# Body Language: The Interplay between Positional Behavior and Gestural Signaling in the Genus *Pan* and Its Implications for Language Evolution

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*ABSTRACT*     *Objectives:* The gestural repertoires of bonobos and chimpanzees are well documented, but the relationship between gestural signaling and positional behavior (i.e., body postures and locomotion) has yet to be explored. Given that one theory for language evolution attributes the emergence of increased gestural communication to habitual bipedality, this relationship is important to investigate.
*Materials and Methods*: In this study, we examined the interplay between gestures, body postures, and locomotion in four captive groups of bonobos and chimpanzees using *ad libitum* and focal video data.
*Results:* We recorded 43 distinct manual (involving upper limbs and/or hands) and bodily (involving postures, locomotion, head, lower limbs, or feet) gestures. In both species, actors used manual and bodily gestures significantly more when recipients were attentive to them, suggesting these movements are intentionally communicative. Adults of both species spent less than 1.0% of their observation time in bipedal postures or locomotion, yet 14.0% of all bonobo gestures and 14.7% of all chimpanzee gestures were produced when subjects were engaged in bipedal postures or locomotion. Among both bonobo groups and one chimpanzee group, these were mainly manual gestures produced by infants and juvenile females. Among the other chimpanzee group, however, these were mainly bodily gestures produced by adult males in which bipedal posture and locomotion were incorporated into communicative displays.
*Discussion:* Overall, our findings reveal that bipedality did not prompt an increase in manual gesturing in these study groups. Rather, body postures and locomotion are intimately tied to many gestures and certain modes of locomotion can be used as gestures themselves. Am J Phys Anthropol 157:592–602, 2015. © 2015 Wiley Periodicals, Inc.

Gestures are integral components of human and non-human primate communication. In humans, gestures appear early in life before verbal communication develops (Knott, 1979) and remain essential to language after the onset of speech (Dunning, 1971; Melinger and Levelt, 2004; Goldin-Meadow and Alibali, 2013). Similarly, non-human primates use gestures both as an independent means of communication and in conjunction with vocalizations and facial expressions. Among African apes, gestures are known to be multi-functional and variable across populations of the same species (de Waal, 1988; Pika *et al.*, 2003, 2005a,b; Tomasello and Call, 2007; Smith, 2011; Roberts *et al.*, 2012; Scott 2013; Smith and Delgado, 2013; Roberts *et al.*, 2014). While much is known about the breadth of gestural repertoires and the contexts in which they are used among chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*), the extent to which factors such as ecology, social dynamics, cognition, and locomotion differentially shape gestural repertoires remains unresolved (Pika *et al.*, 2005a; Smith and Delgado, 2013). In particular, the relationship between gestures and positional behavior (i.e., body postures and modes of locomotion, Prost, 1965; Hunt *et al.*, 1996) has been overlooked in gestural communication research.

Studies into the relationship between positional behavior and gestures are lacking, in part, because of disagreement about how gestures are defined. In humans, gestures can be broadly categorized as speech illustrators (gestures such as gesticulations that accompany speech) and emblems (those that hold referential meaning independent from speech) (Matsumoto and Hwang, 2013). While many human gestures are manual, we also communicate a great deal of information about our emotional states, desires, and intentions through 'body language,' or postures and other movements that are not limited to the arms or hands (Kelly *et al.*, 2002). In the non-human primate gesture literature, there is

disagreement about how to classify gestures and which body movements should be deemed intentionally communicative (i.e., the actor uses body movements in a goal-directed manner with sensitivity to the recipient's attentional state and shows signs of persistence if the goal is not met). Some researchers argue that gestures should be restricted to limb or hand movements (e.g., Pollick and de Waal, 2007; Roberts *et al.*, 2012) or limb and head movements (e.g., Tanner and Byrne, 2010), while others (Pika *et al.*, 2003; Liebal *et al.*, 2004a; Smith, 2011; Scott, 2013; Smith and Delgado, 2013; Roberts *et al.*, 2014) contend that certain body postures and gaits should be considered gestures because they can also be used intentionally to communicate.

In humans, manual gestures and other communicative body movements play essential roles in language production and comprehension (Kelly *et al.*, 2009; Goldin-Meadow and Alibali, 2013). Gestures are a form of embodied cognition in that they express unspoken thoughts (Kinsbourne, 2006) and shape what and how we think (Goldin-Meadow, 2014). For example, in a study on the role of gestures in learning, Goldin-Meadow (2014) found that students who used gestures to solve a math problem (alone or with speech) retained the information longer than those who did not gesture. Furthermore, students who were asked to gesture when reasoning about a moral dilemma were more likely to take on multiple perspectives in their speech than students who spoke without using gestures. In addition, the same neural networks involved in language production and comprehension are activated whether we produce manual or bodily gestures ourselves or we watch others gesture (Arbib, 2005). Given their close evolutionary relationship to humans, we argue that bonobos and chimpanzees also use body movements beyond strict manual gestures to communicate and that postures and locomotor patterns may play a more meaningful role in communication than previously recognized.

Body postures and locomotor patterns (Prost, 1965; Doran, 1993, 1996; Hunt *et al.*, 1996) are also important in the context of communication because they place constraints on the use of gestural signals. For example, individuals are restricted in their use of manual or bodily gestures by certain forms of locomotion like climbing or quadrupedal walking. Thus, we hypothesize that positional behavior can dictate when and how gestures are used in a particular species and in which behavioral contexts. Examining the interplay between manual and bodily gestures and positional behavior is crucial for understanding connections between gestures and the body, and the constraints posture and locomotion can place on communication.

Clarifying the relationship between gestures and the body is also important for understanding the role of gestures in the evolution of language. One proposed factor for the emergence of gestural signaling in humans was the shift toward bipedality in early hominins, which left upper limbs less suited for locomotion and more accessible for other actions such as manual gesturing (Armstrong *et al.*, 1995; Armstrong, 2008; Corballis, 2002, 2003, 2009; see Smith and Delgado, 2013 for a review of the gestural origins hypothesis). This hypothesis posits that gestural signaling provided the foundation for language, and then speech was incorporated into this system as anatomy allowed (Hewes, 1973; Leroi-Gourhan, 1993; Corballis, 2002, 2003; Gentilucci and Corballis, 2006; Corballis, 2009). These early manual gestures may

have been referential gestures like pantomimes, symbolic emblems (or "quotable gestures," Burling, 2005, p. 41), or even a rudimentary form of speech illustrators. Regardless of the types of early gestures hominins may have used initially or the information that these gestures communicated, the first step in testing the gestural origins hypothesis is investigating the relationship between bipedality and manual gesturing. Testing this hypothesis is challenging because the fossil record cannot reveal how communication may have shifted in response to changes in skeletal anatomy and positional behavior. However, we can use our closest living relatives, bonobos and chimpanzees, as models for how early hominins may have used gestures to communicate and to test predictions about how positional behavior influences gestural communication (or vice versa), particularly the use of manual gestures.

Bonobos and chimpanzees are both predominantly knuckle-walkers and have anatomical adaptations for suspensory locomotion (Doran, 1993, 1996; Doran and Hunt, 1996), yet few cross-species comparisons have been done with respect to differences in their locomotor profiles or how these differences may impact communication. Bonobos and chimpanzees are similar in body size, yet there is still significant morphological variation within the genus *Pan* (Morbeck and Zihlman, 1989) and sexual dimorphism in body size among chimpanzees that may influence positional behavior, and in turn, gestural communication. For example, bonobos generally have longer lower limbs and a lower mean intermembral index than chimpanzees (Coolidge and Shea, 1982; Morbeck and Zihlman, 1989; Doran, 1993). Accordingly, one could predict that this anatomical difference may enable bonobos to walk bipedally more efficiently than chimpanzees, which could influence the frequency and type of manual or bodily gestures bonobos use.

Research that explicitly examines positional behavior in bonobos and chimpanzees is scant. Videan and McGrew (2001) compared bipedal postures and locomotion in captive bonobos and chimpanzees and found no species differences in the rates of bipedal locomotion or postures. However, the two species used bipedal postures and locomotion in different contexts: bonobos relied more on bipedality during vigilance and when carrying objects, while chimpanzees used bipedality more frequently during dominance displays (Videan and McGrew, 2001). At Bossou, Carvalho *et al.* (2012) provided chimpanzees with two species of nuts and observed that chimpanzees walked bipedally more often and carried more nuts when transporting the locally unavailable and highly prized coula nut (*Coula edulis*) than the locally available oil palm nut (*Elaeis guineensis*). Chimpanzees have also been observed to use bipedal postures when feeding on fruits in large trees, though at different rates at different sites (0.79 bipedal bouts/hour at the Bwindi Impenetrable Forest in Uganda, Stanford, 2008; 0.17 bipedal bouts/hour in the Mahale Mountains National Park in Tanzania, Hunt, 1994). Thus, bipedal postures and locomotion are important to captive and wild bonobos and chimpanzees in multiple contexts and in varying degrees, but there is no clear picture of how important bipedal postures and locomotion are to their overall locomotor profiles or what impact this behavior has on communication.

Given that patterns of positional behavior vary across groups of the same species and comparative data on durations of positional behavior and rates of bipedality

TABLE 1. Bonobo (Pan paniscus) group compositions

| | San Diego Zoo (n = 8) | | | San Diego Zoo Safari Park (n = 8) | |
|---|---|---|---|---|---|
| Name | Age/Sex Class (DOB) | Dam/Sire | Name | Age/Sex Class (DOB) | Dam/Sire |
| Yenge | AM (12/82) | Unknown | Akili | AM (2/80) | Matata/Bosondjo |
| Junior | AM (1/95) | Lana/Maiko | Erin | AM (12/91) | Loretta/Vernon |
| Lana | AF (4/79) | Linda/Kakowet | Jumanji | AM (5/96) | Marilyn-Lori/Akili |
| Lolita | AF (4/89) | Louise/Vernon | Loretta | AF (1/74) | Linda/Kakowet |
| Ikela | AF (11/91) | Louise/Akili | Connie-Lenore | AF (2/82) | Louise/Vernon |
| Mchumba | JF (12/00) | Lolita/Maiko | Marylin-Lori | AF (11/87) | Louise/Vernon |
| Makasi | IM (4/04) | Loretta/Jumanji | Muhdeblu | JF (4/01) | Marilyn-Lori/Erin |
| Kesi | IF (8/04) | Loretta/Yenge | Kallie | IF (3/05) | Loretta/Jumanji |

AM = adult male, AF = adult female, JF = juvenile female, IM = infant male, IF = infant female. Subjects were categorized by age at the start of data collection.

have been difficult to obtain, the relationship between body postures, locomotion, and gestural communication in *Pan* is not well understood. Nonetheless, this relationship is vital to understanding the variability in gestural repertoires across populations and between species and examining what forces shape gestural communication. To test the hypothesis that early hominins began using their upper limbs more frequently for gestural communication once their upper limbs were freed from the demands of quadrupedal locomotion, it is important to examine how closely related species use manual gestures in relation to their positional behavior.

Here, we examined the extent to which body postures and locomotion influence variability in the gestural repertoires of our closest living relatives, bonobos and chimpanzees. For the purposes of this study, we defined a gesture as a limb movement, head movement, body posture, or gait that is used intentionally to communicate (see Methods). We recognize that locomotor patterns not only influence the modes of gesturing but may also be incorporated into intentionally communicative signals as well. Hence, we examine signaling patterns for both manual (i.e., restricted to upper limbs and hands) and bodily (e.g., using whole-body movements and postures) gestures. We hypothesized that the locomotor profiles of bonobos and chimpanzees would dictate the availability of the upper limbs for gesturing and, thus, the frequency of gestural signaling and the specific gestures used among individuals of each species. Since bonobos possess longer lower limbs than chimpanzees (Coolidge and Shea, 1982; Morbeck and Zihlman, 1989; Doran, 1993), we also predicted that bonobos would walk bipedally more frequently than chimpanzees, thereby allowing their upper limbs to be used more frequently for manual gesturing. To our knowledge, this research is the first to take into account the relationship between positional behavior and gestural communication in any non-human primate.

## MATERIALS AND METHODS
### Study subjects and sites

The subjects of this study were two groups of bonobos and two groups of chimpanzees housed in naturalistic, outdoor enclosures at four captive facilities (see Tables 1 and 2 for group compositions at each site). Bonobos were housed at the San Diego Zoo (SDZ) in a 557 m² enclosure and at the San Diego Zoo Safari Park (SDZSP) in a 4,800 m² enclosure. Chimpanzees were housed at the Saint Louis Zoo (SLZ) in a 5,300 m² enclosure and at the Los Angeles Zoo (LAZ) in a 3,530 m² enclosure.

### Data collection and ethograms

LS collected chimpanzee data from June to August 2007 (SLZ) and September to November 2007 (LAZ), and bonobo data from December 2007 to May 2008 (SDZSP) and March to June 2008 (SDZ), alternating days between bonobo sites from March to May. Data were collected five or six days a week during regular operating hours (approximately 9:30 am to 4:30 pm) in the public viewing areas at SLZ, LAZ, and SDZ. At SDZ, data were also collected from two private viewing areas during feeding periods and when individuals were not visible from public vantage points. At SDZSP, the enclosure was not accessible to the public during the study period so the group was observed from a private grassy area surrounding the enclosure.

To explore the relationship between gestural signaling and positional behavior, we collected two different types of data via video recording using a Sony DCR-DVD403 Handycam and mini-DVDs: 1) *Ad libitum* gestural data when animals were within 5 m of one another to examine the particular posture or mode of locomotion subjects used at the time of gesturing and to assess how gestures were used within each group; and 2) Continuous 15-minute focal animal sampling (Altmann, 1974) to establish comprehensive locomotor and postural profiles for each species independent of gestural signaling. Videos were reviewed, coded, and analyzed according to the coding protocols described below.

We defined a gesture as an intentional movement of the limbs or head, or a body posture or gait that appeared to transfer a communicative message. We divided gestures into manual (those that involved only the upper limbs and/or hands) and bodily (those that involved body postures, locomotion, the head, lower limbs, or feet) to examine how gestures were used in relation to the actor's positional behavior. Because an animal's intention can never be known, we considered a body movement or posture intentional if it appeared goal-directed (i.e., the actor showed signs of expecting a particular response from a recipient or tried an alternative approach if a response was not initially achieved) or if the actor showed sensitivity to the attentional state of the recipient when using gestures (Tanner and Byrne, 1996; Tomasello and Call, 1997; Hostetter *et al.*, 2001; Povinelli *et al.*, 2003; Liebal *et al.*, 2004b). For both species, only gestures that were observed at least two times in at least two individuals were included in analyses to reduce the likelihood of coding non-communicative body movements as gestures. To facilitate more direct comparisons across studies, we used the names and definitions

*TABLE 2. Chimpanzee (*Pan troglodytes*) group compositions*

| Saint Louis Zoo ($n = 11$) | | | Los Angeles Zoo ($n = 13$) | | |
|---|---|---|---|---|---|
| Name | Age/Sex Class (DOB) | Dam/Sire | Name | Age/Sex Class (DOB) | Dam/Sire |
| Smoke | AM (67? wild born) | Unknown | Shaun | AM (7/88) | Nan/Judeo |
| Jimiyu | AM (1/92) | Vicky/M'Chawi | Jerrard | AM (2/90) | Pandora/Judeo |
| Hugo | AM (5/93) | Boo/Roscoe | Glenn | AM (4/94) | Nan/Judeo |
| Rosebud | AF (70? wild born) | Unknown | Ripley | AM (3/96) | Pandora/Judeo |
| Beauty | AF (73? wild born) | Unknown | Pandora | AF (3/67) | Susie/Unknown |
| Mlinzi | AF (12/92) | Kibali/Keo | Nan | AF (12/79) | Bonnie/Johari |
| Cinder | AF (8/94) | Mollie/Smoke | Regina | AF (10/83) | Pandora/Johari |
| Holly | AF (3/98) | Snika/Chester | Joanna | AF (7/85) | Bonnie/Johari |
| Bakhari | AF (4/98) | Ruthie/Koby | Gracie | AF (1/87) | Pandora/Judeo |
| Utamu | JF (12/01) | Rosebud/Niger | Yoshiko | AF (7/90) | Regina/Judeo |
| Tammy | JF (1/02) | Unknown | Jake | JM (6/99) | Regina/Shaun |
| | | | Jean | JF (6/99) | Gracie/Shaun |
| | | | Zoe | JF (8/99) | Unknown |

AM = adult male, AF = adult female, JM = juvenile male, JF = juvenile female. Subjects were categorized by age at the start of data collection.

of gestures from published ethograms as the basis for our gesture ethogram (Table 3). We also established positional behavior ethograms for both species (compiled into one ethogram in Table 4) guided by names and definitions of postures and locomotor behaviors that had been previously defined in the literature (e.g., Hunt *et al.*, 1996).

## Coding protocol for *ad libitum* data

Video recording began whenever individuals were within 5 m of each other. Once recording began, only the gesture that initiated an interaction was coded, not gestures that were produced after a social interaction was initiated. For example, if an individual used the gesture *clap*, the recipient responded with the gesture *grab*, and play ensued, *clap* was coded as the initial gesture and *grab* was the response. All subsequent gestures (such as *push, pull*) that occurred once the interaction between the actor and the recipient was underway were not recorded. A minimum pause of 2 seconds must have occurred before a new gesture was recorded, signifying a new interaction. For example, if the actor used a gesture to restart play after at least a two-second pause, then we regarded that as a new gesture and the interaction as distinct from the previous one.

Videos were reviewed using Intervideo WinDVD 6 software and all gestures made by subjects were coded in terms of: *Actor*: producer of the gesture; *Gesture*: based on the gesture ethogram (Table 3); *Actor's positional behavior while gesturing*: based on the positional behavior ethogram (Table 4). *Recipient*: receiver of the gesture; *Recipient's attentional state*: direct eye contact or head oriented toward actor (*attentive*), or head oriented 90° or more away from actor (*not attentive*); and *Recipient's response*: coded as: *approach*, *move away*, *look toward*, *look away*, *change position*, or respond with another *gesture*. If the recipient did not respond within 4 seconds of the gesture, the response was coded as *no response*. In pilot study videos, most responses occurred within 4 seconds.

## Coding protocol for focal data

We chose the sequence of focal animal sampling by matching age and sex classes across groups, and then using a random rotation. Fifteen-minute focal samples were coded continuously in terms of every posture or mode of locomotion used by the subject (from our ethogram, Table 4), the time spent in each, and whether the subject was holding an object in a hand or foot (labeled "*full*"). The subject must have been engaged in a particular behavior for at least 2 seconds for it to be coded as a distinct positional behavior. Animals were rarely out of view for extended periods in all study sites due to large viewing windows, outdoor viewing areas, and (in some cases) private observation platforms. If a subject was out of sight (OOS) for 1 minute or more, that focal sample was either stopped during recording or discarded during video coding, unless the OOS occurred after 7 minutes and 30 seconds, in which case the focal was halfway complete and it was kept for analysis. All analyses of positional behavior stemming from these focal recordings were done after the total time spent OOS was removed. All timing was determined during video review using the continuous timer on the WinDVD 6 playback toolbar.

## Statistical analyses

Based on behavioral and morphological characteristics (*cf*. Spence and Yerkes, 1937; Hamada *et al.*, 1996), and the accelerated age at maturity for captive animals with increased food availability (Altmann and Alberts, 2005), we assigned all individuals to the following age-classes: Young ($\leq 8$ years old) and Adult ($\geq 9$ years old). Most members of the Adult class had offspring during or prior to data collection. We used parametric tests whenever possible and non-parametric tests when data did not meet the assumptions for parametric statistics (Sokal and Rohlf, 1995; Fowler *et al.*, 1998). The level of significance was set at $P \leq 0.05$ for all statistical tests.

## RESULTS
## Locomotor and postural profiles

In total, we collected 204 hours of 15-minute focal sample video. From bonobos, we collected 58 total hours: 27 h at SDZ (an average of 3.3 h/individual) and 31 h at SDZSP (an average of 3.9 h/individual). From chimpanzees, we collected 146 total hours: 61 h at SLZ (an average of 5.5 h/individual) and 85 h at LAZ (an average of 6.5 h/individual). From these videos, we continuously coded all positional behavior, enabling us to describe locomotor and postural profiles for both species. In the

TABLE 3. Gesture ethogram

| MANUAL | DEFINITION | Bonobos | | Chimpanzees | |
|---|---|---|---|---|---|
| | | SDZ | SDZSP | SLZ | LAZ |
| Arm Raise | Extends arm toward another and holds it out for >2s | ✓ | ✓ | ✓ | ✓ |
| Arm Shake | Loosely shakes hand at wrist while arm is extended toward another | | | | ✓ |
| Bite Offer | Places fingers, wrist, or arm in the mouth of another | | | | ✓ |
| Clap | Palms of hands come into contact with each other or palm comes into contact with sole of foot in one distinct movement | ✓ | ✓ | | |
| Embrace | Wraps arm(s) around the body of another | ✓ | ✓ | ✓ | ✓ |
| Grab | Grasps any part of another's body with the whole hand; fingers are bent | ✓ | ✓ | ✓ | ✓ |
| Long Touch | Gentle and sustained contact with flat hands for >5s | ✓ | ✓ | ✓ | ✓ |
| Object Shake | Waves object in the direction of another or when approaching another | | ✓ | ✓ | ✓ |
| Poke | Taps lightly and repetitively upon another's body with finger-tips or knuckles | ✓ | ✓ | ✓ | |
| Pull | Grasps another forcefully with hand and brings the animal closer | ✓ | ✓ | ✓ | ✓ |
| Push | Presses hand(s) forcefully against another then draws appendage back | ✓ | ✓ | ✓ | ✓ |
| Slap | Approaches another quickly from a distance and hits the animal forcefully with the palm or back of hand then continues traveling | ✓ | ✓ | ✓ | |
| Slap Ground | Hits substrate repetitively with alternating open hands | | ✓ | | |
| Smack | Hits another's body with the palm of hand while in close contact | ✓ | ✓ | ✓ | ✓ |
| Swat | Waves arm or hand at another in close proximity but does not make physical contact | | | ✓ | |
| Take | Grabs an object from another with fingers or whole hand | ✓ | ✓ | ✓ | ✓ |
| Throw | Tosses object (such as branch or food) toward another | | | ✓ | |
| Touch | Gentle contact with another using open hands or feet for <2s | ✓ | ✓ | ✓ | ✓ |
| Touch Genitals | Gentle contact with another's anogenital region using hands or fingers for <2s | ✓ | ✓ | ✓ | ✓ |
| Bodily | Definition | | | | |
| Back Pounce | *Bipedal Swaggers* toward another then bends body or one arm over the other so that physical contact is made | ✓ | ✓ | ✓ | ✓ |
| Bipedal Swagger | While in bipedal posture and rocking side to side, steps in exaggerated manner with feet wide-set and one or both arms waving side to side; piloerection accompanies | | | ✓ | ✓ |
| Bite | Clamps teeth down on any part of another's body | ✓ | ✓ | ✓ | ✓ |
| Body On | Approaches another and sits/lies on or presses body against another for >2s | ✓ | ✓ | ✓ | ✓ |
| Bow | Raises and lowers head and torso with arms outstretched and sometimes hands make contact with substrate below; can be accompanied by *Head Nod* or *Head Shake* | ✓ | ✓ | ✓ | ✓ |
| Chase | Moves quickly and suddenly towards another for >2s | ✓ | ✓ | ✓ | |
| Charge | Sudden and short (<2s) lunge toward another | ✓ | ✓ | | ✓ |
| Drag | *Quadrupedal Running* while holding an object (typically a branch) in one hand and dragging it alongside | ✓ | | | |
| Dropkick | Kicks window, rock, or metal door with both feet while hands are on the ground or other substrate; preceded by piloerection and sometimes *Bipedal Swagger* and/or *Rock* | | | | ✓ |
| Foot Clap | Soles of feet come into contact with each other in one distinct movement | ✓ | ✓ | | |
| Genito-Genital Rub | Repeatedly moves genitals back and forth against another's genitals | | ✓ | | |
| Head Nod | Jerks head up quickly once or several times successively so that the lower face juts out | | | ✓ | ✓ |
| Head Nuzzle | Presses then moves head back and forth against another's body | ✓ | ✓ | ✓ | ✓ |
| Head Shake | Shakes head repeatedly from side to side in a loose, rolling manner | | ✓ | | |
| Inspect Genitals | Makes physical contact with another's genitals with face or mouth for >2s | | ✓ | ✓ | ✓ |
| Kick | Presses foot or feet forcefully against another then draws appendage back | ✓ | ✓ | ✓ | ✓ |
| Mount Pelvic Thrust | Mounts another and repeatedly thrusts pelvis against the animal's body | | ✓ | | |
| Nibble | Opens mouth and gently touches lips or teeth to another's mouth or body | | ✓ | | ✓ |

*TABLE 3. Continued*

| MANUAL | DEFINITION | Bonobos | | Chimpanzees | |
| | | SDZ | SDZSP | SLZ | LAZ |
|---|---|---|---|---|---|
| Object Slide | *Quadrupedal Running* with object (typically flat cardboard box) underneath both hands so that object slides forward underneath the hands as legs propel body forward | ✓ | ✓ | | |
| Peer | Brings face <1ft to the face of a another for >2s | ✓ | ✓ | ✓ | ✓ |
| Present Genitals | Raises genitals up towards another while in a *Crouch* posture (typically female) or thrusts genitals or erection towards another by spreading legs while *Sitting* or in a *Crouch* posture (typically male) | ✓ | ✓ | ✓ | ✓ |
| Rock | Moves upper body side to side while *Sitting* or *Quadrupedal Standing*; usually accompanied by piloerection | | | ✓ | ✓ |
| Somersault | Body rolls and makes at least two rotations either head over feet or sideways | ✓ | ✓ | | |
| Stomp | Brings the sole or heel of foot suddenly and forcibly down upon a substrate | ✓ | ✓ | ✓ | |

The gestures defined in this study listed by gesture type and by group in which gestures were recorded. Manual = gestures using upper limbs or hands only; Bodily = gestures using body postures, locomotion, head, lower limbs, or feet.
Developed in part from: McGrew and Tutin (1978), Nishida (1980), Ingmanson (1987), de Waal (1988), Liebal *et al*. (2004a), Pika *et al*. (2005b), Roberts (2014).

results below, we collapsed the *full* category into the broader positional behavior. For example, *quadrupedal walking* also encompasses *quadrupedal walking full*.

Overall, bonobos and chimpanzees from all age classes spent most of their time in the same three positional behaviors: *sitting*, *lying* and *quadrupedal walking* though in differing proportions. Adult bonobos at SDZ spent 47.0% of their time *sitting*, 40.0% of their time *lying*, and 8.4% of their time *quadrupedal walking*. Every other positional behavior was used less than 5.0% of their time. Adult bonobos at SDZSP spent 36.7% of their time *sitting*, 40.2% of their time *lying*, 13.4% of their time *quadrupedal walking*, and 6.7% of their time *quadupedal standing*. Every other positional behavior was used less than 5.0% of their time. Adult chimpanzees at SLZ spent 60.2% of their time *sitting*, 25.3% of their time *lying*, and 8.9% of their time *quadrupedal walking*. Every other positional behavior was used less than 5.0% of their time. Adult chimpanzees at LAZ spent 61.1% of their time *sitting*, 29.2% of their time *lying*, and 6.6% of their time *quadrupedal walking*. Every other positional behavior was used less than 5.0% of their time.

Young bonobos at SDZ spent 37.3% of their time *sitting*, 33.0% of their time *lying*, and 9.6% of their time *quadrupedal walking*. Every other positional behavior was used less than 5.0% of their time. Young bonobos at SDZSP spent 29.2% of their time *sitting*, 28.0% of their time *lying*, 16.0% of their time *quadrupedal walking*, and 6.9% of their time *quadupedal standing*. Every other positional behavior was used less than 5.0% of their time. Young bonobos did exhibit a wider range of postures and modes of locomotion than adults (e.g., *brachiating*, *riding*, and *hanging*) yet these behaviors still made up less than 5.0% of their time (with the exception of young SDZSP bonobos, who spent 5.6% of their time *riding* on their mothers backs or ventrum). Young chimpanzees at SLZ spent 52.5% of their time *sitting*, 32.6% of their time *lying*, and 5.7% of their time *quadrupedal walking*. Every other positional behavior was used less than 5.0% of their time. Similarly, young chimpanzees at LAZ spent 52.0% of their time *sitting*, 37.8% of their time *lying*, and 7.0% of their time *quadrupedal walking*.

Every other positional behavior was used less than 5.0% of their time.

Contrary to our prediction, bonobos did not engage in more frequent bipedal postures or bipedal locomotion than chimpanzees. In fact, adults of both species spent <1.0% of their time walking or standing bipedally (including time spent carrying objects). Young bonobos in SDZSP spent the greatest amount of time bipedal (1.9% *bipedal standing*) of all age classes in all groups. This posture was used mainly during play bouts between young individuals or when the infant requested rides on the back or ventrum of her mother.

## Gestural repertoires

We collected 336 total hours of *ad libitum* social interactions from which we coded various aspects of gestural signaling, including positional behavior while gesturing. In Table 3, we list the 43 distinct gestures we recorded (19 manual and 24 bodily). There was considerable variation in the frequency of gestural signaling between species and among groups and age-sex classes (Table 5), though young individuals gestured significantly more frequently than adults at SDZSP (1-way ANOVA, df = 1, Fisher *F*-value = 6.274, $P = 0.041$) and at SLZ (1-way ANOVA, df = 1, Fisher *F*-value = 11.939, $P = 0.007$).

Both species used manual and bodily gestures significantly more when recipients were attentive to them compared to when recipients were not attentive (Fig. 1). Bonobos used 1,791 manual gestures when the recipient was attentive versus 492 when not attentive ($\chi^2 = 739.116$, 1 df), 1,059 bodily gestures when the recipient was attentive versus 141 when not attentive ($\chi^2 = 702.270$, 1 df), and 3 manual and bodily gestures used in combination when the recipient was attentive versus 0 when not attentive ($\chi^2 = 4.000$, 1 df). Chimpanzee used 898 manual gestures when the recipient was attentive versus 406 when not attentive ($\chi^2 = 185.632$, 1 df), 638 bodily gestures when the recipient was attentive versus 89 when not attentive ($\chi^2 = 414.582$, 1 df), and 17 manual and bodily gestures used in combination when the recipient was attentive versus 6 when not attentive ($\chi^2 = 5.261$, 1 df).

TABLE 4. *Positional behavior ethogram*

| LOCOMOTOR BEHAVIORS | DEFINITION | Bonobos | | Chimpanzees | |
| --- | --- | --- | --- | --- | --- |
| | | SDZ | SDZSP | SLZ | LAZ |
| Bipedal Running | Rapid locomotion with erect upper body; feet in contact with substrate | | ✓ | ✓ | ✓ |
| Bipedal Running Full | *Bipedal Running* with food or object held in hand(s) | | ✓ | | |
| Bipedal Swaggering | *Bipedal Walking* and stepping in exaggerated manner with feet wide-set and one or both arms waving side to side; piloerection accompanies | | | ✓ | ✓ |
| Bipedal Walking | Slow locomotion with erect upper body; feet in contact with substrate | ✓ | ✓ | ✓ | ✓ |
| Bipedal Walking Full | *Bipedal Walking* with food or object held in hand(s) | ✓ | ✓ | ✓ | ✓ |
| Brachiating | Bimanous locomotion on an arboreal substrate, with swinging propelled by arm over arm movement | ✓ | ✓ | ✓ | ✓ |
| Climbing | Quadrumanous locomotion up or down substrate | ✓ | ✓ | ✓ | ✓ |
| Ice Skating | Pirouettes with hands on substrate or in the air as body twirls around in circles | ✓ | ✓ | | ✓ |
| Jumping | Feet are out of contact with substrate for >2s as body is propelled into the air then lands on substrate or another with any part of the body | ✓ | ✓ | ✓ | ✓ |
| Object Sliding | *Quadrupedal Running* with object (typically flat cardboard box) underneath both hands so that object slides forward underneath the hands as legs propel body forward | ✓ | ✓ | | |
| Quadrupedal Running | Rapid quadrupedal locomotion (knuckle-walking) with hands and feet in contact with substrate | ✓ | ✓ | ✓ | ✓ |
| Quadrupedal Running Full | *Quadrupedal Running* with food or object held in hand(s) or foot (feet) | ✓ | ✓ | ✓ | ✓ |
| Quadrupedal Walking | Slow quadrupedal locomotion (knuckle-walking) with hands and feet in contact with substrate | ✓ | ✓ | ✓ | ✓ |
| Quadrupedal Walking Full | *Quadrupedal Walking* with food or object held in hand(s) or foot (feet) | ✓ | ✓ | ✓ | ✓ |
| Sliding | Movement down smooth substrate (log, rope) with knees slightly bent, hands and feet remain in contact with substrate | ✓ | ✓ | | |
| Somersaulting | Body rolls and makes at least two rotations either head over feet or sideways | ✓ | ✓ | ✓ | ✓ |
| Swingsetting | Hands in contact with substrate while legs swing through arms from back to front. Once feet touch substrate, arms swing forward and entire movement repeats | ✓ | ✓ | | ✓ |
| Bipedal Standing | Stationary with body in erect posture; only feet in contact with substrate | ✓ | ✓ | ✓ | ✓ |
| Bipedal Standing Full | *Bipedal Standing* with food or object held in hand(s) | ✓ | ✓ | ✓ | ✓ |
| Crouching | Body folded in half so that upper body is oriented downwards or knees bent with body in an erect posture | ✓ | ✓ | ✓ | ✓ |
| Hanging | Body is suspended in a vertical position while hand(s) or foot (feet) are grasped around substrate | ✓ | ✓ | ✓ | ✓ |
| Headstanding | *Crouch* posture but with top of head also in contact with substrate for >2s | ✓ | ✓ | | |
| Lying Dorsally | Entire dorsum (and usually back of head) in contact with substrate | ✓ | ✓ | ✓ | ✓ |
| Lying On Side | Side of body in contact with substrate while dorsum and ventrum are not | ✓ | ✓ | ✓ | ✓ |
| Lying Ventrally | Entire ventrum in contact with substrate | ✓ | ✓ | ✓ | ✓ |
| Quadrupedal Standing | Stationary with upper body parallel to substrate and hands and feet in contact with substrate | ✓ | ✓ | ✓ | ✓ |
| Quadrupedal Standing Full | *Quadrupedal Standing* with food or object in hand(s) or foot (feet) | ✓ | ✓ | ✓ | ✓ |
| Riding | Clinging dorsally or ventrally or sitting/standing atop dorsum of another; infants or juveniles only | ✓ | ✓ | ✓ | |
| Sitting | Upper body in erect posture with rear in contact with substrate; legs are straight, bent, or crossed over one another | ✓ | ✓ | ✓ | ✓ |

Modified in part from Hunt *et al.* (1996) and Morcillo *et al.* (2006).

TABLE 5. *Frequencies and rates of gestural signaling*

|  |  | Total gestures recorded | Gestures per hour | Median gestures per individual (range) | Average number of gestures |
|---|---|---|---|---|---|
| Bonobos | SDZ | 1,249 | 15.6 | 104 (45–545) | Adult: 94.4 Young: 259.0 |
|  | SDZSP | 2,237 | 36.7 | 193 (100–954) | Adult: 170.5 Young: 607.0[a] |
| Chimpanzees | SLZ | 1,336 | 14.5 | 76 (30–476) | Adult: 77.7 Young: 318.5[a] |
|  | LAZ | 718 | 6.9 | 45 (26–180) | Adult: 58.8 Young: 43.3 |

Total observation hours: SDZ = 80; SDZSP = 61; SLZ = 92; LAZ = 104.
[a] $P < 0.05$.
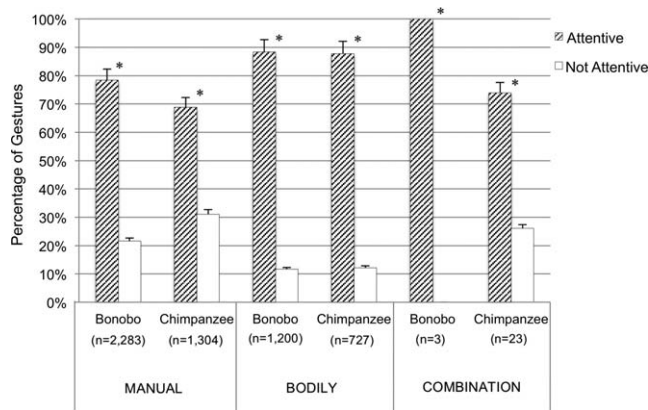


**Fig. 1.** The attentional state of recipients by species and gesture type. Groups are combined for each species. *Attentive* = direct eye contact or head oriented <90° toward actor; *Not Attentive* = head oriented 90° or more away from actor. *Manual* = gestures that involved the upper limbs and/or hands only; *Bodily* = gestures that involved body postures, locomotion, the head, lower limbs, or feet; *Combination* = manual and bodily gestures used simultaneously. *$P < 0.05$



**Fig. 2.** Types of gestures used by bonobos in various positional behaviors. *Manual* = gestures that involved the upper limbs and/or hands only; *Bodily* = gestures that involved body postures, locomotion, the head, lower limbs, or feet; *Combo* = manual and bodily gestures used simultaneously. All individuals from SDZ and SDZSP are combined because the groups were not significantly different. $N = 3,486$ total gestures. Bipedal includes Bipedal Running (Full), Bipedal Standing (Full), Bipedal Walking (Full), and Bipedal Swaggering. Lying includes Lying Dorsally, Lying Ventrally, and Lying on Side. Quadrupedal includes Quadrupedal Running (Full), Quadrupedal Standing (Full), and Quadrupedal Walking (Full).

## Positional behavior while gesturing

From the *ad libitum* social interaction video, we examined the body posture or mode of locomotion the subject was engaged in at the time of gesturing and whether the gesture was manual or bodily. Bonobos gestured most frequently while *lying* (24.0%, $n = 838$), while chimpanzees gestured most frequently while *sitting* (35.5%, $n = 730$). Though neither species spent a large proportion of time engaged in bipedal postures or locomotion in the focal videos, 14.0% ($n = 489$) of all bonobo gestures recorded in the *ad libitum* social videos were produced when bonobos were in a bipedal posture or engaged in bipedal locomotion, and 95.9% ($n = 469$) of these gestures were manual (Fig. 2). Infants were responsible for 93.0% ($n = 436$) of these gestures. *Grab* was the most frequent manual gesture used when in a bipedal posture in both bonobo groups ($n = 215$), and 97.2% of those gestures were produced by the three infants. *Object sliding* was defined as both a bodily gesture (it made up 3.1% of all bonobo gestures) and a mode of locomotion, and bonobos used this as both 107 times (Fig. 2). This gesture occurred 104 times as a gesture (produced by members of all age/sex-classes) in SDZSP's *ad libitum* data but only accounted for 43 seconds of focal video data. *Object sliding* only occurred three times as a gesture in SDZ's *ad libitum* data (produced only by one adult male), but never in focal videos.

Among chimpanzees, 14.7% ($n = 301$) of all gestures recorded in the *ad libitum* social videos were produced when chimpanzees were in a bipedal posture or engaged in
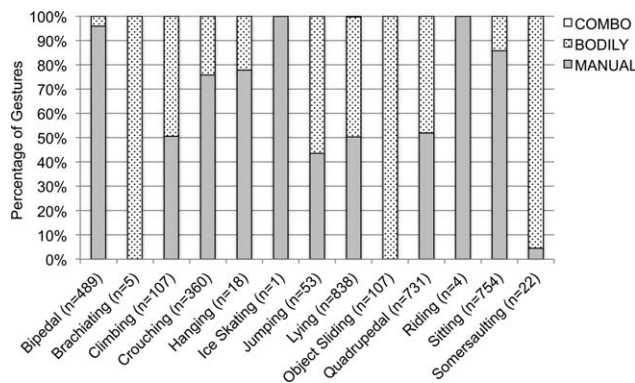
bipedal locomotion (Figs. 3 and 4). However, the types of gestures used when bipedal differed by group. At SLZ, these gestures were predominantly manual (62.1%, $n = 90$) such as *grab*, *object shake*, and *touch*, and produced primarily by juvenile females ($n = 64$). At LAZ, the two bodily gestures *back pounce* and *bipedal swagger* made up 85.9% of the gestures produced when actors were in a bipedal posture or engaged in bipedal locomotion ($n = 134$, Fig. 4) and 97.0% of these gestures were produced by adult males ($n = 130$). As with *object sliding*, *bipedal swagger* doubled as a mode of locomotion and a bodily gesture, and it was produced only by adult males at LAZ ($n = 71$).

## DISCUSSION

Our findings suggest a strong connection between gestures and positional behavior in bonobos and chimpanzees. The gestures we recorded were often linked to body postures and locomotory actions, and certain modes of locomotion were sometimes even used as intentionally communicative signals. We hypothesized that the locomotor profiles of bonobos and chimpanzees would dictate the availability of their upper limbs for gesturing, and thus influence the frequency and type of gestures used. Implicit in this hypothesis was the assumption that if upper limbs were not actively involved in locomotion, they would be recruited for communication. However, our results do not support this
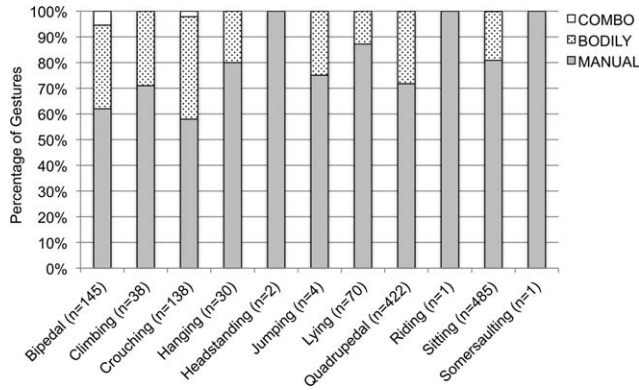
**Fig. 3.** Types of gestures used by SLZ chimpanzees in various positional behaviors. *Manual* = gestures that involved the upper limbs and/or hands only; *Bodily* = gestures that involved body postures, locomotion, the head, lower limbs, or feet; *Combo* = manual and bodily gestures used simultaneously. $N = 1,336$ total gestures from all individuals. Bipedal includes Bipedal Running (Full), Bipedal Standing (Full), Bipedal Walking (Full), and Bipedal Swaggering. Lying includes Lying Dorsally, Lying Ventrally, and Lying on Side. Quadrupedal includes Quadrupedal Running (Full), Quadrupedal Standing (Full), and Quadrupedal Walking (Full).

hypothesis with the caveat that observations in the wild may yield different results. Our findings demonstrate that gestural signaling is not constrained by the availability of the upper limbs; instead, body postures and locomotion are often intimately tied to gestures. Moreover, certain types of locomotion in particular contexts were themselves incorporated into communicative signals. Salient examples from this study included *bipedal swagger*, *drag*, *object sliding* and *somersaulting* (Table 3). As with other manual and bodily gestures we identified in this study, these locomotory actions were used in goal-oriented ways and were produced significantly more
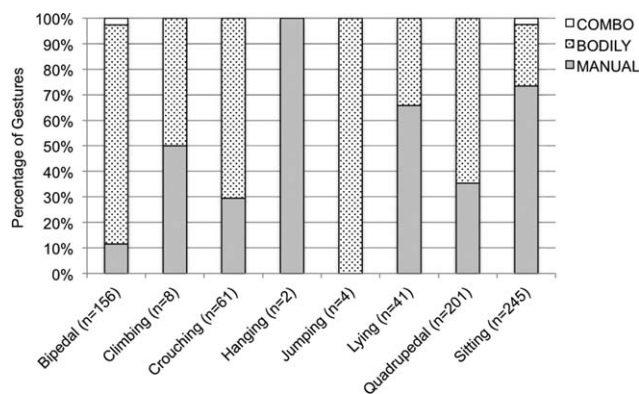


**Fig. 4.** Types of gestures used by LAZ chimpanzees in various positional behaviors. *Manual* = gestures that involved the upper limbs and/or hands only; *Bodily* = gestures that involved body postures, locomotion, the head, lower limbs, or feet; *Combo* = manual and bodily gestures used simultaneously. $N = 718$ total gestures from all individuals. Bipedal includes Bipedal Running (Full), Bipedal Standing (Full), Bipedal Walking (Full), and Bipedal Swaggering. Lying includes Lying Dorsally, Lying Ventrally, and Lying on Side. Quadrupedal includes Quadrupedal Running (Full), Quadrupedal Standing (Full), and Quadrupedal Walking (Full).

when recipients were attentive to the actors than when they were not attentive.

Overall, there were no dramatic differences between the locomotor and postural profiles of bonobos and chimpanzees. Adult chimpanzees and bonobos used the same types of positional behavior and varied only slightly in the percentage of time spent in each. In both species, there were clear age-class differences in the percentage of time devoted to the various kinds of positional behavior. In general, young individuals used a wider range of positional behavior than adults; this was particularly evident in young SLZ chimpanzees and young SDZ bonobos.

Contrary to our prediction that bonobos would rely on bipedal postures and locomotion more than chimpanzees, neither species spent a large portion of time engaged in bipedal postures or locomotion. Bipedal postures and locomotion also served different purposes for different age/sex-classes in both species. In bonobos, young individuals used *bipedal standing* more frequently than adults, and this posture was primarily used when infants requested rides on the backs or ventrum of their mothers (approximately 42%) or during play bouts (approximately 13%). In a study of captive olive baboons, Druelle and Berillon (2013) also found that infants (1-2 years) used bipedal postures and locomotion more frequently than adults. At Lomako, bonobos of all ages have been observed to use bipedal postures and locomotion for displays, during feeding, and when carrying food or infants (Susman *et al.*, 1980). Videan and McGrew (2001) also found that bonobos in captivity used bipedal postures and locomotion mainly for carrying and vigilance, and that bipedality was more frequent in younger individuals. The bonobos in our study used bipedal postures and locomotion occasionally for vigilance or for carrying objects, but they did not use bipedal postures and locomotion for displays. Rather, displays typically included bodily gestures in which actors moving past the group using cardboard boxes provided for enrichment (*object slide*) or dragging large branches (*drag*) past group members. In chimpanzees, however, adults spent more time engaged in bipedal locomotion than young individuals.

Using a gestural origins perspective, we tested the idea that upper limb availability would lead to an increase in gestural signaling using the upper limbs but, based on our gesturing frequency data, this prediction was not supported. In fact, our observations revealed that gestural signaling can and frequently do occur even when both of the upper limbs are actively involved in locomotion. Only 19 of the 43 distinct gestures we recorded can be categorized as expressly manual gestures with no postural or locomotor component. Of the 24 bodily gestures we observed, seven were defined by a locomotor component (such as *somersault, charge*, and *drag*), and the remaining 17 either involved the head only (e.g., *bite, head nod, nibble*) or were dependent on a particular body posture (e.g., *body on, bow, present genitals*). Furthermore, the gestures produced when individuals were in bipedal postures or locomotion and had full use of the upper limbs for gesturing were not always manual gestures. Rather, many were gestures that relied on a particular posture and/or mode of locomotion as part of the communicative act, such as *bipedal swagger*. Gestures, locomotor behavior, and body postures are clearly strongly connected, just not in the limited manner we predicted. Rather than locomotor behavior

restricting the use of certain gestures, it instead appears that body movements, much like body postures, enhance certain gestures. For example, when an actor is standing, any signal can be received presumably by more group members and an erect posture is much more imposing in a dominance display. Thus, the relationships between gestural signaling, locomotion, and postures may not really be determined by upper limb availability but more by the need to maximize visibility and detection by recipients when producing gestures or to make use of the whole body as a communicative tool, rather than confining communication to the upper limbs.

Our results suggest that manual and bodily signaling express the kind of behavioral and locomotor diversity consistent with some aspects of a gestural origins scenario for language evolution. As Kelly *et al.* (2002) argue, "the original functions of communication and language systems [(i.e., demonstrating and indicating)] were perfectly suited for the body, and that the body continued to shape language over time (p. 324)." Body movements can speak volumes about the mood or intentions of another, and gestures can be made more obvious when they are tied to erect postures or locomotion. Our results, however, do not provide support for the freedom of the upper limbs as an impetus for a shift in gestural signaling related to bipedality. However, the types of gestures that early hominins may have been using when bipedality became more habitual were modified and adjusted to fit within a changing locomotor profile. If early hominins were already using gestures similar to *bipedal swagger*, *back pounce*, and *charge* as dominance displays (in addition to a suite of other tactile, visual, and auditory gestures) before the transition to habitual bipedality, then incorporating the upper limbs and an erect body posture would have been a natural transition. We often talk about reading each other's "body language" and seem to take for granted the importance of bodily gestures in our daily interactions. Evidence of the importance of the body as vehicle for communication can be found in child development, sign languages, dance and other performance art, and even in the brain with the discovery of the mirror neuron network (Perrett *et al.*, 1985; Kelly *et al.*, 2009; Beilock and Goldin-Meadow, 2010). Language may now be dominated by speech, but communication is still in many ways rooted in the body.

## ACKNOWLEDGMENTS

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