REVIEW ARTICLE

Considering the Role of Social Dynamics and Positional Behavior in Gestural Communication Research

LINDSEY W. SMITH[1,2]* AND ROBERTO A. DELGADO[2,3]
[1]*Thompson Writing Program, Duke University, Durham, North Carolina*
[2]*New York Consortium in Evolutionary Primatology, New York, New York*
[3]*Section in Human and Evolutionary Biology, Departments of Anthropology and Biological Sciences,
University of Southern California, Los Angeles, California*

While the hominin fossil record cannot inform us on either the presence or extent of social and cognitive abilities that may have paved the way for the emergence of language, studying non-vocal communication among our closest living relatives, the African apes, may provide valuable information about how language originated. Although much has been learned from gestural signaling in non-human primates, we have not yet established how and why gestural repertoires vary across species, what factors influence this variation, and how knowledge of these differences can contribute to an understanding of gestural signaling's contribution to language evolution. In this paper, we review arguments surrounding the theory that language evolved from gestural signaling and suggest some important factors to consider when conducting comparative studies of gestural communication among African apes. Specifically, we propose that social dynamics and positional behavior are critical components that shape the frequency and nature of gestural signaling across species and we argue that an understanding of these factors could shed light on how gestural communication may have been the basis of human language. We outline predictions for the influence of these factors on the frequencies and types of gestures used across the African apes and highlight the importance of including these factors in future gestural communication research with primates. Am. J. Primatol. 75:891–903, 2013.   © 2013 Wiley Periodicals, Inc.

INTRODUCTION

Observe any conversation around the world and it will quickly become clear that gestures are ubiquitous. The gestures themselves vary from gesticulations, used along with speech and pantomimes that represent objects or events, to emblems that hold arbitrary meaning. The meaning behind gestures also varies from person to person and across cultures [Archer, 1997]. Holding up two fingers in the shape of a "v," with the palm facing outward is an emblem for "peace" in the United States, but turn the hand so that the palm faces inward, and you have just insulted someone in the UK. While gestures may vary in form, meaning, and function, the common thread between them is that gestures are prevalent in all human populations. This universality suggests that gestures are fundamental components of human communication.

The wealth of research on human gestures provides support for the idea that gestures are instrumental in communication. Children acquire gestures early in development and use them extensively before speech develops [Iverson et al., 2000; Knott, 1979]. Even after the onset of spoken language, gestures remain important features of communication well into adulthood and are often used in conjunction with speech [Dunning, 1971; Kendon, 1997; Melinger & Levelt, 2004]. However, gestures are not merely tools used to enhance speech. Gestures like emblems and pantomimes function as communicative signals independent of speech. More formalized sign languages of the deaf also represent fully functioning gestural languages that possess properties of syntax originally proposed by Chomsky [1968] and others to be inherent only in human speech [e.g., Armstrong et al., 1995]. Additionally, "homesigns" are rudimentary gestural systems that have emerged in deaf children across the world who are raised in an environment without exposure to formal sign languages [Armstrong & Wilcox, 2007; Goldin-Meadow & Feldman, 1977; Senghas &

*Correspondence to: Lindsey W. Smith, Thompson Writing Program, Duke University, Art Building, Box 90025, Durham, NC 27708. E-mail: lindsey.w.smith@duke.edu

Coppola, 2001]. Homesigns emerge spontaneously without instruction, but they develop into systems of communication with linguistic properties like spatial grammar, in which the meaning of signs can be altered depending on their placement in space [Senghas & Coppola, 2001]. Though homesigns are less syntactically complex than formal sign languages or speech, and they are generally restricted to small communities of deaf people, they demonstrate how gestural systems of communication can emerge in humans and provide us with potential models for language evolution in early hominins [Botha, 2007].

Increasingly, gestures are being regarded as essential parts of language, working with speech to form an integrated system in which both modalities contribute to language production and comprehension [Cartmill et al., 2012; Kelly et al., 2009]. Gestures are so intimately tied to speech that even congenitally blind people gesture as often as sighted people during conversations, and people on the phone often gesture while talking even though the gestures are not visible to their conversation partners [Iverson & Goldin-Meadow, 1998]. Beilock and Goldin-Meadow [2010] have even reported that people are better able to articulate their thoughts by using gestures and argue that gestures themselves can actually facilitate cognitive processes by anchoring thoughts in physical actions. For example, in their study, people had more difficulty describing a physical task they had just performed when the use of one of their hands was restricted, and their second performance of the task subsequently suffered [Beilock & Goldin-Meadow, 2010]. Findings from this research not only provide convincing evidence for the strong connection between speech and gestures and validate the idea that gestures can comprise complete systems of communication independent of speech but also highlight the vital links between gestures and cognition as well as between language and motor actions.

Although growing lines of evidence demonstrate that gestural communication is integral to human language, the role of gestures in the origins and evolution of language in early hominins still remains the subject of interdisciplinary debate. This discourse has centered on whether human language is rooted in primate vocalizations, gestures, or a combination of both. Some scholars [e.g., Chomsky, 1968; Burling, 1993; Pinker & Bloom, 1990] have argued that language arose relatively late in human evolution (e.g., in the Upper Paleolithic) and thus is not based on the communication systems of non-human primates. However, findings from decades of field and experimental research demonstrate compelling ties between human and non-human primate gestures and vocalizations. Two perspectives have emerged among those who support continuity from the communication systems of non-human primates to

human language. A number of primatologists who study vocal signaling contend that certain non-human primate vocalizations are semantic and stem from cognitive mechanisms similar to those that underlie human language [Seyfarth, 2005; Seyfarth et al., 1980, 2005]. Others, however, argue that non-human primate gestures share qualities of human language and that a more productive enterprise for investigating precursors to human language is to explore the gestural signaling of our closest living primate relatives, the African great apes [Müller, 2005; Pika et al., 2005a; Tomasello & Call, 2007].

Answering the question of how language emerged remains challenging. In particular, the selection pressures that favored the anatomical, behavioral, cognitive, and genetic changes that led to the evolution of language in anatomically modern *Homo sapiens* and the timing of these changes are difficult to assess. Additionally, the hominin fossil record cannot inform us on the presence or extent of cognitive traits such as imitation, joint attention, theory of mind, and symbolic representation that were likely pre-adaptations for language. Fortunately, however, because of the close, anatomical, behavioral, and genetic similarities shared between humans and non-human primates—and in particular, the African apes—examining the nature and patterns of great ape gestural communication can provide us with valuable information about how language may have emerged, and how gestures and other forms of non-verbal communication may fit into the puzzle of language origins.

Primatologists and cognitive psychologists have been attempting to measure the linguistic abilities of non-human primates since the 1960s with the onset of research aimed at teaching American Sign Language to apes [e.g., Fouts, 1973; Gardner & Gardner, 1969; Terrrace, 1979]. Since then, the field has expanded to include observational and experimental studies of gestural and vocal signaling of various captive and wild populations of primates. Playback studies and spectrogram analyses of primate calls have demonstrated that species such as vervet monkeys (*Cercopithecus aethiops*) and Campbell's monkeys (*Cercopithecus campbelli*) use certain calls referentially to represent specific predators and that group members respond in predator-appropriate ways to these calls [e.g., Cheney & Seyfarth, 1990; Ouattara et al., 2009a,b; Zuberbühler, 2000]. Other studies have shown that listeners can derive information about a caller, such as kinship and rank, that influences how they perceive and react to certain vocalizations [Cheney & Seyfarth, 1990; Kitchen et al., 2003; Seyfarth et al., 2005]. These studies indicate some flexibility in the ways that certain primate species learn to distinguish, comprehend, and respond to signals, particularly for the listener. However, aside from a report of a captive

orangutan imitating a human whistle without explicit training [Wich et al., 2008], there is no evidence that non-human primates invent new vocalizations without extensive human contact or human enculturation. Additionally, there is only limited evidence of flexible call production or usage outside of fixed social contexts [Hopkins et al., 2007; Janik & Slater, 2000; Marshall et al., 1999; Mitani & Brandt, 1994; Ouattara et al., 2009a; Seyfarth & Cheney, 1997; Seyfarth et al., 1980; Snowdon & Hodun, 1981; Tomasello & Zuberbühler, 2002]. Creating new signals and using them in multiple contexts are key aspects of human language, yet these phenomena are not pervasive in non-human primate vocal communication.

Instead, more robust evidence exists for flexibility in the use of gestural signaling [e.g., Genty et al., 2009; Hobaiter & Byrne, 2011; Müller, 2005; Pika et al., 2003; Pika et al., 2005a,b; Pollick & de Waal, 2007; Smith, 2011; Tomasello & Call, 2007]. Gestural communication may be more flexible than vocal communication because gestures are less tied to emotions [Pollick & de Waal, 2007] and used commonly to communicate less "evolutionarily urgent" information than vocalizations [Pika et al., 2005a, p. 43]. For instance, gestures are employed more often in the contexts of playing, nursing, grooming, and agonism [de Waal, 1988; Pika et al., 2003, 2005a,b]. These contexts are not necessarily tied to immediate survival goals, but they are undoubtedly important for navigating group life and for establishing and maintaining relationships with conspecifics. Vocalizations, on the other hand, are used most often when avoiding predators, traveling as a group, foraging, and defending against aggressors [Tomasello & Zuberbühler, 2002]. Thus, compared to vocalizations, gestures can be more easily incorporated into different social contexts, and shaped over time by repeated social interactions.

The intimate relationship between actor and recipient also distinguishes gestural signaling from vocal signaling because most gestures require a direct interaction between individuals [Cartmill & Byrne, 2010]. Tactile (and to some degree auditory) gestures require physical proximity, and the efficacy of visual gestures depends on the attentional state of the recipient. By contrast, vocal signaling does not require direct contact or rely on the visual attention of a potential recipient. Vocal signals are generally widely broadcast and may be received by all group members indiscriminately, including unintended receivers (i.e., "eavesdroppers"). Group-living primates could certainly obtain adaptive advantages by using non-vocal signals that could be intentionally withheld from certain individuals or restricted to particular dyads.

Here, we review the evidence supporting the idea that gestural signaling served as a precursor to human language and propose previously unexplored factors to consider when conducting gestural communication research with non-human primates. First, we present the salient arguments surrounding the gestural origin theory of language evolution. Then, we review the current status of gestural communication research in African apes. Next, we propose the hypothesis that social dynamics (group composition and the nature of social relationships) and positional behavior (postures and locomotion) play key roles in influencing the frequency and nature of gestural signaling and in shaping the specific gestures used between individuals of each species. We contend that these factors must be taken into account when examining gestural communication in African apes as a means of determining how gestural signaling may have evolved in early hominins.

GESTURAL ORIGINS OF LANGUAGE

The theory that language originated from gestures has a long history, stretching as far back as the eighteenth century. Many scholars credit the initial development of this theory to philosophers such as Condillac [cf. Corballis, 2002], but the gestural origins theory is most often attributed to Hewes [1973], who generated renewed interest by presenting a comprehensive review of the many facets of this theory. Since the 1970s, the gestural origins theory has gained increasing support from subsequent researchers who have each made his or her own contribution [e.g., Arbib et al., 2008; Armstrong & Wilcox, 2007; Armstrong et al., 1995; Copple, 2003; Corballis, 2002, 2003, 2009; Gentilucci & Corballis, 2006; Leroi-Gourhan, 1993].

The central claim of the gestural origins theory is that human language arose from gestural communication rather than vocalizations [Hewes, 1973]. Although Hewes [1973] did not explicitly address the timing of this increased reliance on gestures in human evolution, many scholars have argued that the emergence of bipedality in early hominins approximately 2 million years ago facilitated the use of the upper limbs for activities such as tool manufacture and tool use, carrying objects, and manual (i.e., gestural) communication [Armstrong & Wilcox, 2007; Armstrong et al., 1995; Corballis, 2002, 2003, 2009]. Thus, the shift to obligate bipedality could have been a crucial step in precipitating the use of more frequent and more complex manual gestures. These early symbolic gestures then became the basis for language before more complex and controlled speech was incorporated into this system as evolving vocal anatomy allowed. Donald [1991] even proposed that simple gestural communication was already in place at this point, and the transition toward habitual bipedality may have marked the emergence of more complex gestures and representational gestures like pantomimes.

In recent years, neurological evidence has been incorporated into Hewes' [1973] original theory, which has helped to bolster the claim that gestures shaped language evolution. For example, Broca's area has been traditionally viewed as the speech area, but research reveals that this area is also active when humans perform and observe manual actions [Arbib, 2005]. In fact, even observing a hand grasping an object can influence syllable pronunciation, suggesting further cognitive links between speech and manual actions [Gentilucci, 2003]. An area homologous to Broca's area, F5, has also been discovered in the brains of macaques. In these monkeys, F5 contains neurons dubbed "mirror neurons" that are active when macaques observe and execute facial or manual actions [Arbib, 2005; Perrett et al., 1985]. Interestingly, primate vocalizations are not related to neuronal activity in the F5 region, but rather to the anterior cingulated cortex and other non-cortical regions, which are responsible for autonomic bodily functions [Jürgens, 2002].

A homologue also exists in macaques for Wernicke's area, the region in humans that is involved in language comprehension. In humans and monkeys, this region is also active during facial and forearm movements [Kelly et al., 2002]. Furthermore, Xu et al. [2009] found that symbolic gestures (i.e., pantomimes and emblems that signify actions or objects and stand alone without speech) are processed by the same neural system as spoken language. This research indicates clearly that the brain area traditionally known as the "language network," the inferior frontal and posterior temporal cortices, does not function solely as a speech network but, rather, as an area that processes a broader range of symbolic communication independent of modality [Xu et al., 2009]. Furthermore, humans exhibit a left-hemisphere dominance for speech and language, and some researchers argue [e.g., Corballis, 2002] that this may derive from a pre-existing lateralization for gestural communication in the common ancestor of apes and humans. In a comparative study of handedness among great apes, Hopkins et al. [2012] found significant population-level preferences for right-handed manual gesturing among great apes, particularly for auditory gestures. These results suggest that left hemispheric dominance for communication is not unique to the human lineage, but rather is a shared trait among Hominidae that may stem from an earlier system of gestural communication that was eventually co-opted for speech and language. These important advances in cognitive neuroscience increasingly strengthen an evolutionary scenario in which speech became incorporated into a system based originally on gestural signaling and provide evidence for continuity between gestures in human and non-human primates [Arbib, 2005; Arbib et al., 2008; Corballis, 2002, 2003, 2009].

GESTURAL RESEARCH IN AFRICAN APES

Previous investigations of African ape gestural communication have generally aimed to determine how the ancestors of modern humans may have communicated prior to the evolution of speech and whether certain properties of language exist in other primates. Long-term field studies of African ape behavior first uncovered the use of several communicative gestures [Fossey, 1983; Goodall, 1986; Ingmanson, 1996; Kano, 1982, 1992; McGrew & Tutin, 1978; Nishida, 1980; Schaller, 1963], and these findings sparked further investigation into the importance of non-vocal signaling in these species. In the wild, chimpanzees have been observed using over a dozen distinct gestures in a variety of contexts such as play, agonism, and sex [Goodall, 1986]. Population-wide differences have also been identified in gestures such as leaf-clipping displays [Nishida, 1980] and grooming handclasps [McGrew & Tutin, 1978], both of which have been instrumental in cultural interpretations of geographic variation in chimpanzee behavior [e.g., de Waal, 1999; McGrew, 2004; Whiten et al., 1999]. As for the other African apes, species-specific displays such as chest beating have been observed in wild gorillas [Fossey, 1983; Schaller, 1963] and early studies of captive bonobos identified many unique gestures not seen in other apes, such as frequent genito-genital rubbing [de Waal, 1988]. Since these initial observations, researchers have compiled ethograms of gestures for several captive and wild populations (Table I) and have set out to explore more explicitly the role and diversity of gestures in African ape communication.

Thus far, research on gestural signaling in African apes has addressed spontaneous gestural use within species [e.g., de Waal, 1988; Genty et al., 2009; Hobaiter & Byrne, 2011; Kalan & Rainey, 2009; Liebal et al., 2004a; Savage-Rumbaugh et al., 1977; Smith, 2011; Tanner & Byrne, 1996], examined the learning mechanisms involved in creating and maintaining gestures within groups such as phylogenetic ritualization and ontogenetic ritualization [e.g., Liebal & Call, 2012; Pika et al., 2003; Tomasello et al., 1997], and explored individual capacities to learn language systems and use them to communicate with conspecifics and humans [e.g., Fouts, 1973; Gardner & Gardner, 1969; Savage-Rumbaugh et al., 1998]. Together, this body of research has revealed that African ape gestures can vary across populations of the same species, and many gestures are used in versatile ways to achieve multiple communicative ends. This flexibility within and across groups is a universal characteristic of gestural signaling and differentiates it from vocal signaling, which is more often tied to specific contexts. Gestures are also used at different rates among different age- and sex-classes, reflecting a need for different types of gestures at different

TABLE I. Gestures Recorded Among African Apes From Published Ethograms*

Gesture	Signal category	Species observed
Arm On	Tactile	*Gorilla gorilla*[l]; *Pan troglodytes*[h,i]; *Pan paniscus*[l]
Arm Raise/Arm Up	Visual	*P. troglodytes*[h,k]; *P. paniscus*[f]
Back Pounce	Tactile	*P. troglodytes*[l]; *P. paniscus*[l]
Beg	Visual	*P. paniscus*[f]
Bipedal Swagger	Visual	*P. troglodytes*[h,l]; *P. paniscus*[f]
Bite	Tactile	*G. gorilla*[j,l]; *P. troglodytes*[k,l]; *P. paniscus*[l]
Bite Offer	Tactile	*P. troglodytes*[l]
Body Beat	Auditory	*G. gorilla*[g,j,l]
Body On	Tactile	*G. gorilla*[l]; *P. troglodytes*[l]; *P. paniscus*[l]
Body/Belly Slap	Auditory	*G. gorilla*[g]; *P. troglodytes*[h]
Bow	Visual	*G. gorilla*[g,j]; *P. troglodytes*[k,l]; *P. paniscus*[l]
Charge	Visual	*G. gorilla*[l]; *P. troglodytes*[l]; *P. paniscus*[f,l]
Chase	Visual	*G. gorilla*[l]; *P. troglodytes*[l]; *P. paniscus*[l]
Chest Beat	Auditory	*G. gorilla*[a,d,g,l]; *P. paniscus*[f]
Chuck Up	Visual	*G. gorilla*[g]
Clap	Auditory	*G. gorilla*[g,j,l]; *P. troglodytes*[e,h,k]; *P. paniscus*[f,l]
Concave Back	Visual	*P. paniscus*[f]
Dropkick	Auditory	*P. troglodytes*[l]
Drum	Tactile	*G. gorilla*[j,l]; *P. troglodytes*[k]
Duck Face	Visual	*P. paniscus*[f]
Embrace	Tactile	*G. gorilla*[g,l]; *P. troglodytes*[h,k,l]; *P. paniscus*[f,l]
Finger Flex	Visual	*P. paniscus*[f]
Foot Clap	Auditory	*P. paniscus*[e,f,l]
Formal Bite	Visual	*G. gorilla*[g,l]; *P. troglodytes*[i]
Funny Faces	Visual	*P. paniscus*[f]
Gallop	Visual	*G. gorilla*[g,j,l]; *P. troglodytes*[k]; *P. paniscus*[g]
Genital Offer	Visual	*P. troglodytes*[i]
Genital Massage	Tactile	*P. paniscus*[f]
Genito-Genital Rub	Tactile	*P. paniscus*[f,l]
Gentle Touch	Tactile	*P. troglodytes*[h]
Grab	Tactile	*G. gorilla*[g,j,l]; *P. troglodytes*[k,l]; *P. paniscus*[i,l]
Grab-Pull-Push	Tactile	*G. gorilla*[g,j]; *P. troglodytes*[k]; *P. paniscus*[i]
Groom	Tactile	*P. paniscus*[f]
Grooming Hand Clasp	Tactile	*P. troglodytes*[b]
Hand On	Tactile	*G. gorilla*[g,j]; *P. troglodytes*[k]
Head Bang	Visual	*G. gorilla*[l]
Head Bob	Visual	*P. troglodytes*[h,k]; *P. paniscus*[i,l]
Head Nod	Visual	*P. troglodytes*[l]
Head Nuzzle	Tactile	*G. gorilla*[l]; *P. troglodytes*[l]; *P. paniscus*[l]
Hunch-Over	Tactile	*P. paniscus*[f]
Ice Skate/Pirouette	Visual	*G. gorilla*[g,j,l]; *P. troglodytes*[k]; *P. paniscus*[i]
Inspect Genitals	Visual	*P. troglodytes*[l]
Jump	Visual	*G. gorilla*[g,j]; *P. troglodytes*[h,k]; *P. paniscus*[i]
Kick	Tactile	*P. paniscus*[i]
Lead	Tactile	*P. troglodytes*[h]
Leaf-Clipping Display	Auditory	*P. troglodytes*[c,k]
Lip Lock	Tactile	*P. troglodytes*[h]
Look At	Visual	*P. paniscus*[i]
Long Touch	Tactile	*G. gorilla*[g,l]; *P. troglodytes*[l]; *P. paniscus*[l]
Mount	Tactile	*P. paniscus*[f]
Mount Pelvic Thrust	Tactile	*G. gorilla*[l]; *P. paniscus*[l]
Mount Walk	Tactile	*P. paniscus*[f]
Mouth Kiss	Tactile	*P. paniscus*[f]
Move	Visual	*G. gorilla*[g]; *P. paniscus*[i]
Nibble	Tactile	*G. gorilla*[l]; *P. troglodytes*[l]; *P. paniscus*[l]
Object Slide	Visual	*P. paniscus*[l]
Offer	Visual	*P. troglodytes*[h]
Oral Sex	Tactile	*P. paniscus*[f]
Pat	Tactile	*G. gorilla*[j]; *P. paniscus*[f]
Peer	Visual	*G. gorilla*[g,l]; *P. troglodytes*[k,l]; *P. paniscus*[i,l]

(Continued)

TABLE I. Continued

Gesture	Signal category	Species observed
Play Face	Visual	*P. paniscus*[f]
Present	Visual	*P. troglodytes*[k,l]; *P. paniscus*[f,i,l]
Prod/Poke At	Tactile	*G. gorilla*[g]; *P. troglodytes*[h,k,l]; *P. paniscus*[l]
Pull	Tactile	*G. gorilla*[g,l]; *P. troglodytes*[h]; *P. paniscus*[i,l]
Punch	Tactile	*G. gorilla*[g,j]; *P. troglodytes*[k]; *P. paniscus*[e,h]
Push (Object/Body)	Tactile	*G. gorilla*[g,j,l]; *P. troglodytes*[h,k,l]; *P. paniscus*[i,l]
Reach Arm	Visual	*G. gorilla*[g,j]; *P. troglodytes*[h,k]; *P. paniscus*[f,i]
Rock	Visual	*P. troglodytes*[l]
Shake (**Arm/Object**/Head)	Visual	*G. gorilla*[g,j,l]; *P. troglodytes*[h,k,l]; *P. paniscus*[f,i,l]
Silent Pout	Visual	*P. paniscus*[f]
Silent Teeth Bare	Visual	*P. paniscus*[f]
Slap	Tactile	*G. gorilla*[g,j,l]; *P. troglodytes*[k,l]; *P. paniscus*[f,i,l]
Slap Ground	Auditory	*G. gorilla*[g,j,l]; *P. troglodytes*[h, k]; *P. paniscus*[f,l]
Smack	Tactile	*G. gorilla*[l]; *P. troglodytes*[l]; *P. paniscus*[l]
Somersault	Visual	*G. gorilla*[g,l]; *P. troglodytes*[k]; *P. paniscus*[i,l]
Staredown	Visual	*G. gorilla*[l]
Stiff Stance	Visual	*G. gorilla*[g,j]; *P. troglodytes*[k]
Stamp Trot	Auditory	*P. paniscus*[f]
Stomp	Auditory	*G. gorilla*[g]; *P. troglodytes*[h,k,l]; *P. paniscus*[f,i,l]
Straw Wave	Visual	*G. gorilla*[g]
Take	Tactile	*G. gorilla*[l]; *P. troglodytes*[l]; *P. paniscus*[l]
Tense Mouth	Visual	*P. paniscus*[f]
Touch	Tactile	*G. gorilla*[g,j,l]; *P. troglodytes*[k,l]; *P. paniscus*[i,l]
Touch Genitals	Tactile	*G. gorilla*[l]; *P. troglodytes*[l]; *P. paniscus*[l]
Throw	Visual/tactile	*G. gorilla*[g]; *P. troglodytes*[h,k,l]
Wrist/Hand Shake	Visual	*P. troglodytes*[k]; *P. paniscus*[f]

[*]We combined gestures if they appeared to be the same based on names and descriptions. Manual gestures are in bold; gestures that are tied to positional behavior but not restricted to the upper limbs are in italics.
[a]Schaller [1963].
[b]McGrew and Tutin [1978].
[c]Nishida [1980].
[d]Fossey [1983].
[e]Ingmanson [1987].
[f]de Waal [1988].
[g]Pika et al. [2003].
[h]Liebal et al. [2004a].
[i]Pika et al. [2005b].
[j]Genty et al. [2009].
[k]Hobaiter and Byrne [2011].
[l]Smith [2011].

developmental stages and within certain social relationships. For example, sub-adults and juveniles tend to gesture more frequently than any other age class [Pika et al., 2003, 2005b; Smith, 2011], and they frequently gesture to other young individuals or to their mothers [Smith, 2011]. Furthermore, African apes (particularly the genus *Pan*) show sensitivity to audience effects when gesturing, evident in a higher prevalence of visual gestures (as opposed to tactile or auditory gestures) when recipients are oriented toward the signaler [Bodamer & Gardner, 2002; Genty et al., 2009; Hostetter et al., 2001; Liebal et al., 2004b; Pika et al., 2003, 2005a; Povinelli et al., 2003; Smith, 2011; Tanner & Byrne, 1996]. This attention to the orientation and perception of another individual is a crucial indicator that gestures are used to communicate intentionally with others.

While much has been learned about the use of gestural signaling in African apes, there is still much to be explored, particularly with respect to understanding how gestures are expressed within and across groups of different species. We feel that two questions are important to ask in future studies that aim to use gestural communication among African apes as a model for how gestural communication may have influenced language evolution in early hominins. First, do the frequencies of gestural signaling and the types of gestures used within a population differ as a function of social dynamics (e.g., levels of affiliation, agonism, and sexual behavior) across species? Second, how do locomotor and postural behaviors (e.g., time spent bipedal, climbing, sitting, or quadrupedal) vary across species and are these differences reflected in the ways that species communicate gesturally? Our theoretical framework builds upon the existing knowledge of the gestural repertoires of African apes and provides insights into how social dynamics and positional behavior may shape

non-vocal communication and underlie variability in the gestural repertoires of African apes. This, in turn, can provide valuable clues as to how gestural signaling may have evolved in humans.

THE IMPORTANCE OF SOCIAL DYNAMICS

Clearly, gestural communication is instrumental to African ape communication; yet, the extent to which factors such as ecology, locomotion, cognition, and social dynamics differentially shape gestural repertoires across the African apes has not been fully explored [Pika et al., 2005a]. Social dynamics is of particular importance because of the proposed relationship between social complexity and communicative complexity [Freeberg et al., 2012]. Specifically, species with more complex social systems, as quantified by larger group size and a higher frequency of interactions with individuals of differing social roles across various contexts over time, are hypothesized to favor more complex forms of communication in terms of the number of structurally distinct signaling elements. For example, among North American wrens, song repertoire size is not only closely related to mating patterns (males in polgynous societies have a larger repertoire size compared to monogamous males), but species occurring at higher densities with high intraspecific encounter rates have larger and more complex repertoires than those occurring at lower densities [Kroodsma, 1977]. Among non-primate mammalian taxa, the number of distinct alarm calls in sciurid rodents is positively correlated to social complexity [Blumstein & Armitage, 1997; Pollard & Blumstein, 2012] and more social species of mongoose have a more diverse system of calls compared to solitary species, particularly in affiliative signals [Le Roux et al., 2009]. Similarly, the complexity of isolation calls among infant bats is strongly positively correlated with colony size [Wilkinson, 2003]. Together, these reported findings indicate a strong relationship between social dynamics and signaling patterns.

Among non-human primates, Maestripieri [2005] compared the diversity of gestures among three species of macaques in relation to their varying levels of social cohesion and found that they were similar in their use of dominance and submissive gestures but differed in those gestures associated with affiliation. As predicted [Maestripieri, 1997], stumptail macaques (*Macaca arctoides*), the most despotic species with the highest amount of social avoidance, relied on the fewest number of gestures compared to the two other more socially complex species and affiliative rhesus (*Macaca mulatta*) or pigtail (*Macaca nemestrina*) macaques [Maestripieri, 2005]. Furthermore, in a comparative study of 12 non-human primate species, Dobson [2009] also found that the diversity of facial expressions is most strongly positively correlated with group size. Hence, even as Darwin [1872] long considered, among

species living in socially complex systems, gestures and other forms of non-vocal signaling are expected to be important modes of communication and influenced by social dynamics.

In the case of the African apes, gorillas have been described as having a despotic social structure, thus their gestural repertoire is expected to be smaller than either species of the genus *Pan*. However, gorillas appear to have comparable (and in some cases larger) gestural repertoires compared to chimpanzees and bonobos [Genty et al., 2009; Pika et al., 2003; Smith, 2011]. Because the social structures of African apes are so diverse, an examination of the factors that shape gestural communication across species may help to resolve this reported discrepancy and elucidate how the social environment can influence patterns of communication (see Table II for our predictions based on social dynamics).

In the wild and in captivity, African apes are remarkably varied with regard to agonism, sexual behavior, dominance relationships, group size, and intra-sexual interactions [reviewed in King, 2004]. Here, we use *social dynamics* as a broad term to describe the types of social relationships that exist within a species and the patterns of social grouping. Hence, particular social dynamics can be determined by the time individuals spend in proximity, how often individuals groom, the frequency of agonistic encounters, and the stability of dominance hierarchies within communities and populations. Examining communicative interactions within and within and across different age- and sex-class dyads will shed light on the social dynamics of these three species and provide clues about the ways in which individuals interact and communicate information.

Consequently, we feel it is important to test the hypothesis that gestural signaling should differ among dyads as a function of the frequency of interactions between individuals and the nature of those interactions. For example, rates of gesturing and the types of gestures used between adult females may vary across the African apes depending on the nature and frequency of interactions in female–female dyads. Among gorillas, affiliative behavior between adult females is not a common occurrence. In over 800 hr of observation with western lowland gorillas at Mbeli Bai, Stokes [2004] observed no grooming and very little affiliative behavior between adults of both sexes. When adult females do exhibit affiliative behavior, it is typically directed towards their offspring or the silverback, but rarely towards other adult females [Stokes, 2004]. Similarly, among chimpanzees, adult females in the wild often forage in small parties with their close kin or travel alone, so females do not spend as much time with each other as do males [Wrangham & Smuts, 1980]. Even in captivity, where females cannot emigrate, females tend to socialize very little with each other (but see Baker and Smuts [1994] for evidence of increased

TABLE II. Predictions for the Influence of Social Dynamics and Positional Behavior on Gestural Signaling in African Apes*

	Gorilla gorilla	*Pan troglodytes*	*Pan paniscus*
Social structure	Despotic	Intermediate[a]	Egalitarian
Predicted degree of interaction among sex dyads	Male–male: low Male–female: low Female–female: low	Male–male: high Male–female: medium Female–female: medium	Male–male: low Male–female: high Female–female: high
Predicted frequency of gestural signaling in social contexts	Highest: agonistic Lowest: affiliative	Highest: affiliative/agonistic Lowest: sexual	Highest: sexual Lowest: agonistic
Predicted degree of interaction among age dyads	Adult–adult: low Adult–young: medium Young–young: high	Adult–adult: medium Adult–young: medium Young–young: high	Adult–adult: medium Adult–young: medium Young–young: high
Predicted frequency of upper limb involvement in gesturing	Highest	Lowest–medium	Medium–highest
Predicted gesture repertoire size	Smallest	Medium–large	Largest
Reported gesture repertoire size	24 [Smith, 2011] 32 [Smith, 2011] 33 [Pika et al., 2003] 102 [Genty et al., 2009]	27 [Smith, 2011] 28 [Smith, 2011] 66 [Hobaiter & Byrne, 2011]	20 [Pika et al., 2005a] 27 [Smith, 2011] 28 [de Waal, 1988] 33 [Smith, 2011]

*Following Maestripieri [2005], we define despotic social structures as those with high levels of spatial avoidance, low levels of interaction across age/sex classes, and clearly identified dominance hierarchies; egalitarian social structures are those with low levels of spatial avoidance, higher levels of interaction across age/sex classes, and more fluid dominance relationships. Repertoire size refers to the total number of distinct gestures recorded per study group. Predictions are relative to the other species, not absolute values. Young = individuals ≤8 years old; Adult = individuals ≥9 years old.
[a]Data demonstrate that *Pan troglodytes* is more despotic than *Pan paniscus*, yet more egalitarian than *Gorilla gorilla*, thus we have designated this species as having an intermediate social structure.

adult female affiliation in captivity), and overt dominance interactions between females tend to be rare [de Waal, 1982]. In wild and captive environments, dominant, resident females have been shown to form coalitions against subordinate, immigrant females (at Gombe: Goodall [1986], Pusey [1980]; at Mahale: Nishida [1989]; in captivity: Baker and Smuts [1994]). Finally, bonobos exhibit flexibility in group size and composition, as well as diversity in their social relationships. A dramatic difference between chimpanzee and bonobo social behavior is that females are often dominant to males in bonobo society, though dominance hierarchies are not always straightforward [Paoli et al., 2006; White & Wood, 2007]. Females even form coalitions with each other in agonistic encounters against males or when defending food sources against males [Kano, 1992; Parish, 1994], and interact with each other regularly via sexual behavior [Hohmann & Fruth, 2000; Hohmann et al., 1999]. We recommend that researchers examine who is gesturing to whom, how frequently, in what social contexts, and with what specific gestures to determine how these diverse social dynamics are reflected in the gestural repertoires and patterns of gestural signaling for each species.

How often individuals communicate with each other and the nature of that communication can also depend on the number of young individuals in the group, the presence of dependent offspring, and even the particular personalities and leadership styles of high-ranking individuals. We suspect that general patterns of gestural signaling can be used as measures of the social dynamics of a species, but the frequency of gestural signaling among certain individuals and within particular social contexts can stray from these patterns because of specific relationships within a group, particularly within a behaviorally flexible genus like *Pan*. Data on the influence of social dynamics on African ape gestural communication can inform us about particular social contexts that give rise to more frequent gestural signaling, and this could shed light on how early hominin societies may have used gestural communication to meet their social needs.

THE IMPORTANCE OF POSITIONAL BEHAVIOR

The influence of locomotion and body posture on gestural signaling has thus far been neglected in investigations of gestural signaling in the African apes. Though all African apes are predominantly knuckle-walkers and have anatomical adaptations for suspensory locomotion, few cross-species comparisons have been done and thus no definitive conclusions have been reached as to exactly how African apes differ in their locomotor profiles. In particular, quantitative data are lacking with respect to terrestrial positional behavior and the degree of arboreality of wild apes because researchers have been unable to consistently follow wild bonobos [Doran, 1996; Doran & Hunt, 1994] or gorillas [Doran, 1996; Remis,

1995, 1998, 1999] through dense vegetation. Doran and Hunt [1994] pooled data from various chimpanzee and mountain gorilla field sites and reported that more than 85% of their locomotor activities were quadrupedal and 90% of their postural activities were attributed to sitting and lying. More detailed accounts of time spent in various postures or locomotion or specific positional behaviors used when terrestrial versus arboreal, however, have not been obtained due to the dearth of reliable field data for bonobos and western lowland gorillas. As a result, the relationship between positional behavior and gestural communication in the African apes has been difficult to establish.

We argue that the connection between locomotion and gestural signaling must be considered when exploring the variability in gestural repertoires among the African apes and when examining the evolution of non-vocal communication. To test the hypothesis that early hominins started using more manual gestures once their upper limbs were freer, it is critical to examine the relationship between gestures and locomotion, and whether greater freedom of the hands indeed encourages gestural signaling in the African apes. We hypothesize that the locomotor profiles of African apes (which depend on environmental conditions, body size, and skeletal anatomy) should dictate the availability of the upper limbs for gesturing and the frequency with which gestural communication is employed [see Table II for our predictions based on positional behavior].

To explore the relationship between gestural signaling and positional behavior, we propose that researchers should examine the proportions of time spent in various positional behaviors, the frequencies of these behaviors, and the degree of arboreality versus terrestriality. For example, because of their large body size, especially for adult males, we would expect gorillas to spend more time on the ground in seated postures than either species of *Pan*, thus freeing their upper limbs to gesture; hence, gorillas gestures should have a relatively high frequency of upper limb involvement in gesturing. Bonobos generally have longer lower limbs than chimpanzees or gorillas [Coolidge & Shea, 1982; Doran, 1993; Morbeck & Zihlman, 1989], which may enable them to walk bipedally more efficiently. As a result of this "liberation" of hands [Copple, 2003, p. 54], the frequency with which upper limbs are available for gesturing among bonobos should be higher than among chimpanzees, whose upper limbs we expect to be occupied more often in knuckle-walking. As a result of the predicted increased terrestriality and seated postures of gorillas (which also frees their upper limbs for gesturing) and the increased bipedal locomotion of bonobos, we expect gorillas and bonobos to have greater freedom to gesture with their upper limbs, and thus gesture at a higher rate than chimpanzees. Furthermore, researchers should ex-

amine the particular posture or mode of locomotion actors used at the time of gesturing to determine whether upper limb availability influenced gestural signaling. Manual gestures that are restricted to the upper limbs (such as *arm raise*) could certainly be more easily produced when in a bipedal or seated posture, and other gestures that are not restricted to the upper limbs, but are tied to a particular body posture or have a locomotor component (such as *gallop*) are also very much influenced by the positional behavior of the animal producing the gesture. Manual gestures and those that rely on positional behavior but are not restricted to the upper limbs are identified in Table I. Despite the proposed importance of body postures and locomotion to the gestural origins theory, the relationship between gestural signaling and positional behavior has yet to be resolved. Thus, this is a critical aspect of gestural signaling that could offer insight into the physical contexts that influence gestural signaling.

DISCUSSION

Our goals in this paper have been twofold: (1) to emphasize how comparative studies of human and African ape gestural communication can be useful for understanding the origins and evolution of language and (2) to propose that social dynamics and positional behavior must be considered carefully when examining gestural communication in African apes and when attempting to uncover how human language may have emerged. The theory that language originated from gestures is based, in part, on the flexibility of gestures in human and non-human primates, and the fact that gestures are universal in modern human communication. In fact, gestures are more than just a universal means of communication. As Cartmill et al. [2012] recently stated, "the movements we make with our hands both reflect our mental processes and help to shape them [129]." A growing body of research has also shown that neural networks involved in language production and comprehension are active during body movements and gesture production and processing, and these networks have correlates in non-human primates [e.g., Arbib, 2005; Perrett et al., 1985]. Collectively, these findings demonstrate evolutionary continuity between language and motor actions in primates [Arbib, 2005; Kelly et al., 2002] as well as illustrate an important feature of gestural signaling—that body movements are inherently connected to language comprehension and production. The question now becomes: what can we learn about the origins and evolution of human language by studying the gestural communication of African apes and how can we best investigate this connection?

Tomasello and Call [2007] assert that: (1) flexible gestural signaling, (2) increased sensitivity to audience effects inherent in comprehending visual

signals, and (3) the development of an interest in sharing intentional states with others were three milestones of language evolution. The authors argue that these developments were more likely the basis for symbolic communication than were vocalizations [Tomasello & Call, 2007]. The ability to adjust communication based on the attentional states of others was likely a building block for the development of more advanced cognitive abilities like shared intentionality, decision-making, joint attention, theory of mind, and self-awareness [Liebal & Tomasello, 2009; Pika & Mitani, 2006; Pollick & de Waal, 2007; Tomasello & Herrmann, 2010], and these abilities were clearly important to human language evolution, perhaps even forming the basis for intermediate stages of "protosign" and "protolanguage" [Arbib et al., 2008].

Referential gestures like declarative and imperative pointing, emblems, and pantomimes are vital components of human gestural signaling, yet there seems to be a great divide between these prominent human gestures and the meaningful yet limited gestures of African apes [Tomasello & Herrmann, 2010]. Gestures like declarative pointing to direct one's attention to something external or imperative pointing to recruit another to cooperate or attend to a shared goal are crucial to opening up the dyadic interactions between actors and recipients to involve third parties or external objects [Povinelli & Davis, 1994; Tomasello & Call, 1997]. Humans develop these abilities in infancy as they learn to follow their mothers' gazes, focus jointly on objects or events with others, and begin pointing to direct others' attentions elsewhere [Liebal & Tomasello, 2009; Striano & Stahl, 2005]. Although pointing is quite common in human communication, it has rarely been observed among apes. Language-trained apes in captivity have been reported to point to humans and to conspecifics (see Leavens [2012] for a review), but consistently reliable accounts of spontaneous pointing among conspecifics are noticeably lacking in captive and wild populations of apes. Understanding the thoughts and intentions of others and being able to communicate about external events or objects by using gestures are essential social skills necessary for language development, and these skills were presumably important for the evolution of language as well.

Limited evidence for referential gesturing has been reported among non-human primates, but they are not abundant in the African ape gestural repertoire. No observations of pointing have been reported for untrained captive or wild non-human primates. Savage-Rumbaugh et al. [1977] reported the use of referential gestures in language-trained bonobos, and Tanner and Byrne [1996] reported that a captive silverback gorilla used a referential gesture (referred to as "iconic") to direct a female's movements by making a downward motion with his hand.

One instance of referential gesturing was reported between pairs of adult male chimpanzees in the wild when actors used a "directed scratch" gesture to direct recipients' attention to their own bodies, presumably to request that the recipients groom there [Pika & Mitani, 2006]. This type of signaling has never been reported elsewhere and the gesture was not referential in the sense that it directed another's attention to an external referent since the gesture was directed at the actor's own body. A recent examination of 20 years of data on free-ranging, rehabilitated orangutans in Borneo uncovered the use of pantomimes mainly as tools to enhance unsuccessful requests [Russon & Andrews, 2010]. Fourteen of the 18 pantomimes Russon and Andrews [2010] identified were used during interactions with humans, while the remaining four were used by orangutans to communicate with conspecifics. The authors suggest that pantomimes are more widespread than previously assumed, but this has yet to be confirmed.

More directed research that aims to explicitly examine the functional and intentional meanings behind ape gestures [e.g., Cartmill & Byrne, 2010], explore the nature of collaborative and triadic interactions [e.g., Tanner & Byrne, 2010], and discover new experimental approaches for investigating the cognitive underpinnings of gestures [e.g., Hare et al., 2001; Vonk & Povinelli, 2006] will aid in our understanding of this flexible, multi-functional, highly variable mode of communication. Understanding how certain cognitive abilities differ within and between humans and African apes can provide more information about the origins and evolution of these abilities and their impact on the evolution of language. Exploring how gestural signaling varies according to different dyadic relationships and social contexts can reveal more information about how the social environment shapes communication and may have facilitated the transition from simple manual gestures to the more complex, referential gestures used by modern humans.

The theory that language originated in gestures is also based on a shift toward bipedality in early hominins that provided an opportunity for the upper limbs to become more available for gestural signaling. Using the upper limbs, perhaps along with facial expressions, communication could be achieved between group members over long distances without drawing attention from predators like vocalizations potentially could. Kelly et al. [2002] argue that "the original functions of communication and language systems were perfectly suited for the body, and that the body continued to shape language over time [324]." Donald [1991] contends that the transition to obligate bipedality could have sparked the development of "mimetic culture," in which pantomimes of the hands and body were used to communicate about external events. This type of gesturing, along with

the use of increasingly controlled speech, could have been the basis of human language. Similarly, Arbib et al. [2008] propose that symbolic gestures such as pantomimes that followed syntactical rules eventually gave rise to "protosign," which laid the groundwork for the emergence of "protolanguage" and eventually language in early hominins.

These theories regarding how communication may have flourished in response to changes in locomotion and body posture hinge on a presumed connection between positional behavior and gestural communication that has yet to be explicitly examined, though one of us is beginning to do so with observational studies on captive African apes [Smith, 2011]. If the shift toward bipedality was indeed instrumental in advancing gestural signaling and, thus, language in early hominins, then exploring how African apes use gestures in relation to their positional behavior could reveal key information about the relationship between gestural signaling and body postures and locomotion. Ongoing [Smith & Delgado, unpublished data] and future work regarding the interconnectedness of cognition, social dynamics, positional behavior, and gestural communication will contribute to our understanding of just how intimately connected gestural signaling is to the bodies and minds of its users and what factors may have sparked the emergence of language in early hominins.

REFERENCES

Arbib MA. 2005. From monkey-like action recognition to human language: an evolutionary framework for neurolinguistics. Behav Brain Sci 28:105–168.

Arbib MA, Liebal K, Pika S. 2008. Primate vocalization, gesture, and the evolution of human language. Curr Anthropol 49:1053–1076.

Archer D. 1997. Unspoken diversity: cultural differences in gestures. Qual Sociol 20:79–105.

Armstrong DF, Wilcox SE. 2007. The gestural origin of language. New York (NY): Oxford University Press. 151 p.

Armstrong DF, Stokoe WC, Wilcox SE. 1995. Gesture and the nature of language. Cambridge (UK): Cambridge University Press. 272 p.

Baker KC, Smuts BB. 1994. Social relationships of female chimpanzees. In: Wrangham RW, McGrew WC, de Waal FBM, Heltne PG, editors. Chimpanzee cultures. Cambridge (MA): Harvard University Press. p 227–242.

Beilock SL, Goldin-Meadow S. 2010. Gesture changes thought by grounding it in action. Psychol Sci 21:1605–1610.

Blumstein DT, Armitage KB. 1997. Does sociality drive the evolution of communicative complexity? A comparative test with ground-dwelling Sciurid alarm calls. Am Nat 150:179–200.

Bodamer MD, Gardner RA. 2002. How cross-fostered chimpanzees (Pan troglodytes) initiate and maintain conversations. J Comp Psychol 116:12–26.

Botha R. 2007. On homesign systems as a potential window on language evolution. Lang Commun 27:41–53.

Burling R. 1993. Primate calls, human language, and nonverbal communication. Curr Anthropol 34:25–53.

Cartmill EA, Byrne RW. 2010. Semantics of primate gestures: intentional meanings of orangutan gestures. Anim Cogn 13:793–804.

Cartmill EA, Beilock S, Goldin-Meadow S. 2012. A word in the hand: action, gesture, and mental representations in humans and non-human primates. Philos Trans R Soc B 367:129–143.

Cheney DL, Seyfarth RM. 1990. How monkeys see the world: inside the mind of another species. Chicago (IL): University of Chicago Press. 388 p.

Chomsky N. 1968. Language and mind. 1st edition. New York (NY): Harcourt Brace. 186 p.

Coolidge HJ, Shea BT. 1982. External body dimensions of Pan paniscus and Pan troglodytes chimpanzees. Primates 23:245–251.

Copple M. 2003. Gesture and speech: André Leroi-Gourhan's theory of the co-evolution of manual and intellectual activities. Gesture 3:47–94.

Corballis MC. 2002. From hand to mouth, the origins of language. Princeton (NJ): Princeton University Press. 272 p.

Corballis MC. 2003. From mouth to hand: gesture, speech, and the evolution of right-handedness. Behav Brain Sci 26:190–260.

Corballis MC. 2009. The evolution of language. The Year in Cognitive Neuroscience 2009. Ann N Y Acad Sci 1156:19–43.

Darwin C. 1872. The expression of the emotions in man and animals. London (UK): John Murray (reprinted by University of Chicago Press, 1965). 370 p.

de Waal FBM. 1982. Chimpanzee politics: power and sex among apes. New York (NY): Harper & Row. 256 p.

de Waal FBM. 1988. The communicative repertoire of captive bonobos (Pan paniscus) compared to that of chimpanzees. Behaviour 106:183–251.

de Waal FBM. 1999. Cultural primatology comes of age. Nature 399:635–636.

Dobson SD. 2009. Socioecological correlates of facial mobility in nonhuman anthropoids. Am J Phys Anthropol 139:413–420.

Donald M. 1991. Origins of the modern mind. Cambridge (MA): Harvard University Press. 424 p.

Doran DM. 1993. Comparative locomotor behavior of chimpanzees and bonobos: the influence of morphology on locomotion. Am J Phys Anthropol 91:83–98.

Doran DM. 1996. The comparative positional behavior of the African apes. In: McGrew W, Nishida T, editors. Great ape societies. Cambridge (UK): Cambridge University Press. p 213–224.

Doran DM, Hunt KD. 1994. Comparative locomotor behavior of chimpanzees and bonobos: species and habitat differences. In: Wrangham RW, McGrew WC, de Waal FBM, Heltne PG, editors. Chimpanzee cultures. Cambridge (MA): Harvard University Press. p 93–108.

Dunning GB. 1971. Research in nonverbal communication. Theory Pract 10:250–258.

Fossey D. 1983. Gorillas in the mist. London (UK): Hodder & Stoughton. 400 p.

Fouts RS. 1973. Acquisition and testing of gestural signs in four young chimpanzees. Science 180:978–980.

Freeberg TM, Dunbar RIM, Ord TJ. 2012. Social complexity as a proximate and ultimate factor in communicative complexity. Phil Trans R Soc B 367:1785–1801.

Gardner RA, Gardner BT. 1969. Teaching sign language to a chimpanzee. Science 165:664–672.

Gentilucci M. 2003. Grasp observation influences speech production. Eur J Neurosci 17:179–184.

Gentilucci M, Corballis MC. 2006. From manual gesture to speech: a gradual transition. Neurosci Biobehav Rev 30:949–960.

Genty E, Breuer T, Hobaiter C, Byrne RW. 2009. Gestural communication of the gorilla (Gorilla gorilla): repertoire, intentionality and possible origins. Anim Cogn 12:527–546.

Goldin-Meadow S, Feldman H. 1977. The development of language-like communication without a language model. Science 197:401–403.

Goodall J. 1986. The chimpanzees of Gombe: patterns of behavior. Cambridge (MA): Belknap Press. 673 p.

Hare B, Call J, Tomasello M. 2001. Do chimpanzees know what conspecifics know? Anim Behav 61:139–151.

Hewes GW. 1973. Primate communication and the gestural origin of language. Curr Anthropol 12:5–24.

Hobaiter C, Byrne RW. 2011. The gestural repertoire of the wild chimpanzee. Anim Cogn 14:745–767.

Hohmann G, Fruth B. 2000. Use and function of genital contacts among female bonobos. Anim Behav 60:107–120.

Hohmann G, Gerloff U, Tautz D, Fruth B. 1999. Social bonds and genetic ties: association and affiliation in a community of bonobos (Pan paniscus). Behaviour 136:1219–1235.

Hopkins WD, Taglialatela JP, Leavens DA. 2007. Chimpanzees differentially produce novel vocalizations to capture the attention of a human. Anim Behav 73:281–286.

Hopkins WD, Pika S, Liebal K, et al. 2012. Handedness for manual gestures in great apes: a meta-analysis. In: Pika S, Liebal K, editors. Current developments in non-human primate gesture research. Amsterdam (The Netherlands): John Benjamins Publishing. p 93–111.

Hostetter AB, Cantero M, Hopkins WD. 2001. Differential use of vocal and gestural communication by chimpanzees (Pan paniscus) in response to the attentional state of a human (Homo sapiens). J Comp Psychol 115:337–343.

Ingmanson EJ. 1987. Clapping behavior: Non-verbal communication during grooming in a group of captive pygmy chimpanzees. Am J Phys Anthropol 72:214.

Ingmanson EJ. 1996. Tool-using behavior in wild Pan paniscus: social and ecological considerations. In: Russon AE, Bard KA, Parker ST, editors. Reaching into thought: the minds of the great apes. Cambridge (UK): Cambridge University Press. p 190–210.

Iverson JM, Goldin-Meadow S. 1998. Why people gesture when they speak. Nature 396:228.

Iverson JM, Tencer HL, Lany J, Goldin-Meadow S. 2000. The relation between gesture and speech in congenitally blind and sighted language-learners. J Nonverbal Behav 24:105–130.

Janik VM, Slater PJB. 2000. The different roles of social learning in vocal communication. Anim Behav 60:1–11.

Jürgens U. 2002. Neural pathways underlying vocal control. Neurosci Biobehav Rev 26:235–258.

Kalan AK, Rainey HJ. 2009. Hand-clapping as a communicative gesture by wild female swamp gorillas. Primates 50:273–275.

Kano T. 1982. The social group of pygmy chimpanzees (Pan paniscus) of Wamba. Primates 23:171–188.

Kano T. 1992. The last ape: pygmy chimpanzee behavior and ecology. Stanford (CA): Stanford University Press. 276 p.

Kelly SD, Iverson JM, Terranova J, Niego J, Hopkins M, Goldsmith L. 2002. Putting language back in the body: speech and gesture on three time frames. Dev Neuropsychol 22:323–349.

Kelly SD, Özyürek A, Maris E. 2009. Two sides of the same coin: speech and gesture mutually interact to enhance comprehension. Psychol Sci 21:260–267.

Kendon A. 1997. Gesture. Annu Rev Anthropol 26:109–128.

King BJ. 2004. The dynamic dance: nonvocal communication in African apes. Cambridge (MA): Harvard University Press. 304 p.

Kitchen DM, Seyfarth RM, Fischer J, Cheney DL. 2003. Loud calls as indicators of dominance in male baboons (Papio cynocephalus ursinus). Behav Ecol Sociobiol 53:374–384.

Knott GP. 1979. Nonverbal communication during early childhood. Theory Pract XVII:226–233.

Kroodsma DE. 1977. Correlates of song organization among North American wrens. Am Nat 111:995–1008.

Le Roux A, Cherry MI, Manser M. 2009. The vocal repertoire in a solitary foraging carnivore, Cynictis penicillata, may reflect facultative sociality. Naturwissenschaften 96:575–584.

Leavens DA. 2012. Joint attention: twelve myths. In: Seemann A, editor. Joint attention: new developments in pyschology, philosophy of mind and social neuroscience. Cambridge (MA): MIT Press. p 43–72.

Leroi-Gourhan A. 1993. Gesture and speech. Berger AB, trans. Cambridge (MA): MIT Press. 453 p.

Liebal K, Call J. 2012. The origins of non-human primates' manual gestures. Philos Trans R Soc B 367:118–128.

Liebal K, Tomasello M. 2009. Infants appreciate the social intention behind a pointing gesture. Commentary on "Children's understanding of communicative intentions in the middle of the second year of life" by Aureli T, Perucchini P, Genco M. Cogn Dev 24:13–15.

Liebal K, Call J, Tomasello M. 2004a. Use of gesture sequences in chimpanzees. Am J Primatol 64:377–396.

Liebal K, Pika S, Call J, et al. 2004b. To move or not to move: how apes adjust to the attentional state of others. Interact Stud 5:199–219.

Maestripieri D. 1997. The evolution of communication. Lang Commun 17:269.

Maestripieri D. 2005. Gestural communication in three species of macaques (Macaca mulatta, M. nemestrina, M. arctoides): use of signals in relation to dominance and social context. Gesture 5:57–73.

Marshall AJ, Wrangham RW, Arcadi AC. 1999. Does learning affect the structure of vocalizations in chimpanzees? Anim Behav 58:825–830.

McGrew WC. 2004. The cultured chimpanzee: reflections on cultural primatology. Cambridge (UK): Cambridge University Press. 262 p.

McGrew WC, Tutin CEG. 1978. Evidence for a social custom in wild chimpanzees? Man 13:234–251.

Melinger A, Levelt WJM. 2004. Gesture and the communicative intention of the speaker. Gesture 4:119–141.

Mitani J, Brandt K. 1994. Social factors influence the acoustic variability in the long-distance calls of male chimpanzees. Ethology 96:233–252.

Morbeck ME, Zihlman AL. 1989. Body size and proportions in chimpanzees, with special reference to Pan troglodytes schweinfurthii from Gombe National Park, Tanzania. Primates 30:369–382.

Müller C. 2005. Gestures in human and nonhuman primates, why we need a comparative view. Gesture 5:259–283.

Nishida T. 1980. The leaf-clipping display: a newly-discovered expressive gesture in wild chimpanzees. J Hum Evol 9:117–128.

Nishida T. 1989. Social interactions between resident and immigrant female chimpanzees. In: Heltne P, Marquardt L, editors. Understanding chimpanzees. Cambridge (MA): Harvard University Press. p 68–89.

Ouattara K, Lemasson A, Zuberbühler K. 2009a. Campbell's monkeys concatenate vocalizations into context-specific call sequences. Proc Natl Acad Sci USA 106:22026–22031.

Ouattarra K, Zuberbühler K, Eliezer K, Gombert J, Lemasson A. 2009b. The alarm call system of female Campbell's monkeys. Anim Behav 78:35–44.

Paoli T, Palagi E, Borgognini Tarli SM. 2006. Reevaluation of dominance hierarchy in bonobos (*Pan paniscus*). Am J Phys Anthropol 130:116–122.

Parish AR. 1994. Sex and food control in the "uncommon chimpanzee." How bonobo females. overcome phylogenetic legacy of male dominance. Ethol Sociobiol 15:157–179.

Perrett DI, Smith PAJ, Mistlin AJ, et al. 1985. Visual analysis of body movements by neurons in the temporal cortex of the macaque monkey. Behav Brain Res 16:153–170.

Pika S, Mitani J. 2006. Referential gestural communication in wild chimpanzees (*Pan troglodytes*). Curr Biol 16:191–192.

Pika S, Liebal K, Tomasello M. 2003. Gestural communication in young gorillas (*Gorilla gorilla*): gestural repertoire, learning and use. Am J Primatol 60:95–111.

Pika S, Liebal K, Call J, et al. 2005a. The gestural communication of apes. Gesture 5:41–56.

Pika S, Liebal K, Tomasello M. 2005b. Gestural communication in subadult bonobos (*Pan paniscus*): repertoire and use. Am J Primatol 65:39–61.

Pinker S, Bloom P. 1990. Natural language and natural selection. Behav Brain Sci 13:707–784.

Pollard KA, Blumstein DT. 2012. Evolving communicative complexity: insights from rodents and beyond. Philos Trans R Soc B 367:869–878.

Pollick AS, de Waal FBM. 2007. Ape gestures and language evolution. Proc Natl Acad Sci 104:8184–8189.

Povinelli DJ, Davis DR. 1994. Differences between chimpanzees (*Pan troglodytes*) and humans (*Homo sapiens*) in the resting state of the index finger: implications for pointing. J Comp Psychol 108:134–139.

Povinelli DJ, Theall LA, Reaux JE, Dunphy-Lelii S. 2003. Chimpanzees spontaneously alter the location of their gestures to match the attentional orientation of others. Anim Behav 65:71–79.

Pusey AE. 1980. Inbreeding avoidance in chimpanzees. Anim Behav 28:543–552.

Remis MJ. 1995. Effects of body size and social context on the arboreal activities of lowland gorillas in the Central African Republic. Am J Phys Anthropol 97:413–433.

Remis MJ. 1998. The effects of body size and habitat on the positional behavior of lowland and mountain gorillas. In: Strasser E, Fleagle J, Rosenberger A, McHenry HM, editors. Primate locomotion—recent advances. New York (NY): Plenum Press. p 95–106.

Remis MJ. 1999. Tree structure and sex differences in arboreality among western lowland gorillas (*Gorilla gorilla gorilla*) at Bai Hokou, Central African Republic. Primates 40:383–396.

Russon A, Andrews K. 2010. Orangutan pantomime: elaborating the message. Biol Lett 7:627–630.

Savage-Rumbaugh S, Wilkerson BJ, Bakesman R. 1977. Spontaneous gestural communication among conspecifics in the pygmy chimpanzee (*Pan paniscus*). In: Bourne GH, editor. Progress in ape research. New York (NY): Academic Press. p 97–116.

Savage-Rumbaugh S, Shanker SG, Taylor TJ. 1998. Apes, language, and the human mind. New York (NY): Oxford University Press. 256 p.

Schaller GB. 1963. The mountain gorillas: ecology and behavior. Chicago (IL): University of Chicago Press. 448 p.

Senghas A, Coppola M. 2001. Children creating language: how Nicaraguan Sign Language acquired a spatial grammar. Psychol Sci 12:323–328.

Seyfarth RM. 2005. Continuities in vocal communication argue against a gestural origin of language. Behav Brain Sci 28:144–145.

Seyfarth RM, Cheney DL. 1997. Some general features of vocal development in nonhuman primates. In: Snowdon CT, Hausberger M, editors. Social influences on vocal development. Cambridge (UK): Cambridge University Press. p 249–273.

Seyfarth RM, Cheney DL, Marler P. 1980. Monkey responses to three different alarm calls: evidence for predator classification and semantic communication. Science 210:801–803.

Seyfarth RM, Cheney DL, Bergman TJ. 2005. Primate social cognition and the origins of language. Trends Cogn Sci 9:264–266.

Smith LW. 2011. The effects of social dynamics and positional behavior on gestural communication among African apes [dissertation]. New York (NY): City University of New York Graduate Center. 200 p. ProQuest Dissertations and Theses, ID: 1 883387049.

Snowdon CT, Hodun A. 1981. Acoustic adaptations in pygmy marmoset contact calls: locational cues vary with distance between conspecifics. Behav Ecol Sociobiol 9:295–300.

Stokes EJ. 2004. Within-group social relationships among females and adult males in wild western lowland gorillas (*Gorilla gorilla gorilla*). Am J Primatol 64:233–246.

Striano T, Stahl D. 2005. Sensitivity to triadic attention in early infancy. Dev Sci 8:333–343.

Tanner JE, Byrne RW. 1996. Representation of action through iconic gesture in a captive lowland gorilla. Curr Anthropol 37:162–173.

Tanner JE, Byrne RW. 2010. Triadic and collaborative play by gorillas in social games with objects. Animal Cognition 13:591–607.

Terrrace HS. 1979. Nim. New York (NY): A.A. Knopf. 303 p.

Tomasello M, Call J. 1997. Primate cognition. New York (NY): Oxford University Press. 528 p.

Tomasello M, Call J. 2007. Ape gestures and the origins of language. In: Tomasello M, Call J, editors. The gestural communication of apes and monkeys. Mahwah (NJ): Lawrence Erlbaum Associates. p 221–239.

Tomasello M, Herrmann E. 2010. Ape and human cognition: what's the difference? Curr Dir Psychol Sci 19:3–8.

Tomasello M, Zuberbühler K. 2002. Primate vocal and gestural communication. In: Bekoff M, Allen C, Burghardt GM, editors. The cognitive animal: empirical and theoretical perspectives on animal cognition. Cambridge (MA): MIT Press. p 293–300.

Tomasello M, Call J, Warren JA, et al. 1997. The ontogeny of chimpanzee gestural signals: a comparison across groups and generations. Evol Commun 1:223–259.

Vonk J, Povinelli DJ. 2006. Similarity and difference in the conceptual systems of primates: the unobservability hypothesis. In: Wasserman E, Zentall T, editors. Comparative cognition: experimental explorations of animal intelligence. Cambridge, UK: Oxford University Press. p 363–387.

White FJ, Wood KD. 2007. Female feeding priority in bonobos, *Pan paniscus*, and the question of female dominance. Am J Primatol 69:837–850.

Whiten A, Goodall J, McGrew WC, et al. 1999. Cultures in chimpanzees. Nature 399:682–685.

Wich SA, Swartz KB, Hardus ME, et al. 2008. A case of spontaneous acquisition of a human sound by an orangutan. Primates 50:56–64.

Wilkinson GS. 2003. Social and vocal complexity in bats. In: de Waal FBM, Tyack PL, editors. Animal social complexity: intelligence, culture, and individualized societies. Cambridge (MA): Harvard University Press. p 322–341.

Wrangham RW, Smuts BB. 1980. Sex differences in the behavioural ecology of chimpanzees in Gombe National Park. Tanzania J Reprod Fertil S28:13–31.

Xu J, Gannon PJ, Emmorey K, Smith JF, Braun AR. 2009. Symbolic gestures and spoken language are processed by a common neural system. Proc Natl Acad Sci 106:20664–20669.

Zuberbühler K. 2000. Referential labelling in Diana monkeys. Anim Behav 59:917–927.