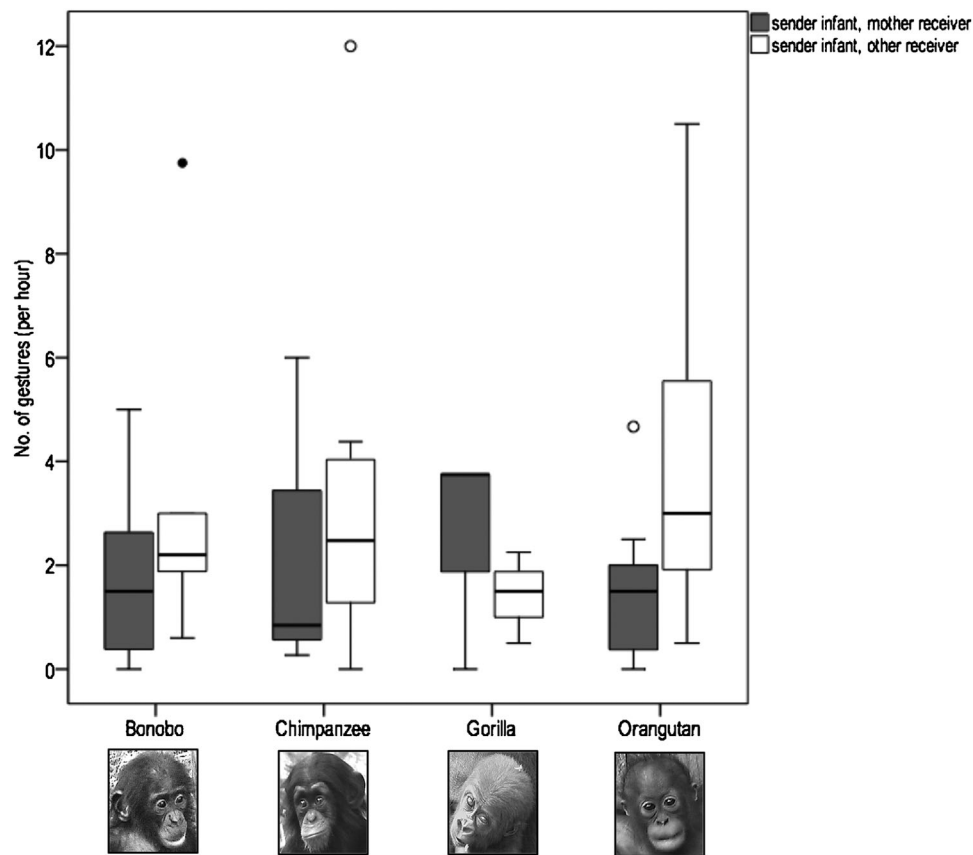


FIGURE 2 Boxplots showing the median number of gestures (per hour) infants directed to their mothers and other group members (referred to as “other”) across the four nonhuman great ape species (bonobos, $n = 6$; chimpanzees, $n = 8$; gorillas, $n = 3$; orangutans, $n = 7$)

four species, infants did not statistically differ in their responses to gestures from their mothers (median response ratios between 0.8 and 1); $H(3) = 4.03$, $p = 0.272$, $N = 21$; and from other group members (ratios between 0.75 and 1); $H(3) = 1.88$, $p = 0.621$, $N = 24$. Mothers,

across species, also did not statistically differ in their response ratio to infants' gestures (ratios between 0.27 and 0.67), $H(3) = 3.02$, $p = 0.420$, $N = 20$; or to other group members' gestures (ratios between 0.41 and 0.67), $H(3) = 4.7$, $p = 0.205$, $N = 23$ (Figure 3).

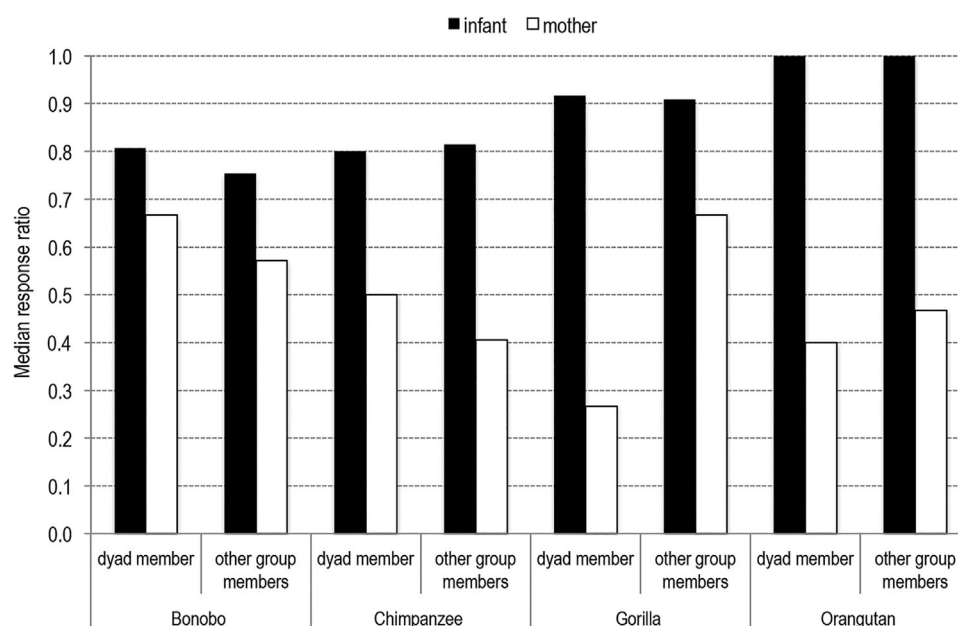


FIGURE 3 Median response ratio for both mothers and infants when receiving gestures from respective dyad member and other group members across the four nonhuman great ape species

As we observed no significant differences in mothers' or infants' response behaviors across species we amalgamated and contrasted both their response ratio scores. Infants (median response ratio 0.92; $n = 21$) were significantly more likely to react to gestures than mothers (0.5; $n = 20$), $U = 98.5$, $z = -2.96$, $p = 0.003$, $r = -0.46$. Similarly, infants (0.85; $n = 24$) reacted significantly more to gestures from other group members than mothers (0.5; $n = 23$), $U = 131$, $z = -3.1$, $p = 0.002$, $r = -0.45$ (Figure 3).

4 | DISCUSSION

We observed distinct and subtle differences in the way mothers "give" (i.e., direct gestures to infants) and "respond" (to gestures) in bonobos, chimpanzees, gorillas, and orangutans. Bonobo mothers differed in their gesturing toward infants from other ape species in two important ways. First, they produced more infant-directed gestures than gorillas and orangutans (but not chimpanzees), and second, only bonobo mothers gestured significantly more toward their infants than they did to other group members. However, bonobo mothers were along with other ape mothers, "ambivalent" in their responsiveness (i.e., in the sense of being as likely to react as not) to gestures produced by infants (or other group members). In contrast, infants of all species were more likely to react "pervasively" to gestures from both mothers and other group members (i.e., in the sense of being more likely to react than not to react).

4.1 | Bonobo mothers are the most proactive in communicating to their infants

In support of our initial prediction that bonobos are more proactive in their gesturing towards infants when compared with other species, our findings are consistent with established and emergent evidence that bonobos are more subtly attuned and motivated to attend to the nuances of social interaction (e.g., De Waal, 1988; Kano et al., 2015; Pollick & de Waal, 2007; Schneider et al., 2010). In this way, bonobos may share important commonalities with human mothers who (as evidenced in Western cultures) are proactive in communication with their infants (e.g., Kaye, 1979; Keller et al., 1999; Masur et al., 2005; cf., Reck et al., 2004).

Bonobos clearly differed from gorillas and orangutans in their rates of infant-directed gesturing, but they were less distinguishable from chimpanzees. While chimpanzees did not share bonobos' tendency to direct more gestures to their infants than to other group members, they were not statistically dissimilar in the numbers of infant-directed gestures they presented. These observed commonalities in mother-infant gesturing are not surprising given that fundamental communicative similarities have been previously identified in genus *Pan*, for example, use of similar gesture repertoires for same-age peers (De Waal, 1988; Schneider et al., 2012b). However, our correlational analyses considering group sizes indicates that while elements of "sociability" may be mapped in *Pan* species, "qualitative" behavior differences may be present. For example, chimpanzees directed more gestures to other group members as group sizes increased, whereas

bonobo mothers were "unaffected" by the group size they resided in. While this strengthens our finding that bonobos "invested" more in their interactions with infants, further clarification of the nuances in early mother-infant communication in these species is needed.

Despite the small sample, our finding that gorilla mothers were initiating less gestural interactions with their infants than bonobos fits to what we know about gorillas' limited social intra-group interactions (Watts, 1996, 2003). It also supports previous research (Maestriperi, Ross, & Megna, 2002), where gorilla mothers generally showed "little or no encouragement" toward their infants (e.g., in object manipulation and food sharing), and, unless an infant was at risk, remained uninvolved in their "social and nonsocial activities." Like gorillas, we observed orangutan mothers to also be less proactive than bonobo mothers in their gesturing to infants. This is an interesting finding given, across species, orangutan offspring spend the longest period in close proximity with their mother and are judged to manifest a particular tight bond (Van Noordwijk et al., 2009). Moreover, compared with other ape species, dyads live as relatively independent units with respect to conspecifics surrounding them in their natural habitats (Van Schaik, 1999). And yet, as Van Noordwijk et al. (2009) noted, orangutan mothers generally play infrequently with their infants and, compared with other apes, are less likely to groom them. Orangutan infants, on the other hand, carefully watch their mothers' feeding behavior (Van Noordwijk et al., 2009; Van Schaik, 2004), and, as the current study demonstrates, are (similar to gorillas) highly responsive to their mothers' and others' gestures. Thus, while orangutan mother-infant dyads establish a close unit, this does not seem to extend to increased levels of communication from the mother; a finding which may be contextualized in a generally less interactive "parenting style" in orangutans.

Compared to other apes, the increased motivation observed in bonobos to socially engage and communicate, specifically in the context of the close mother-infant relationship, is likely to be adaptive and embedded in the broadly, more diffused and egalitarian structures they live in and have evolved in (De Waal, 1988; Hare et al., 2007; Kano, 1992; Palagi, 2006; Paoli, Palagi, & Tarli, 2006; for possible ecological explanations of these structures see Hare, Wobber, & Wrangham, 2012; Wilson et al., 2014). Moreover, it has been argued that bonobos' advanced social-problem-solving abilities are likely to be anchored in their "balanced" emotional temperament, which affords more cooperative behavior opportunities (Hare & Tomasello, 2005).

An alternative explanation for the more pronounced mother-to-infant gesturing in bonobos may be that mothers simply gesture more frequently due to their increased playfulness across the lifespan when compared to other species (e.g., Demuru, Ferrari, & Palagi, 2015; Hare et al., 2012; Palagi, 2008). Previous studies (including those considering mother-offspring dyads) have documented that *play* is particularly important as a communicative platform for gesture occurrence in all ape species (Call & Tomasello, 2007; Schneider et al., 2012b). While we recorded the behavioral contexts in which gestures occurred, a meaningful statistical analysis was not possible due to the limited number of gestures that remained after contexts were broken down by individual. However, although we are unable to fully rule out playfulness as an influential factor, we know from previous studies that play-related

gestures are most prominent in mother–infant interactions in all apes; not just bonobos (Schneider et al., 2012a,b).

4.2 | Ape infants are “pervasively” responsive, while mothers are more “ambivalent”

While it is important to note that maternal response styles vary across cultures (e.g., Bornstein, Tamis-LeMonda, Hahn, & Haynes, 2008; Ochs & Schieffelin, 1982; Richman, Miller, & LeVine, 1992), and may diminish in certain impoverished and vulnerable environments (e.g., mothers developing postpartum depression develop passivity and reduced responsiveness; Reck et al., 2004); humans have the potential to be highly responsive to their infant's behavior (both vocally and non-vocally; e.g., Lloyd & Masur, 2014). Our study highlights that while bonobo mothers appear to resemble “human-like” potential to communicatively (albeit non-vocally) “address” their infants, they—along with mothers from other ape species—were less likely to “react” and extend the communicative interaction in receipt of an infant gesture. This generic “ambivalent” gesture responsiveness observed in ape mothers is a new and intriguing finding. Moreover, it may support the idea that adult nonhuman great apes lack the full capacity to acknowledge and incorporate the “other” in their communication efforts; and highlight humans' unique potential for cooperative communication and for their understanding of shared conventions—which carries obvious and important implications for the evolution of language (e.g., Call & Tomasello, 2008; Grice, 1975; Tomasello, 2008).

The current study raises important questions about what impact ape mothers' “ambivalence” in responsiveness has on infants' communicational and wider development (e.g., Tronick, 1989). Plooiij (1979) observed, for example, unresponsive chimpanzee mothers led to a “deprivation” state which elicited more self-stimulating behaviors (e.g., self-biting, sucking cheeks inward and rocking) in infants. Moreover, the importance of emotional engagement, and how it positively affects young, captive-born chimpanzees' social cognition, has been previously reported by Bard, Bakeman, Boysen, and Leavens (2014). More specifically, addressing the question of early gestural acquisition, the observation that bonobo mothers were less likely to respond to their infants' gestures (despite presenting more gestures to them) resonates with previous reports that infants of the genus *Pan* seem unlikely to learn gestures from their mothers (Schneider et al., 2012b); that is, a diminished responsiveness in ape mothers may be implicated in this absence of learning.

Interestingly, and in contrast to their mothers, infants of all four species were “pervasive” in their gestural responsiveness (toward both mothers and other group members). This may be indicative of an “intrinsic motivation” for the young to make *effect* in their environment (White, 1959; see also Csibra, 2010). White (1959) proposed, there was a predisposition for “effectance motivation” which manifested in earliest infancy in humans and other species. Individuals from birth develop essential adaptive “competence” through proactive and pervasive exploration, action, and reaction in their environment, which becomes more refined and discriminant as they develop into adulthood. White (1959) proposed that the motivation to make pervasive *effect* changes will therefore be reliant on the constituent parts of the environment

itself. For example, as ape infants grow older, they become more actively involved in the complex hierarchical structures existing in their “societies” (Mitani, Call, Kappeler, Palombit, & Silk, 2012; Smuts, Cheney, Wrangham, & Struhsaker, 1987) and will, as a result, “constrain” or differentiate their social behavior accordingly.

Infants' *pervasive responsiveness*, paired with their mothers' *ambivalent responsiveness*, opens up the intriguing possibility that communicative development is predominantly driven by interactions and contexts outside the mother–infant dyad, for example, peer interactions in play (for similar reports in stump-tail macaques, *Macaca arctoides*, see Chevalier-Skolnikoff, 1974). This is further supported by emergent evidence indicating that an infant ape's independence from, rather than contact with, their mother may be an important antecedent for gestural development (Schneider et al., 2012a,b). Moreover, infants' *pervasive responsiveness* may, in itself, be an essential phylogenetic characteristic shared by all ape species (i.e., including humans), which enables the infant to communicatively adapt and develop in the social environment they are born into, regardless of the “stimulation” afforded. In certain non-Western cultures and vulnerable Western settings, for example, where human caregivers investment in infant's communication is less apparent (e.g., Ochs & Schieffelin, 1982; Reck et al., 2004), infants still learn to communicate effectively.

4.3 | Limitations and future directions

The current study is, to our knowledge, the first systematic analysis of gesture behavior and response patterns within mother–infant dyads across all four nonhuman great ape species. However, the strength of our interpretations and conclusions are affected by data limitations; not least our (unique but still) small sample sizes and modest number of gestures available restricted analytical options (e.g., the potential to integrate behavioral context). Furthermore, current findings and interpretations are based on captive individuals living in constrained, predetermined environments; hence, extrapolation power should be treated with caution until verified in other populations, including those living in natural habitats. Given the logistical and pragmatic challenges involved in extending this type of data set (especially in wild conspecifics), merging data from independent research groups would be a worthwhile direction to further validate our current findings and to obtain answers to important questions raised in this study. Finally, a more fine-grained analysis of “responsiveness” will afford opportunities to investigate interactional communicative *processes*, rather than simple and—as it currently stands—relatively broad *outcomes* alone. To delve more deeply into the nuanced action-and-reaction patterns between mother and infant, dyadic-interactional designs, where the sequence and streams of behavior are analyzed (e.g., Bakeman & Quera, 2011), appear particularly fruitful and would best replace the current unidirectional approach.

5 | CONCLUSIONS

Our comparative investigation of mother–infant gestural communication identified bonobo mothers to be the most proactive in their

gesturing to infants across all apes. This finding adds to a growing body of research indicating bonobos are more “socially attuned and motivated” when compared with other nonhuman great apes. However, the observation that bonobo and other species’ mothers were “ambivalent” in their responses to infant gestures begs the questions: to what extent ape mothers have the potential to *mutually engage* in interactions with infants, and whether social attunement and motivation are, in themselves, enough. At the same time we observed *pervasive responsiveness* in infants of all four species, which we, and others, propose is shared with humans, and is likely to play an essential role in gestural and social development in general.

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SUPPORTING INFORMATION

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