

- Kopp, Stefan, Paul Tepper and Justine Cassell 2004. Towards integrated microplanning of language and iconic gesture for multimodal output. In: *Proceedings of the International Conference on Multimodal Interfaces (ICMI '04)*, 97–104. New York, NY: ACM Press.
- Kopp, Stefan and Ipke Wachsmuth 2002. Model-based animation of coverbal gesture. In: *Proceedings of Computer Animation 2002*, 252–257. Los Alamitos, CA: IEEE Press.
- Kopp, Stefan and Ipke Wachsmuth 2004. Synthesizing multimodal utterances for conversational agents. *Computer Animation and Virtual Worlds* 15(1): 39–52.
- Krenn, Brigitte and Hannes Pirker 2004. Defining the gesticon: Language and gesture coordination for interacting embodied agents. In: *Proceedings AISB-2004 Symposium on Language, Speech and Gesture for Expressive Characters*, 107–115. University of Leeds, UK.
- McNeill, David 2005. *Gesture and Thought*. Chicago: Chicago University Press.
- Neff, Michael, Michael Kipp, Irene Albrecht and Hans-Peter Seidel 2008. Gesture modeling and animation based on a probabilistic recreation of speaker style. *ACM Transactions on Graphics* 27(1): 1–24.
- Poggi, Isabella 2001. The lexicon and the alphabet of gesture, gaze, and touch. In: *Proceedings of IVA 2001. Lecture Notes in Computer Science*, Volume 2190, 235–236. Heidelberg: Springer Verlag.
- Reiter, Ehud and Robert Dale 2000. *Building Natural-Language Generation Systems*. Cambridge: Cambridge University Press.
- Ruttkay, Zsofi 2007. Presenting in style by virtual humans. In: Anna Esposito (ed.), *Verbal and Nonverbal Communication Behaviours*, 23–36. Berlin/Heidelberg: Springer Verlag.
- Stone, Matthew, Douglas DeCarlo, Insuk Oh, Christian Rodriguez, Adrian Stere, Alyssa Lees and Chris Bregler 2004. Speaking with hands: Creating animated conversational characters from recordings of human performance. *ACM Transactions on Graphics* 23(3): 506–513.
- Swartout, William, Jonathan Gratch, Randy Hill, Ed Hovy, Stacy Marsella, Jeff Rickel and David Traum 2006. Toward virtual humans. *AI Magazine* 27(2): 96–108.
- Thórisson, Kristin R. 1997. Gandalf: an embodied humanoid capable of real-time multimodal dialogue with people. In: *Proceedings of AGENTS '97*, 536–537. New York, NY: ACM Press.

Stefan Kopp, Bielefeld (Germany)

153. The psychology of gestures and gesture-like movements in non-human primates

1. What are nonhuman primates?
2. What is a gesture?
3. What is a psychological approach?
4. What is intentional communication?
5. Which cognitive aspects are of interest?
6. Conclusion and outlook
7. References

Abstract

Research into gestural communication of nonhuman primates is often inspired by an interest in the evolutionary roots of human language. The focus on intentionally used behaviors is central to this approach that aims at investigating the cognitive mechanisms characterizing

gesture use in monkeys and apes. This chapter describes some of the key characteristics that are important in this context, and discusses the evidence the claim is built on that gestures of nonhuman primates represent intentionally and flexibly used means of communication.

This chapter will first provide a brief introduction into what primates are and how a gesture is defined, before the psychological approach to gestural communication is described in more detail, with focus on the cognitive mechanisms underlying gesture use in nonhuman primates.

1. What are nonhuman primates?

The order primates has been traditionally divided into prosimians (lemurs, lorises, tarsiers) and anthropoids (Old World monkeys, New World monkeys, apes, humans) (Fleagle 1999). While humans inhabit all continents and almost every climate zone of the world, nonhuman primates live in the tropical and subtropical regions of Africa, Asia, and the Americas. Unlike other mammalian orders, primates lack a shared characteristic that is unique to this group. However, one major behavioral trait of primates is their tendency to be highly social throughout all life stages. In contrast to the typically short-term associations of other mammals, group membership in primates tends to be highly regular (Smuts et al. 1987).

2. What is a gesture?

Although the term *gesture* is frequently used in the scientific world and in everyday life, definitions can vary significantly, i.e., in regard to the body parts that execute gestures, the considered modalities, and the relationship of these non-verbal communicative means with language. For example, human gestures can be defined as a form of non-verbal communication in which visible bodily actions communicate particular messages, either in place of speech or closely intertwined with spoken words (Kendon 2004). However, because nonhuman primates do not have language, researchers usually adopt definitions and criteria from research into gestures of pre-verbal children (Bates et al. 1979; Leavens, Russell, and Hopkins 2005). Thus, gestures of nonhuman primates are commonly defined as mechanically ineffective behaviors that are directed at a particular recipient and are tailored to the attentional state of the audience and which are characterized by the sender's persistence and elaboration when the initial communicative attempts fail (Call and Tomasello 2007; Leavens, Russell, and Hopkins 2005) (see section 5). Unlike research into human gestures that focuses on the visual modality, researchers interested in nonhuman primates also consider auditory gestures, which generate sound from body parts other than the vocal cords, as well as tactile gestures, which involve physical contact between the two interacting partners. Furthermore, many researchers do not restrict gestures to the use of hands but include movements of limbs or the head and body postures. Some studies also consider facial expressions as facial gestures (Ferrari et al. 2003; Maestripietri 1999), while others refer to facial expressions as a separate mode of visual communication (Call and Tomasello 2007). Unlike facial expressions and vocalizations, gestures are not identified based on specific structural properties, but are generally classified according to their function or use (but see Roberts et al. 2012).

3. What is a psychological approach?

The communication of nonhuman animals receives considerable attention from a variety of disciplines such as biology and psychology, but also anthropology, linguistics, or neu-

rosience. One major reason for this interest in animal communication is the search for the evolutionary roots of human language and the assumption that by comparing humans and other animals, it is possible to identify those behaviors that are uniquely human and those that are shared with other species, which might represent potential precursors to human language (Slocombe, Waller, and Liebal 2011; Wilcox 1999).

Biologists and psychologists traditionally use different – though related – perspectives when studying animal behavior. While biologists focus more on the *ultimate* aspects of behavior and are particularly interested in why and how a specific behavior has evolved, psychologists are more interested in the *proximate* aspects, which include cognitive, emotional, or physiological mechanisms underlying behavior and the development of behavior during an individual's lifetime (Tinbergen 1963; Waller et al. 2013).

This has important implications for research into the gestural communication of non-human primates. Here researchers mostly use a psychological approach, which centers on the proximate aspects and thus on the cognitive mechanisms underlying gesture use (see section 5). Key to this approach is the question whether gestural communication in nonhuman primates is intentional, as the intentional use is one of the major characteristics of human language.

4. What is intentional communication?

In gesture research, the term “intentional communication” is used to describe purposeful, goal-directed behavior, with the sender having voluntary control over the production of a particular signal (Benga 2005). At the same time, this does not necessarily imply that the recipient understands that this signal is an intentional act of communication (Genty et al. 2009).

The aim of this approach to primate communication is to identify those signals that are characterized by variability between individuals and flexibility in use as opposed to signals that are used by all individuals of one species, often for very specific functions and in very specific contexts (Tomasello 2008). In contrast to those phylogenetically ritualized signals that have evolved under very specific selection pressures, intentionally used signals are most likely acquired by some form of learning during an individual's lifetime. Thus, research into primate gestures is particularly motivated by an interest in the cognitive aspects of primate communication, because the intentional use of signals implies voluntary control and thus potential for a more flexible and sophisticated use of these signals.

5. Which cognitive aspects are of interest?

In the following, different features are discussed that are commonly used to identify acts of intentional communication in nonhuman primates (for a detailed discussion, see Liebal et al. 2013: Chapter 8).

5.1. Presence and attentional state of the audience

The sender's sensitivity to the presence of an audience is defined as audience effect, and refers to a signal only being used when someone is present and thus able to perceive the signal (Rogers and Kaplan 2000). Most existing studies focus on great apes' interactions

with a human experimenter and demonstrate that they only produce gestures in the presence, but not absence of the human (e.g., Hostetter, Cantero, and Hopkins 2001; Poss et al. 2006).

There is considerably more research that investigates if and how nonhuman primates adjust their gestures to the recipient's attentional state. While tactile and auditory gestures can be perceived regardless of whether the recipient is attending or not, visual gestures require the visual attention of the recipient. In interactions with conspecifics, several species including monkeys, gibbons, and great apes use visual gestures only if the recipient is visually attending (see Call and Tomasello 2007). In interactions with humans, both great apes and monkeys adjust their gesture use to the attentional state of a human experimenter: They gesture more and use visual gestures only if the human is oriented towards them (e.g., Anderson et al. 2010; Hostetter, Cantero, and Hopkins 2001; Maille et al. 2012). However, in more complex situations with two human experimenters with differing attentional states and varying body orientations, chimpanzees did not seem to show sensitivity to the attentional state of the human when producing pointing gestures (Povinelli and Eddy 1996). However, there is some evidence that the apes use the orientation of the human's face to conclude whether the human can perceive the their pointing gestures, while the body orientation informs the ape whether the human is able to give any food at all. Thus, the orientation of the face and the body provide different information (Kaminski, Call, and Tomasello 2004).

5.2. Use of attention-getters

Closely related to the previous section is the question whether nonhuman primates use particular gestures to attract the attention of a non-attending individual. Studies that focused on interactions between conspecifics found that both siamangs and orangutans do not use auditory and tactile gestures more if the recipient is not attending indicating that these potential attention-getting gestures are used regardless of the attentional state of the recipient (Liebal, Pika, and Tomasello 2004, 2006). Furthermore, there is little evidence that great apes use attention-getting gestures first to attract the recipient's attention before producing a visual gesture (Liebal, Call, and Tomasello 2004; Tempelmann and Liebal 2012). Thus, it is currently unclear whether nonhuman primates use specific gestures to attract the attention of others or whether such gestures are used to trigger others into action (Liebal and Call 2012).

In interactions with humans, great apes use more auditory gestures and vocalizations if a human experimenter is turned away and thus not attending (Hostetter, Cantero, and Hopkins 2001; Poss et al. 2006). However, if great apes are given the opportunity to change their position in relation to the orientation of a human experimenter, they preferably walk in front of the human where they use visual gestures to beg for food rather than using auditory or tactile gestures behind the human to attract her attention (Liebal et al. 2004). Thus, rather than manipulating the attentional state of their partner, chimpanzees move into the visual field of another individual to ensure that their communicative behaviors are perceived (Liebal, Call, and Tomasello 2004).

5.3. Flexible use across different contexts

Gesture researchers usually highlight the flexible use of these signals (Call and Tomasello 2007; Tomasello 2008), but flexibility can be defined in different ways. It can refer to

the flexible usage of gestures across different contexts, or to the ability to combine components of an existing repertoire into longer sequences to enable a more flexible use of a relatively limited repertoire.

In regard to the flexible usage, great apes use the majority of gestures for more than one function, and several gestures can be used to achieve the same goal (e.g., Genty et al. 2009; Tomasello et al. 1997). As a consequence of this flexible use across different contexts, many gestures do not have a specific meaning, but the information they convey is defined by the context in which they are used.

In regard to the combination of gestures, sequences are described for several great ape species in both captive and wild settings (Hobaiter and Byrne 2011; Liebal, Pika, and Tomasello 2004; Tanner 2004). Altogether, there is little evidence that gesture combinations are used for new or other functions than their single components, thus indicating that great apes do not create sequences to communicate new meanings. Instead, they seem to represent the sender's communicative strategies to flexibly react to the recipient's behavior. For example, gesture sequences of chimpanzees emerge if the recipient does not respond to the initial gesture (Liebal et al. 2004) and gorillas use sequences as means to adjust the communicative interactions between two individuals (Genty et al. 2009; Tanner 2004). Interestingly, there is some evidence that gesture sequences of chimpanzees reflect some kind of developmental process since they shift from initially long and redundant sequences of rapid-fire gestures in youngsters to selecting more effective single iterative gestures as adults (Hobaiter and Byrne 2011). Thus, across these studies gesture sequences are not used as premeditated constructs to increase the flexibility or efficacy of gesture use, but they seem to represent strategies to react appropriately to the recipient's behavior.

5.4. Persistence and elaboration

Instances in which a recipient does not react to the first gesture are very interesting, since they reveal how flexibly nonhuman primates can react in such situations. If the sender persists in their communicative attempts, they can either repeat the same signal or elaborate gesture use by changing the type or intensity of the gesture in order to achieve the recipient's response.

In interactions with conspecifics, there is evidence that both wild and captive chimpanzees persist in their communicative attempts after their initial gesture failed (Hobaiter and Byrne 2011; Liebal, Call, and Tomasello 2004), while gorillas and orangutans are less likely to continue to gesture if there is no response of the recipient (Genty and Byrne 2010; Tempelmann and Liebal 2012). Whether these results reflect differences between species or are caused by different methodologies across studies is currently unclear.

Most gesture sequences of great apes, however, are repetitions of the same gesture. Even if different gesture types are combined, there is little evidence that these elaborated sequences are more successful in obtaining an appropriate response from the recipient than single gestures (Genty and Byrne 2010; Liebal, Call, and Tomasello 2004; Tempelmann and Liebal 2012). Most evidence for elaboration in gesture use comes from studies on great apes' interactions with humans. For example, orangutans adjust their communicative behavior when begging for food from a human depending on whether the human's response met their goal fully, only partly, or not at all (Cartmill and Byrne 2007). Thus, orangutans stop gesturing when they get the whole banana, they repeat the same gesture if they receive only half instead of the whole banana indicating persistence, and they switch to other gestures in case the human offers them a completely different food item than they requested.

5.5. Learning of novel gestures

This section specifically refers to novel gestures that are created by particular individuals and which are not part of a species' repertoire, but which may spread across individuals within one group. This would indicate some form of flexibility in a way that new gestures can be added to a species repertoire. For example, an eye-covering gesture has been documented for mandrills in only one out of many groups (Laidre 2008). In chimpanzees, the hand-clasp is unique to certain communities, suggesting that this gesture was newly created and was subsequently acquired by other individuals within the group (van Leeuwen et al. 2012). However, very little is known about how nonhuman primates acquire their gestures and more longitudinal studies are needed to identify the mechanisms underlying gesture acquisition (Schneider, Call, and Liebal 2012a, b).

6. Conclusion and outlook

Research on gestural communication in nonhuman primates usually takes a psychological perspective and thus focuses on the cognitive mechanisms underlying gesture use in monkeys and apes. The intentional use of gestures is of central importance in this field of research and a variety of cognitive skills are used to identify intentional acts of communication. An increasing body of research on several species of apes but also some monkey species shows that nonhuman primates use their gestures only in the presence of an audience, they adjust them to the attentional state of the recipient, and persist in their communicative attempts if their initial gestures fails to elicit a response of the recipient. However, studies examining the use of specific attention-getting gestures to manipulate the recipient's attentional state revealed inconsistent findings, as did studies on the function of gesture sequences. Furthermore, some communicative strategies seem to vary depending on whether apes are interacting with other conspecifics or a human experimenter. It is important to emphasize, however, that the majority of knowledge on gesture use is from studies on great apes in captive settings. Therefore, future research needs to consider other primate species, particularly monkeys, in both captive and wild settings. Furthermore, little is known about the developmental processes and the factors that influence gesture acquisition during ontogeny. Finally, gesture is only one out of several modalities nonhuman primates use to communicate with others, in addition to facial expressions, vocalizations, and olfactory signals. Future research should specifically address these different facets of primate communication and the ways these modalities interact with and influence each other.

7. References

- Anderson, James R., Hika Kuroshima, Yuko Hattori and Kazuo Fujita 2010. Flexibility in the use of requesting gestures in squirrel monkeys (*Saimiri sciureus*). *American Journal of Primatology* 72(8): 707–714.
- Bates, Elizabeth, Laura Benigni, Inge Bretherton, Luigia Camaioni and Virginia Volterra 1979. *The Emergence of Symbols: Cognition and Communication in Infancy*. New York: Academic Press.
- Benga, Oana 2005. Intentional communication and the anterior cingulate cortex. *Interaction Studies* 6(2): 201–221.
- Call, Josep and Michael Tomasello (eds.) 2007. *The Gestural Communication of Apes and Monkeys*. Mahwah/NJ: Erlbaum.

- Cartmill, Erica A. and Richard W. Byrne 2007. Orangutans modify their gestural signaling according to their audience's comprehension. *Current Biology* 17(15): 1345–1348.
- Ferrari, Pier F., Vittorio Gallese, Giacomo Rizzolatti and Leonardo Fogassi 2003. Mirror neurons responding to the observation of ingestive and communicative mouth actions in the monkey ventral premotor cortex. *European Journal of Neuroscience* 17(8): 1703–1714.
- Fleagle, John G. 1999. *Primate Adaptation and Evolution*. San Diego, CA: Academic Press.
- Genty, Emilie, Thomas Breuer, Catherine Hobaiter and Richard W. Byrne 2009. Gestural communication of the gorilla (*Gorilla gorilla*): Repertoire, intentionality and possible origins. *Animal Cognition* 12(3): 527–546.
- Genty, Emilie and Richard W. Byrne 2010. Why do gorillas make sequences of gestures? *Animal Cognition* 13(2): 287–301.
- Hobaiter, Catherine and Richard W. Byrne 2011. Serial gesturing by wild chimpanzees: Its nature and function for communication. *Animal Cognition* 14(6): 827–838.
- Hostetter, Autumn B., Monica Cantero and William D. Hopkins 2001. Differential use of vocal and gestural communication by chimpanzees (*Pan troglodytes*) in response to the attentional status of a human (*Homo sapiens*). *Journal of Comparative Psychology* 115(4): 337–343.
- Kaminski, Juliane, Josep Call and Michael Tomasello 2004. Body orientation and face orientation: Two factors controlling apes begging behavior from humans. *Animal Cognition* 7(4): 216–233.
- Kendon, Adam 2004. *Gesture: Visible Action as Utterance*. Cambridge, UK: Cambridge University Press.
- Laidre, Mark E. 2008. Do captive mandrills invent new gestures? *Animal Cognition* 11(2): 179–187.
- Leavens, David A., Jamie L. Russell and William D. Hopkins 2005. Intentionality as measured in the persistence and elaboration of communication by chimpanzees (*Pan troglodytes*). *Child Development* 76(1): 291–306.
- Liebal, Katja and Josep Call 2012. The origins of non-human primates' manual gestures. *Philosophical Transactions of the Royal Society B: Biological Sciences* 367(1585): 118–128.
- Liebal, Katja, Josep Call, Simone Pika and Michael Tomasello 2004. To move or not to move: How apes adjust to the attentional state of others. *Interaction Studies* 5(2): 199–219.
- Liebal, Katja, Josep Call and Michael Tomasello 2004. The use of gesture sequences in chimpanzees. *American Journal of Primatology* 64(4): 377–396.
- Liebal, Katja, Simone Pika and Michael Tomasello 2004. Social communication in siamangs (*Symphalangus syndactylus*): Use of gestures and facial expressions. *Primates* 45(1): 41–57.
- Liebal, Katja, Simone Pika and Michael Tomasello 2006. Gestural communication of orangutans (*Pongo pygmaeus*). *Gesture* 6(1): 1–38.
- Liebal Katja, Bridget M. Waller, Anne M. Burrows and Katie E. Slocombe 2013. *Primate Communication: A Multimodal Approach*. Cambridge, UK: Cambridge University Press.
- Maestripieri, Dario 1999. Primate social organization, gestural repertoire size, and communication dynamics: A comparative study of macaques. In: Barbara J. King (ed.), *The Evolution of Language: Assessing the Evidence from Nonhuman Primates*, 55–77. Santa Fe: School of American Research.
- Maille, Audrey, Lucie Engelhart, Marie Bourjade and Catherine Blois-Heulin 2012. To beg, or not to beg? That is the question: Mangabeys modify their production of requesting gestures in response to human's attentional states. *Plos One* 7(7): e41197.
- Poss, Sarah R., Chris Kuhar, Tara Stoinski and William D. Hopkins 2006. Differential use of attentional and visual communicative signaling by orangutans (*Pongo pygmaeus*) and gorillas (*Gorilla gorilla*) in response to the attentional status of a human. *American Journal of Primatology* 68(10): 978–992.
- Povinelli, Daniel J. and Timothy J. Eddy 1996. Factors influencing young chimpanzees' (*Pan troglodytes*) recognition of attention. *Journal of Comparative Psychology* 110(4): 336–345.
- Roberts, Anne I., Sarah J. Vick, Sam G. B. Roberts, Hannah M. Buchanan-Smith and Klaus Zuberbühler 2012. A structure-based repertoire of manual gestures in wild chimpanzees: Statistical analyses of a graded communication system. *Evolution and Human Behavior* 33(5): 578–589.
- Rogers, Lesley J. and Gisela Kaplan 2000. *Songs, Roars, and Rituals: Communication in Birds, Mammals, and other Animals*. Cambridge, MA: Harvard University Press.

- Schneider, Christel, Josep Call and Katja Liebal 2012a. What role do mothers play in the gestural acquisition of *Pan paniscus* and *Pan troglodytes*? *International Journal of Primatology* 33: 246–262.
- Schneider, Christel, Josep Call and Katja Liebal 2012b. Onset and early use of gestural communication in nonhuman great apes. *American Journal of Primatology* 74: 102–113.
- Slocombe, Katie E., Bridget M. Waller and Katja Liebal 2011. The language void: the need for multimodality in primate communication research. *Animal Behaviour* 81(5): 919–924.
- Smuts, Barbara B., Dorothy L. Cheney, Robert M. Seyfarth, Richard W. Wrangham and Thomas Struhsaker 1987. *Primate Societies*. Chicago, IL: University of Chicago Press.
- Tanner, Joanne E. 2004. Gestural phrases and gestural exchanges by a pair of zoo-living lowland gorillas. *Gesture* 4(1): 1–24.
- Tempelmann, Sebastian and Katja Liebal 2012. Spontaneous use of gesture sequences in orangutans: A case for strategy? In: Simone Pika and Katja Liebal (eds.), *Recent Developments in Primate Gesture Research*, 73–91. Amsterdam: John Benjamins.
- Tinbergen, Niko 1963. On aims and methods of ethology. *Zeitschrift für Tierpsychologie* 20(4): 410–433.
- Tomasello, Michael 2008. *Origins of Human Communication*. Cambridge, MA: MIT Press.
- Tomasello, Michael, Josep Call, Jennifer Warren, Thomas G. Frost, Malinda Carpenter and Katherine Nagell 1997. The ontogeny of chimpanzee gestural signals: A comparison across groups and generations. *Evolution of Communication* 1(2): 223–259.
- van Leeuwen, Edwin J. C., Katherine A. Cronin, Daniel B. M. Haun, Roger Mundry and Mark D. Bodamer 2012. Neighbouring chimpanzee communities show different preferences in social grooming behaviour. *Proceedings of the Royal Society B: Biological Sciences* 279(1746): 4362–4367.
- Waller, Bridget M., Katja Liebal, Anne M. Burrows and Katie E. Slocombe 2013. How can a multimodal approach to primate communication help us understand the evolution of communication? *Evolutionary Psychology: An International Journal of Evolutionary Approaches to Psychology and Behavior* 11: 538–549.
- Wilcox, Sherman 1999. The invention and ritualization of language. In: Barbara J. King (ed.), *The Evolution of Language: Assessing the Evidence from Nonhuman Primates*, 351–384. Santa Fe: School of American Research.

Katja Liebal, Berlin (Germany)

154. An evolutionary perspective on facial behavior

1. Asking the right questions
2. The ultimate function(s) of facial behavior
3. Conclusion
4. References

Abstract

The field of human facial expression contains an impressive record of psychological research on the developmental, emotional, and social aspects of facial behavior. Although most psychological research on facial behavior refers to Darwin's (1872) ideas about emotional