

From grasping to pointing: The evolution of referentiality in man and animals

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ABSTRACT Pointing with the help of the index finger may be one of the most conspicuous human behavioral patterns. Even though similar behaviors can occasionally be seen in some great apes, the ritualized form of using a special pointing finger to show or explain something to a conspecific suggests that this behavior has become anatomically internalized by our species. Pointing in its various forms represents such a frequently used behavior that human cooperation would be barely imaginable without it. In addition, even the modern digital world still heavily relies on pointing devices, such as the computer mouse or a joystick. Hence, it appears justifiable to treat this unique motor pattern as one of the possible evolutionary ignition sparks which, approximately 6 to 7 million years ago, caused humans and apes to continuously drift apart with regard to their specific socio-cognitive abilities. In other words, the distinct social world of human symbolic communication in all its manifold facets may have begun with the invention of the act of pointing. This review attempts to show that it is possible to develop the following evolutionary scenario: First, the original grasping behavior, as already displayed by primitive primate species (lemurs) slowly evolved into a characteristic begging movement involving the extended hand (in monkeys), and finally, then into a ritualized pointing gesture using the index finger with a clear referential meaning in the *Hominoidea* (apes and humans). Second, during phylogeny the production of any higher cognitive behavior, such as pointing, always preceded its comprehension when shown by a conspecific. Third, young human

infants show grasping and then begging attempts toward remote objects before eventually pointing at them in an intentional manner, which supports the idea that ontogeny recapitulates phylogeny (the so-called *Biogenetic Law*). Fourth, relaxed environmental selection conditions might have been favorable to the evolution of referential pointing in primates. In sum, this may explain why humans and apes, to a certain degree, can communicate with each other in a clearly referential manner about concrete aspects of the world.

KEYWORDS Biogenetic Law, evolution of pointing, grasping, referential gesture, relaxed selection

1 INTRODUCTION

A short review of the literature shows that among higher vertebrates, true pointing gestures primarily occur in the family of primates (see, e.g., Leavens & Hopkins, 1999; Vea & Sabater-Pi, 1998). Few other animals appear to understand pointing (e.g., wolves and dogs: Kubinyi, Virányi, & Miklósi, 2007; seals: Shapiro, Janik, & Slater, 2003; and elephants: Smet & Byrne, 2013), or are capable of producing pointing-like behaviors themselves (e.g., horses: Malavasi & Huber, 2016; dolphins: Xitco, Gory, & Kuczay, 2001; fish: Vail, Manica, & Bshary, 2013; chickens: Evans & Evans, 2007; common ravens: Pika & Bugnyar, 2011, Australian magpies: Kaplan, 2011). However, their points typically consist of moving the whole body in a certain direction, while they never point by indicating a remote position in space with the same precision as does pointing with the index finger by an ape or a human. This obviously has to do with the fact that the hands of a primate are special organs which possess enormous degrees of freedom compared to the forelegs of most other vertebrates. In the latter case, locomotion still represents the main function and therefore strongly limits the options for producing pointing gestures.

It is important to note that not all primates point in the same manner as humans do. Most prosimians, for example, evolutionarily more primitive primates that have retained a wet nose (*rhinarium*) are unable to do so even though they have hands that – from a purely anatomical view – are quite similar to those of monkeys and humans. Their thumbs can be



Figure 1. Monkey and human infant displaying *begging* behavior consisting of grasping with the whole hand in a requestive manner for an object out of reach. Note the emotional expression on the infant's face (monkey picture reprinted with permission of photographer Audrey Maille, see Maille et al., 2012; right picture photographed by author).

opposed to the other fingers in nearly the same way as in monkeys. Nevertheless, there are no known instances in which a prosimian primate has been shown to point with the hand. This does not preclude that lemurs can be artificially trained to point at a particular location by grasping toward it or extending their arms in the direction of an object (Genty & Roeder, 2006), but they never do so spontaneously and with an extended index finger. This limitation may have to do with a basic inability to visually guide the movements of their forelimbs (Kaas, Stepniewska, & Gharbawie, 2012). But even monkeys with their agile hands and fingers are far from being pointing experts. In captivity, they occasionally show *begging* behaviors using their whole hands (Blaschke & Ettliger, 1987; Bourjade et al., 2014; Maille, Engelhart, Bourjade, & Blois-Heulin, 2012) that resemble the requestive form of pointing in human infants (see Figure 1), but so far they have never been observed pointing with the index finger neither in captivity nor in the wild.

By contrast, apes have been observed to show clearly recognizable pointing movements in the wild. At least in bonobos and chimpanzees, a few cases of either pointing with the whole hand (Hobaiter, Levens,

& Byrne, 2013; Pika & Mitani, 2006), the index finger (Veà & Sabater-Pi, 1998; Povinelli, 1991), or the feet (*foot-pointing*: Douglas & Moscovice, 2015) have been reported. Compared to the natural habitat, however, pointing is much more common among apes held in captivity, even without any previous training. Captive orangutans, gorillas, chimpanzees and bonobos from time to time produce pointing gestures with their hands and fingers that are easily recognizable as such by a human observer (see, e.g., Call & Tomasello, 1994; Leavens, Hopkins, & Bard, 2005, 2008; Patterson, 1978; Savage-Rumbaugh & Fields, 2000), and thus are used by the animals to get otherwise unreachable food or toys outside their enclosure (see Table 1 in Leavens & Hopkins, 1999). The animals sometimes point in a very human-like manner with their extended index fingers (see Figure 2) but usually use all their fingers and point with the whole hand. However, there is one exception, and this is the group of the language-trained chimpanzees who use their index finger even more frequently than young human infants between the age of one and two years (Leavens & Hopkins, 1999). Some researchers have proposed to qualify pointing with the whole hand as a mere *reaching* behavior, without any social connotation. Yet the fact that it occurs only when a caregiver is present and never or very rarely when the animals are alone (Leavens, Hopkins, & Bard, 1996), indicates at least a *requestive intention* by the subject. Similar to human infants, apes raised in captivity develop pointing without having been trained to do so, suggesting that they behave in a spontaneous manner.

2 POINTING AS THE FOUNDING STONE OF LANGUAGE

What makes pointing – a rather inconspicuous behavior per se – so special a phenomenon that a multitude of studies have investigated its origin and development? True pointing in the sense of creating a *spatial reference* to parts of the external world is an exceptional behavior because it can be treated as providing access to all subsequent kinds of referencing behaviors. By pointing, the subject tries to develop a spatially well-defined proto-semantic reference to an external object or event. This apparently trivial kind of *showing things to others* represents the precondi-



Figure 2. In captivity, great apes sometimes point with the index finger at interesting objects (e.g. food) in a clearly human-like and referential manner, easily recognizable through the ritualized, repetitive character of the behavior (picture taken from <https://www.youtube.com/watch?v=oDjwaWbrm8Y>).

tion for spoken language for the simple reason that vocalizations alone always remain ambiguous with regard to the attribution of meaning to particular entities of the external world. Hence, even though a young baby starts uttering a variable number of more or less distinct noises from very early on, it is not before the age of about one year that the first clear references to particular objects become recognizable (Mayo et al., 2013). It is at this age that one observes an important switch from the initial pointing with the whole hand, which still has a strong requestive and primarily dyadic character (“I want this object”), to the later canonical form of pointing with the help of the index finger, the nature of which is clearly more indicative in the sense of “Look, there is an object” (Franco & Butterworth, 1996; Leavens & Hopkins, 1999).

The necessity of the pointing gesture for creating the first semantic references has to do with the purely physical fact that an acoustic signal, in contrast to a visual gesture like pointing, is by itself necessarily unable to indicate a particular position in space. In air, sound waves propagate uniformly into all three spatial dimensions and thus are not qualified for

establishing any concrete semantic reference¹. For the growing child, a new word simply spoken into air without any simultaneous spatial reference to a concrete object makes no sense. Somewhat later in a child's life, as soon as at least a small repertoire of well-defined semantic meanings has been installed with the help of pointing, further vocabulary development is achieved by using primarily vocal referencing. Nevertheless, as soon as there exists some degree of uncertainty with regard to the concrete meaning of an utterance, even adult humans usually *regress* to the basic stage of gestural referencing, which means consciously going back to explicit manual pointing to avoid any semantic ambiguity (and this occurs also at the highest level of scientific work: see the use of laser pointers to clarify details in pictures).

By producing well-defined references, pointing automatically becomes a conscious social act. Neither animals nor humans, unless under some special conditions (e.g., rehearsal of a scene by an actor, gestural preparation of a speech before performance, counting by use of the index finger), would point at an object or event when alone. This apparently paradoxical asymmetry between pointing in a social context, the so-called *triadic* relationship between the *pointing agent*, the *referenced object* and the *addressee* (Bates et al., 1979; Bruner, 1981; Trevarthen & Aitken, 2001), and the total absence of any pointing behavior if nobody else other than the subject is present, is also readily explained by the perceptual substrate of reference. Knowing the object of reference by looking at it, the subject does not need to point at it to understand what s/he is looking at. Taken together, both basic features of true pointing, that is a) a clear spatial relationship to an external phenomenon, and b) an equally clear involvement of a conspecific through gaze alternation between object and addressee, presuppose that the pointing agent firstly understands the meaning of what a spatial direction (a geometrical line) is, and secondly uses pointing with the conscious intention of showing something to a conspecific. These requirements explain why true pointing, in its mature form, is quite rare among living beings or, in the words

¹ Alarm calls of some colony-forming (e.g., marmots, ground squirrels) or group living (e.g., monkeys, most hoofed animals) mammals are no exceptions to this rule since they do not work without a moving cue (predator, competitor) in an otherwise static visual scenery.

of modern developmental psychology: “Pointing things out for others seems like an exceedingly simple act. But it turns out that [...] it rests on a very complex and mostly hidden social-cognitive, social-motivational infrastructure” (Tomasello, Carpenter, & Liszkowski, 2007, p. 719). Ultimately, pointing necessitates the presence of a self-conscious agent that intentionally proceeds to instruct other group members about specific aspects of the surrounding world.

3 **UNDERSTANDING POINTING PRESUPPOSES BEING ABLE TO POINT BY ONESELF**

When we see another person pointing at an object we immediately understand what s/he is doing because we, too, already know how to point at an object and what that act is intended to signal to the addressed person. In our mind’s eye we follow an imagined straight line that extends in the indicated spatial direction of the index finger to a given point in space. This is valid for both the pointing person as well as the observing person and requires a basic understanding of visual perspective. By moving around while pointing, for instance during pointing at one and the same object from different angles, we construct a three-dimensional space of linear vectors that can be arbitrarily used for referencing purposes. In other words, understanding pointing is a rather demanding cognitive achievement that clearly exceeds simple perception.

All the more surprising, there are quite a few animal species that appear to perfectly comprehend pointing when performed by a human experimenter in front of them. By contrast, species that are capable of producing points themselves are much rarer. In a review by Miklósi and Soproni (2006), still the most comprehensive overview of animal pointing to date, dogs, wolves, cats, horses, goats, dolphins and seals appear to learn quite rapidly to correctly interpret helpful human pointing gestures when confronted with the problem of choosing between two non-transparent containers of which only one is baited with a reward. Surprisingly, our closest relatives among the primates, monkeys and apes do not perform markedly better than most other tested species. In these so-called *object choice tasks*, monkeys achieve results that are more

(Anderson, Sallaberry, & Barbier, 1995; Vick & Anderson, 2000) or less (Anderson, Montant, & Schmitt, 1996) comparable to other successful mammals like dogs and cats. Surprisingly, apes, with which we share the closest possible evolutionary ancestry of all animals, fared even worse: they seemed to have severe problems understanding that kind of experimental test (see Itakura, Agnetta, Hare, & Tomasello, 1999; Tomasello, Call, & Hare, 1998).

Since pointing is a *cooperative behavior* where the pointing agent consciously tries to draw the attention of the addressee to a particular place or object in the surrounding world, one explanation for their surprising failure in object choice tasks could be that chimpanzees and other great apes just do not engage in cooperative behaviors to the same extent than humans do (Hare, 2001). In other words, the social relationships of great apes may simply be of a more competitive nature. Alternatively, human experimenters were often located quite close to the objects at which they pointed during the experimental tasks and the tested apes could have interpreted this proximity as a demonstration of ownership on the part of the humans rather than as a sign of cooperativeness, which would explain the apes' generally poor performance. In fact, the behavior that was shown by the majority of chimpanzees during these tests – mostly nervousness and unfocused movements – supports such an interpretation.² However, a range of methodological issues surrounding object choice tasks in primates and other animals (see, e.g., Mulcahy & Hedge, 2012) should warn about reaching premature conclusions on the topic of point comprehension.

From an evolutionary standpoint, it is rather unlikely that distantly related species like dogs and cats are better at understanding the human pointing gesture than our closest relatives, the great apes. Despite superficial similarities between the domestication of these house pets and a presumed human *self-domestication* (see Hare, Wobber, & Wrangham, 2012), this apparent *pointing gulf* between apes and humans is difficult to reconcile with a largely identical evolutionary past. A closer analysis of what has been documented so far in the field of animal pointing brings

² Video showing mentality-based difficulties of chimpanzees with understanding human pointing: <https://www.youtube.com/watch?v=wdTEYQX3s2o>, retrieved on December 20, 2017.

the phylogenetic perspective readily into play again. The majority of research findings stem from object choice studies, in which the indicated object, the pointing agent and the addressee were located in close spatial proximity to one another. Some researchers attempted to elicit so-called *distal pointing* in different animal species, but even there, the distance between the pointing gesture and the object was not more than 50 cm (defined as *out of reach* by Miklósi & Soproni, 2006). However, pointing distances of several meters – not uncommon in human pointing – have rarely been tested with nonhuman animals. This suggests that purely associative and/or specific perceptual mechanisms could be responsible for the results of most of those experiments. Since proximity between objects is an important criterion for association to take place, many animals could have simply learned that the position and/or the movement of the human hand is related in a meaningful way to a particular resource, for instance hidden food (see Shapiro et al., 2003).

Dogs, like many other predatory species, are extremely sensitive toward even the slightest changes in their visual field that could code for the movement of potential prey. They are able to react rapidly by extrapolating the likely direction of flight. The details of the underlying perceptual mechanism were first described by Shaffer, Krauchunas, Eddy and McBeath in 2004. They observed dogs catching frisbees and found the same basic mechanism of intercepting the linear trajectory of a moving object as is in place in human baseball players. During play, this mechanism can be easily instigated in any dog by humans making short intention movements in different directions. The dog will instantaneously track and react to every small movement of its owner (Figure 3). Translated into the situation of an object choice test in which pointing gestures are used to indicate the spatial location of hidden food, dogs and cats should not show any difficulties in solving these tasks; and in fact, they often solve these tasks from the first moment on, without much associative learning required (Miklósi, Pongrácz, Lakatos, Topál, & Csányi, 2005).

In some object choice experiments, subtle indicators like gaze movement were used as a substitute of manual gestures to indicate the location of the hidden food, and yet most tested species had no serious problems solving the tasks. Instead of necessitating the formulation of a special *gaze following mechanism*, this merely speaks in favor of a very high sen-



Figure 3. Dog intently watching his owner (author) before searching for a tossed object in the classical stick fetching game. The animal very precisely foresees the correct trajectory of the object without attributing any referential meaning of an abstract *direction* to the observed movement (Shaffer et al., 2004; photographs by author).

sitivity of the underlying motion extrapolating perceptual mechanism as already described by Shaffer et al. (2004). This interpretation is corroborated by the fact that newborn human babies correctly understand to follow the gaze of an experimenter as long as they can see the movement of the pupils (Farroni, Johnson, & Csibra, 2004).

The only reliable method to verify whether different animal species are truly able to understand the meaning of human pointing is to confront them with gestures that refer to remote objects which are so far away that it is not possible to create a purely perceptual association based on proximity aspects and/or use simple visual reactions based on movement direction itself. Unfortunately, this has not been done with most species. With dogs, a simplified version of this method can be employed by any dog owner whereby it is comparatively easy to show that these animals are completely unable to understand human pointing gestures. For this purpose, it is sufficient to play a game of fetch with a dog in a meadow with high grass and wait until the dog, due to restricted vision, has difficulties finding the stick in the high grass. Then one would simply start pointing to the remote location where the stick is lying and

observe what the dog does. First, the dog may likely follow the pointing gesture if the gesture is done dynamically (i.e., with movement) and repeatedly. However, as soon as the arm is held static while pointing in the correct direction without movement, the dog, from that moment on, will ignore the indicated point in space. In fact, despite seeing the extended arm with the index finger pointing in a well-defined spatial direction, the dog usually runs around in circles that have nothing to do with the direction indicated. This provides support for the view that dogs do not interpret the human pointing gesture the same way humans do, namely as a referential gesture with the meaning of indicating a spatial direction.

Compared with dogs, apes perform surprisingly poorly in object choice tasks on pointing comprehension. Following conventional wisdom, they do so due to some hard to define disturbing factors mostly linked to the presence of a human experimenter which creates a competitive situation (for a critique of this view, see Mulcahy & Hedge, 2012, and Hopkins, Russell, McIntryre, & Leavens, 2013). But this does not mean that apes are unable to understand the referential nature of pointing. The fact that chimpanzees very well understand human pointing has been demonstrated by a recent experiment conducted by Roberts et al. (2014) on distal pointing with a distance of at least several meters between indicating subject and indicated object. In this experiment, the animals first witnessed how a human experimenter hid a valuable object (container with reward) somewhere outside of their enclosure. The objects were first shown to the chimpanzees at close distance and then buried at a remote but still visible place in the area surrounding the enclosure. Next, a second human experimenter who was ignorant of the hiding place came into play. This person was known to the chimpanzees as a very helpful familiar person who, in the recent past, had repeatedly provided food to them. When this person appeared, the chimpanzees immediately tried to elicit their help in retrieving the hidden food. Apparently, the animals knew from the start that the second experimenter could not know the place where the container with the tidbits was hidden. As a result, they immediately proceeded to guide the cooperative, but ignorant, human partner to the right place by basically deploying a strategy that we humans – if we assume having lost our voice for the moment – would also deploy in such a situation. They pointed with the extended index finger exactly to the place where the food was hidden and, by doing so, succeed-

ed in guiding the cooperative experimenter to the right place. Every time the experimenter stopped or deviated from the correct way to the envisaged goal, the chimpanzees started gesturing and indicated again the precise location with the help of the index finger. Finally, the closer the experimenter came to the unknown hiding place the more frequently the chimpanzees began to produce purely affirmative intentional gestures, like shaking the hand or bobbing the head, to signal to the experimenter that he was already very close to the desired location. Even though only two human-raised animals were tested in the study, the results are more than clear-cut: in 11 out of 12 trials the animals reached their goal by successfully leading the ignorant experimenter to the hiding place. The supplementary videos nicely illustrate the communicative expertise of these chimpanzees (see Roberts et al., 2014).

Generally, chimpanzees as well as all other ape species, including gibbons (Inoue, Inoue, & Itakura, 2004), appear to be qualified to use pointing in the same referential manner as humans. A female gorilla has recently even been shown to use a tool – different sticks which she specifically prepared – for various intentional pointing purposes (Luef & Heschl, 2017). But does this finding mean that they also interpret the pointing of another person, be it a conspecific or a human, in the same way we do? Unfortunately, no comparative experimental data exists to date on this topic. What appears to be overdue in this case is a simple role reversal of the actions of chimpanzees and humans as shown in Roberts et al.'s study from 2014. In such an experiment, a human experimenter would try to guide chimpanzees (or any other ape species) to a particular place in their enclosure by merely indicating via gestures the way to a previously hidden resource (e.g., covered feeding site). The traditional object choice tasks are inappropriate for this purpose because the average distances between indicator and object are normally too short to exclude purely associatively learned coincidences that have little to do with a true comprehension of referential meaning. This explains why a recent study done with capuchin monkeys, in which the cue giver was once a conspecific (another monkey reaching for one of two containers) and once a human person pointing to the baited container, ended with the disappointing conclusion that “results may be explained by simple rules of association learning and stimulus generalization” even though

nearly all monkeys tested perfectly mastered the task (Essler, Schwartz, Rossetti, & Judge, 2017, p. 1).

So how is a reliable decision on whether monkeys are able to understand the referential aspect of pointing feasible? Again, the answer can be found in the videos made by Roberts et al. (2014) as well as in similar recordings on the internet. One particularly revealing video on YouTube, taken by chance by a zoo visitor, shows a chimpanzee pointing with the index finger at diverse objects lying outside the enclosure with the intention of inducing the visitors to either channel it through a hole in the glass pane (fruit juice) or to throw it (banana) over the pane into the cage.³ The decisive element in the behavior of this chimpanzee is the repetitive accentuation in the pointing movements. It is this ritualization of the pointing movement which shows that the animal really wants *to say something*, in exactly the same manner as humans who make a pointing gesture in an *unmistakable* and *urgent* manner. So far, no monkey has been observed producing such a clearly intentional pointing gesture. And – as we will see in the next section – since the comprehension of pointing done by a conspecific always follows the production of pointing, it can be excluded that monkeys are able to understand the referential character of the pointing gesture done by a human (see also Hess, Novak, & Povinelli, 1993). This is valid for both ontogeny and phylogeny.

4 ONTOGENY EXPLAINS PHYLOGENY

When observing the behavior of young human infants during ontogeny we realize that the ability to point always develops before (according to Leavens & Hopkins, 1999, at the age of 14-15 months) the ability to comprehend the pointing gesture as a referential signal (according to Morissette, Ricard, & Décarie, 1995, at around 18 months)⁴. Around the

³ Video “Smart chimpanzee wants to drink coke”: <https://www.youtube.com/watch?v=oDjwaWbrm8Y>; https://www.youtube.com/watch?v=yrI2_v_FhLs; https://www.youtube.com/watch?v=SG8d52cVG_E, retrieved on December 20, 2017.

⁴ Much earlier reported times for the onset of pointing comprehension are either based on simpler perceptual, non-cognitive mechanisms (see Bertenthal,

age of 11 months, the young baby starts grasping for objects that are out of reach by moving the hand with all its fingers extended toward the targeted object, seemingly ignoring the insurmountable distance between her/himself and the object (Leavens & Hopkins, 1999). However, this so-called *whole-hand point*, a seemingly non-functional grasping behavior, is only shown when another person is present who could help the baby in procuring the intended object. The behavior is usually accompanied by loud vocal utterances that signal the current mood of the baby, usually hunger, thirst or the wish to play with the object. Then, slowly, this characteristic *begging* behavior (see Figure 1) develops into a more clearly symbolic activity in which both the form of the behavioral pattern and the accompanying vocalizations begin to change. Around the age of 12 months, the whole-hand gesture starts to disappear and the characteristic pointing movement with the extended index finger becomes dominant (Leavens & Hopkins, 1999). At the same time, the loud vocalizations that accompany the young infant's pointing efforts change into less requestive and instead more indicative⁵ utterances that, for the first time, appear to *denote* specific objects in the environment. In other words, the young infant begins to speak with the help of the first pointing attempts with the index finger (see Figure 4, Butterworth, 2003). By doing so, the infant's inner urge to actively communicate with her social milieu meets a perfectly pre-adapted behavioral reaction by the parents/caregivers: as soon as the infant points at a concrete object, parents/caregivers automatically feel compelled to utter the corresponding name for the object. In this way, the child gradually enters the semantic world of her/his social environment and acquires a first, though still relatively limited,

Boyer, & Harding, 2014) or demonstrate that even slight modifications of the pointing gesture (e.g., angular pointing) are not understood (see Schmitow, Kochukhova, & Nyström, 2016).

⁵ The transition from predominantly emotional to the first pre- and proto-semantic vocalizations (*babbling* > use of *proto words*) becomes manifest by the infant's first use of consonants (Oller, 1980) which, in contrast to vowels, restrict airflow through the respiratory tract and thus are mainly produced when strong or negative emotions are absent (Scheiner et al., 2002). This important step is accompanied by a change from dyadic to triadic forms of looking that begin to coordinate one's own perspective, outer world, and social environment (Kutsuki et al., 2007).



Figure 4. A 13-month-old human infant points at an object and tries to repeat the naming (“lamp”) given by an adult (author). Note the relaxed expression on the infant’s face. Through pointing, the young child actively provides herself with a basic semantic vocabulary during the second year of life (photographed by author).

set of words allowing her/him nevertheless to finally conquer the whole mental cosmos of its culture in the years to come (Bates et al., 1994; Colonna, Stams, Koster, & Noom, 2010). This close relationship between pointing and language is nicely corroborated by the fact that in human adults, a significant correlation between manual and semantic/verbal laterality exists in the brain (see also Luef in this volume). In the vast majority of humans, Wernicke’s and Broca’s area are located in exactly the same hemisphere as the motor areas that control the dominant, which is the pointing hand (Stein & Stoodley, 2006; for a detailed analysis of the neuroanatomical connections between pointing behavior and spoken language see Peeters et al., 2017).

The fact that the production of pointing tends to precede the comprehension and social imitation of pointing during a child’s ontogeny merits its own attention. Starting at the age of 12 months, a close correlation between production and comprehension of pointing characterizes the socio-cognitive development of the young infant (see Behne, Liszkowski, Carpenter, & Tomasello, 2012). Provided Haeckel’s so-called *Biogenetic Law* (Haeckel, 1866) has at least some empirical value for the evolution

of behavior (see Parker & Gibson, 1979), this special temporal relationship between production and comprehension would also be applicable to the phylogeny of pointing. The implication would be that all animals that are unable to point in a clearly referential manner, as for instance dogs, cats and monkeys, should also be unable to *understand* the referential meaning of pointing. The question is why this should be the case and why not the opposite. After all, if the comprehension of pointing develops first, then the young animal could simply learn by mere observation and subsequent imitation how to correctly perform pointing at an object without struggling with the many details of an independent elaboration of the behavior. The answer has to do with the specific sensorimotor mechanisms that are associated with pointing. First of all, the young infant must learn how to visually control the movements of her/his hands and fingers. As soon as this is accomplished around the age of 9 months (see McDonnell, 1975), the infant starts grasping for objects that are within her/his reach. Only when such basic, visually guided reaching behaviors have been perfected, can the infant proceed to more distal forms of intentionally reaching and requesting in which the eye aligns hand and finger orientation with a remote object. Finally, the transition from such a still *begging*-like form of grasping with the whole hand to a fine-tuned targeting of a specific point in space with the help of the extended index finger makes the behavior referential in the proper sense of the word, that is translatable into the general meaning of “Look, there is something”. Only at this point does pointing by a conspecific become understandable for the young child because s/he can now transfer the observed scenery into her/his own perceptual interpretation frame. In the end, it is basically the same functional relationship that exists between reaching for an object by oneself and imitating an observed reaching movement of a conspecific with the help of so-called *mirror neurons* (Rizzolatti, Fadiga, Gallese, & Fogassi, 1996). Here, too, the production of the behavior always precedes its comprehension and imitation during ontogeny (Kanakogi & Itakura, 2011).

By about 18 months of age, young children have already acquired a basic *expressive lexicon* of about 50 words that serves as a kind of semantic starting basis for all ensuing, much more elaborate utterances. After several years of continuous cognitive development, logically structured sentences with increasing syntactical complexity emerge (Peltzer-Karpf,

2012). Realizing that every word must have a concrete meaning, young children around the age of 2 years start to experience a regular *naming* or *vocabulary explosion* during which 10 words or more are acquired per day with relative ease by simply asking questions like “What (is this)?”. This vocabulary growth spurt continues through the third year during which the famous “Why?” questions emerge and persist (see McCarthy, 1954). It was found that a child who has not achieved the critical number of approximately 50 words by the age of 18 months must be called a *late talker* who needs additional time of socio-cognitive training to clear her/his backlog in linguistic competence (Thal and Tobias, 1992). Pointing plays a crucial role in vocabulary learning and is therefore immensely important for the acquisition of spoken language. During the second half of the second year, another developmental milestone appears that crucially shapes the mental faculties of the growing infant, namely the ability to recognize her/himself in the mirror (*mirror self-recognition* or MSR⁶, see Bertenthal & Fischer, 1978). This suggests that the acquisition of a first primitive *ego* represents a necessary step toward language, confirmed by the appearance of the word “me” shortly after the first successful instances of MSR. At the same time, pointing with the whole hand markedly decreases at this age in favor of the much more precise canonical form of pointing with the extended index finger (Leavens & Hopkins, 1999), an observation that nicely mirrors the emerging intention of the self-conscious mind to be as precise as possible in all of its actions, be they self-related, object-related and/or communicative.

The findings from human cognitive ontogeny should help predict the occurrence of pointing in nonhuman species, in particular for answering the question of which animal candidates come into question for a true, meaning referential, understanding of pointing. Apes (Parker, 1991) including gibbons (Heschl & Fuchsichler, 2009), dolphins (Reiss & Marino, 2001) and elephants (Plotnik, de Waal, Moore, & Reiss, 2010) have been shown to be able to recognize themselves in the mirror. By

⁶ Spontaneously acquired, not trained self-recognition in a mirror represents one of the basic requirements for self-consciousness (see Chang et al., 2017; Liu et al., 2017). Behaviorally, it is the expression of the rare ability of just a few vertebrate species to visually guide their locomotion (for details see Heschl & Fuchsichler, 2009).

implication this means that dogs, cats and even monkeys – who generally fail in mirror-self-recognition tests – should be unable to understand the referential meaning of pointing despite their comparatively successful performance in object choice tasks.⁷ Only self-conscious animals are able to produce referential pointing gestures, either with their hands (apes: Roberts et al., 2014), heads (dolphins: Xitco et al., 2001) or trunks (elephants: Smet & Byrne, 2013). Though monkeys can learn how to beg for food with the extended open hand, and do so even when the experimenter is turned away and unable to see the addressed object (proving that the animals do not understand perspective; for more details see LaMaury, Cochet, & Bourjade, 2017), they have never been observed producing a clearly intentional pointing gesture with the index finger (see Essler, Schwartz, Rossettie, & Judge, 2017), which correlates with their lack of a basic form of self-consciousness. For the most intelligent bird taxa, the corvids and parrots, which are at least potential candidates for self-consciousness (see Pepperberg, Garcia, Jackson, & Marconi, 1995; Prior, Schwarz, & Güntürkün, 2008), research on referential pointing is still in its infancy, but it may only be a question of time until a larger body of research will detail their exact referential abilities (a first step in this direction is Pika & Bugnyar’s study on ‘pointing’ ravens from 2011).

5 **RELAXED SELECTION CONDITIONS FAVOR THE EMERGENCE OF POINTING**

Finally, if we want to reconstruct the phylogeny of pointing we need to know the presumed selection conditions that may have favored the emergence of this behavior. Apes that are raised by humans spontaneously develop manual pointing gestures; however, in wild apes, pointing appears

⁷ Dogs are often overrated with regard to their cognitive abilities due to their impressive social behavior (see Moore, Mueller, Kaminski, & Tomasello, 2014), whereas cats, bears and monkeys clearly reach a basic level of higher cognition based on visually guided reaching, without however fulfilling *all* criteria of a whole body-related self-consciousness as given in hominids, cetaceans and elephants.

to be rather rare. So far the only documented instance is an individual bonobo was observed during the production of a pointing gesture at a group of slowly approaching human observers in a presumed attempt to alert her conspecifics to their presence (Veà & Sabater-Pi, 1998). The fact that pointing is rare in wild apes is revealing because it suggests a theoretical question that is not easy to answer: Why is pointing in nature not much more frequent when the ability to silently alert other group members to potential danger with the help of pointing should be extremely advantageous from an evolutionary perspective?

Leavens, Hopkins and Bard (2005) proposed the hypothesis that it is the rather confined conditions in an artificial enclosure that force animals to develop various gestures to communicate with the outside world (e.g., for requesting food). The situation in a narrow enclosure may indeed very well favor such a behavior, however, apart from the unavoidable spatial restrictions, zoo animals are at the same time provided with some specific ecological advantages. They are well-fed and for this reason do not need to worry about procuring food. In addition, any possibly *paralyzing* effect of stress on cognition, arising from a threat by potential predators, is widely lacking. Hence, instead of enforcing pointing through spatial limitation, it rather appears to be a question of allowing this new kind of behavior to emerge which may explain why it is so rarely shown in nature. The relaxed selection conditions that prevail in a captive setting could even represent the crucial impetus that is needed for apes to engage in referential pointing. If true, the hypothesis would predict that the most impressive examples of chimpanzee pointing should be found in rather relaxed situations, as given in zoos in which only a comparatively small extra portion of food in form of tidbits is the main goal of the behavior. This prediction is directly confirmed by the existing studies on pointing in captive apes. Consequently, pointing in wild apes should occur only under relatively relaxed environmental conditions when the animals are unrestrained from external or other pressures that impact their behavior.

Countless observations of chimpanzees in their natural habitat produced only a few rare indications of a possible whole hand pointing gesture (Hobaiter et al., 2013), whereas the still relatively poorly studied wild bonobo delivered the hitherto sole clear evidence of human-like pointing with the index finger (Veà & Sabater-Pi, 1998). The common chimpanzee

practices a more terrestrial lifestyle, whereas the bonobo spends most of its time high up in the trees and is therefore much more protected from potential predators (Rowe, 1996). This explains why chimpanzees are a comparatively frequent prey of leopards, whereas bonobos only rarely suffer such a fate (D'Amour, Hohmann, & Fruth, 2006; Zuberbühler & Jenny, 2002). From an adaptationist point of view, it should thus be extremely advantageous for chimpanzees to use pointing as an effective counter-strategy to avoid predation by leopards. By contrast, bonobos would not really need to develop any pointing habits at all for that special purpose. However, the exact opposite appears to be true. Wild bonobos have been observed pointing with the index finger and wild chimpanzees have not.

From a molecular biological perspective, new behaviors are always accompanied by genetic changes and the sequence difference in DNA between free-living and zoo-raised chimpanzees is probably not large enough to attribute differences in behavior to a change in the new genetic make-up. Since the DNA of wild and captive animals can be assumed to be more or less identical, the ability to produce referential pointing gestures must have evolved already in the natural habitat, maybe as a consequence of a general propensity for communicating in a semantically meaningful way, be it by means of gestures and/or vocal utterances. In this way, the impressive structural complexity of modern human languages might have been originated in the course of repeated phases of relaxed selection during our more recent phylogeny that allowed further semantic *explosions* to take place (Deacon, 2010).

6 CONCLUSION

Concerning our primate relatives, future studies should focus on free-living populations that live under *more favorable* environmental conditions, such as in those primate species that occur in variable habitats, to determine how specific socio-ecological circumstances, and maybe a significant decrease in general selection pressure, can influence the manifestation of referential behavior in a given species. Based on the observation of how fragile and comparatively rare higher cognitive skills usually are

in the wild, it seems that two renowned pioneers of classical field primatology were already heading in the right direction with the following remark:

Innovative behaviour achieved through exploration, learning and insight heavily depends on certain motivational, social and ecological conditions of short duration. We propose that more attention should be given to what these conditions are and where they are realized in natural groups of non-human primates. Only to the extent that such favourable conditions were frequently realized in a social structure or an extraspecific environment could selective pressures act on innovative abilities. There is hope that research into field conditions of innovative behaviour will help to identify its selectors in evolution (Kummer & Goodall, 1985, p. 203).

REFERENCES

- Anderson, J. R., Montant, M., & Schmitt, D. (1996). Rhesus monkeys fail to use gaze direction as an experimenter-given cue in an object-choice task. *Behavioral Processes*, *37*, 47-55.
- Anderson, J. R., Sallaberry, P., & Barbier, H. (1995). Use of experimenter given cues during object-choice tasks by capuchin monkeys. *Animal Behaviour*, *49*, 201-208.
- Bates, E. (1979). *The emergence of symbols: Cognition and communication in infancy*. New York: Academic Press.
- Bates, E., Marchman, V., Thal, D., Fenson, L., Dale, P., Reznick, J. S., ... Hartung, J. (1994). Developmental and stylistic variation in the composition of early vocabulary. *Journal of Child Language*, *21*, 85-123.
- Behne, T., Liskowski, U., Carpenter, M., & Tomasello, M. (2012) Twelve-month-olds' comprehension and production of pointing. *British Journal of Developmental Psychology*, *30*, 359-375.
- Berthenthal, B. I., Boyer, T. W., & Harding, S. (2014). When do infants begin to follow a point? *Developmental Psychology*, *50*, 2036-2048.
- Berthenthal, B. I., & Fischer, K. W. (1978). Development of self-recognition in the infant. *Developmental Psychology*, *14*, 44-50.
- Blaschke, M., & Ettlinger, G. (1987). Pointing as an act of social communication by monkeys. *Animal Behaviour*, *35*, 1520-1523.

- Bourjade, M., Meguerditchian, A., Maille, A., Gaunet, F., & Vauclair, J. (2014). Olive baboons, *Papio anubis*, adjust their visual and auditory intentional gestures to the visual attention of others. *Animal Behaviour*, *87*, 121-128.
- Bruner, J. S. (1981). The social context of language acquisition. *Language & Communication*, *1*, 155-178.
- Butterworth, G. (2003). Pointing is the royal road to language for babies. In S. Kita (Ed.), *Pointing: Where language, culture, and cognition meet* (pp. 9-33). Mahwah: Erlbaum.
- Call, J., & Tomasello, M. (1994). Production and comprehension of referential pointing by orangutans (*Pongo pygmaeus*). *Journal of Comparative Psychology*, *4*, 307-317.
- Chang, L., Zhang, S., Poo, M. M., & Gong, N. (2017). Spontaneous expression of mirror self-recognition in monkeys after learning precise visual-proprioceptive association for mirror images. *Proceedings of the National Academy of Sciences USA*, *114*, 3258-3263.
- Colonesi, C., Stams, G. J. J. M., Koster, I., & Noom, N. J. (2010). The relation between pointing and language development: A meta-analysis. *Developmental Review*, *30*, 352-366.
- D'Amour, D. E., Hohmann, G., & Fruth, B. (2006). Evidence of leopard predation on bonobos (*Pan paniscus*). *Folia Primatologica*, *77*, 212-217.
- Deacon, T. W. (2010). Colloquium paper: A role for relaxed selection in the evolution of the language capacity. *Proceedings of the National Academy of Sciences USA*, *107*, 9000-9006.
- Douglas, P. H., & Moscovice, L. R. (2015). Pointing and pantomime in wild apes? Female bonobos use referential and iconic gestures to request genito-genital rubbing. *Scientific Reports*, *5*, 13999.
- Essler, J. L., Schwartz, L. P., Rossettie, M. S., & Judge, P. G. (2017). Capuchin monkeys' use of human and conspecific cues to solve a hidden object-choice task. *Animal Cognition*, *5*, 985-998.
- Evans, C. S., & Evans, L. (2007). Representational signaling in birds. *Biology Letters*, *3*, 8-11.
- Farroni, T., Johnson, M. H., & Csibra, G. (2004). Mechanisms of eye gaze perception during infancy. *Journal of Cognitive Neuroscience*, *16*, 1320-1326.
- Franco, F., & Butterworth, G. (1996). Pointing and social awareness: Declaring and requesting in the second year. *Journal of Child Language*, *23*, 307-336.
- Genty, E., & Roeder, J. J. (2006). Can lemurs learn to deceive? A study in the black lemur (*Eulemur macaco*). *Journal of Experimental Psychology: Animal Behavior Processes*, *32*, 196-200.
- Haeckel, E. (1866). *Generelle Morphologie. II: Allgemeine Entwicklungsgeschichte der Organismen*. Berlin: Reimer-Verlag.
- Hare, B. (2001). Can competitive paradigms increase the validity of experiments on primate social cognition? *Animal Cognition*, *4*, 269-280.

- Hare, B., Wobber, V., & Wrangham, R. (2012). The self-domestication hypothesis: Evolution of bonobo psychology is due to selection against aggression. *Animal Behaviour*, *83*, 573-585.
- Heschl, A., & Fuchsichler, C. (2009). Siamangs (*Hylobates syndactylus*) recognize their mirror image. *International Journal of Comparative Psychology*, *22*, 221-233.
- Hess, J., Novak, M. A., & Povinelli, D. J. (1993). 'Natural pointing' in a rhesus monkey, but no evidence of empathy. *Animal Behavior*, *46*, 1023-1025.
- Hobaiter, C., Leavens, D. A., & Byrne, R. W. (2013). Deictic gesturing in wild chimpanzees, (*Pan troglodytes*)? Some possible cases. *Journal of Comparative Psychology*, *128*, 82-87.
- Hopkins, W. D., Russell, J., McIntyre, J., & Leavens, D. A. (2013). Are chimpanzees really so poor at understanding imperative pointing? Some new data and an alternative view of canine and ape social cognition. *PLoS ONE*, *8*, e79338.
- Inoue, Y., Inoue, E., & Itakura, S. (2004). Use of experimenter-given directional cues by a young white-handed gibbon (*Hylobates lar*). *Japanese Psychological Research Short Report*, *46*, 262-267.
- Itakura, S., Agnetta, B., Hare, B., & Tomasello, M. (1999). Chimpanzee use of human and conspecific social cues to locate hidden food. *Developmental Science*, *2*, 448-456.
- Kaas, J. H., Stepniewska, I., & Gharbawie, O. (2012). Cortical networks subserving upper limb movements in primates. *European Journal of Physical and Rehabilitation Medicine*, *48*, 299-306.
- Kanakogi, Y., & Itakura, S. (2011). Developmental correspondence between action prediction and motor ability in early infancy. *Nature Communications*, *2*, 341.
- Kaplan, G. (2011). Pointing gesture in a bird: Merely instrumental or a cognitively complex behavior? *Current Zoology*, *57*, 453-467.
- Kubinyi, E., Virányi, Z., & Miklósi, A. (2007). Comparative social cognition: From wolf and dog to humans. *Comparative Cognition & Behavior Reviews*, *2*, 26-46.
- Kummer, H., & Goodall, J. (1985). Conditions of innovative behaviour in primates. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *308*, 203-214.
- Kutsuki, A., Egami, S., Ogura, T., Nakagawa, K., Kuroki, M., & Itakura, S. (2007). Developmental changes of referential looks in 7- and 9-month-olds: A transition from dyadic to proto-referential looks. *Psychologia*, *50*, 319-329.
- Lamaury, A., Cochet, H., & Bourjade, M. (2017). Acquisition of joint attention by olive baboons gesturing toward humans. *Animal Cognition*. Advance online publication. doi: 10.1007/s10071-017-1111-9
- Leavens, D. A., & Hopkins, W. D. (1999). The whole-hand point: The structure and function of pointing from a comparative perspective. *Journal of Comparative Psychology*, *113*, 417-425.

- Leavens, D. A., Hopkins, W. D., & Bard, K. A. (1996). Indexical and referential pointing in chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, *110*, 346-353.
- Leavens, D. A., Hopkins, W. D., & Bard, K. A. (2005). Understanding the point of chimpanzee pointing: Epigenesis and ecological validity. *Current Directions in Psychological Science*, *14*, 185-189.
- Leavens, D. A., Hopkins, W. D., & Bard, K. A. (2008). The heterochronic origins of explicit reference. In J. Zlatev, T. P. Racine, F. Sinha, & E. Itkonen (Eds.), *The shared mind: Perspectives on intersubjectivity* (pp. 187-214). Amsterdam: John Benjamins Publishing.
- Liu, X., Liu, T., & Huang, X. (2017). Commentary: Spontaneous expression of mirror self-recognition in monkeys after learning precise visual-proprioceptive association for mirror images. *Frontiers in Psychology*, *8*, 1151.
- Luef, E. M., & Heschl, A. (2017). Triadic interactions with tools in a gorilla. *Animal Behavior & Cognition*, *4*, 136-145.
- Maille, A., Engelhart, L., Bourjade, M., & Blois-Heulin, C. (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*, e41197.
- Malavasi, R., & Huber, L. (2016). Evidence of heterospecific referential communication from domestic horses (*Equus caballus*) to humans. *Animal Cognition*, *19*, 899-909.
- Mayo, J., Chlebowski, C., Fein, D., & Eigsti, I. (2013). Age of first words predicts cognitive ability and adaptive skills in children with ASD. *Journal of Autism and Developmental Disorders*, *43*, 253-264.
- McCarthy, D. (1954). Language development in children. In L. Carmichael (Ed.), *Manual of child development* (pp. 492-630). New York: Wiley.
- McDonnell, P. M. (1975). The development of visually guided reaching. *Perception & Psychophysics*, *18*, 181-185.
- Miklósi, A., Pongrácz, P., Lakatos, G., Topál, J., & Csányi, V. (2005). A comparative study of dog-human and cat-human interactions in communicative contexts. *Journal of Comparative Psychology*, *119*, 179-186.
- Miklósi, A., & Soproni, K. (2006). A comparative analysis of animals' understanding of the human pointing gesture. *Animal Cognition*, *9*, 81-93.
- Moore, R., Mueller, B., Kaminski, J., & Tomasello, M. (2015). Two-year-old children but not domestic dogs understand communicative intentions without language, gestures, or gaze. *Developmental Science*, *18*, 232-242.
- Morissette, P., Ricard, M., & Décarie, T. G. (1995). Joint visual attention and pointing in infancy: A longitudinal study of comprehension. *British Journal of Developmental Psychology*, *13*, 163-175.
- Mulcahy, N. J., & Hedge, V. (2012). Are great apes tested with an object-choice task? *Animal Behaviour*, *83*, 313-321.

- Oller, D. K. (1980). The emergence of the sounds of speech in infancy. In G. Yeni-Komshian, J. Kavanagh, & C. A. Ferguson (Eds.), *Child phonology, Vol. 1, Production* (pp. 93-112). New York: Academic Press.
- Parker, S. T. (1991). A developmental approach to the origins of self-recognition in great apes. *Human Evolution, 6*, 435-449.
- Parker, S. T., & Gibson, K. R. (1979). A developmental model for the evolution of language and intelligence in early hominids. *Behavioral and Brain Sciences, 3*, 367-408.
- Patterson, F. G. (1978). The gestures of a gorilla: Language acquisition in another pongid. *Brain and Language, 5*, 72-97.
- Peeters, D., Snijders, T. M., Hagoort, P., & Ozyurek, A. (2017). Linking language to the visual world: Neural correlates of comprehending verbal reference to objects through pointing and visual cues. *Neuropsychologia, 95*, 21-29.
- Peltzer-Karpf, A. (2012). The dynamic matching of neural and cognitive growth cycles. *Nonlinear Dynamics: Psychology and Life Sciences, 16*, 61-78.
- Pepperberg, I., Garcia, S. E., Jackson, E. C., & Marconi, S. (1995). Mirror use by African grey parrots (*Psittacus erithacus*). *Journal of Comparative Psychology, 109*, 182-195.
- Pika, S., & Bugnyar, T. (2011). The use of referential gestures in ravens (*Corvus corax*) in the wild. *Nature Communications, 2*, 560.
- Pika, S., & Mitani, J. (2006). Referential gestural communication in wild chimpanzees (*Pan troglodytes*). *Current Biology, 16*, R191-R192.
- Plotnik, J. M., de Waal, F. B., Moore, D., & Reiss, D. (2010). Self-recognition in the Asian elephant and future directions for cognitive research with elephants in zoological settings. *Zoo Biology, 29*, 179-191.
- Povinelli, D. J. (1991). *Social intelligence in monkeys and apes* (Unpublished doctoral dissertation). Yale University, Connecticut.
- Prior, H., Schwarz, A., & Güntürkün, O. (2008). Mirror-induced behavior in the magpie (*Pica pica*): Evidence of self-recognition. *PLoS Biology, 6*, e202.
- Reiss, D., & Marino, L. (2001). Mirror self-recognition in the bottlenose dolphin: A case of cognitive convergence. *Proceedings of the National Academy of Sciences USA, 98*, 5937-5942.
- Rizzolatti, G., Fadiga, L., Gallese, V., & Fogassi, L. (1996). Premotor cortex and the recognition of motor actions. *Brain Research: Cognitive Brain Research, 3*, 131-141.
- Roberts, A. I., Vick, S.-J., Roberts, S. G. B., & Menzel, C. R. (2014). Chimpanzees modify intentional gestures to coordinate a search for hidden food. *Nature Communications, 5*, 3088.
- Rowe, N. (1996). *The pictorial guide to the living primates*. Charlestown: Pogonias Press.
- Savage-Rumbaugh, E. S., & Fields, W. M. (2000). Linguistic, cultural and cognitive capabilities of bonobos (*Pan paniscus*). *Culture and Psychology, 6*, 131-153.

- Scheiner, E., Hammerschmidt, K., Jurgens, U., & Zwirner, P. (2002). Acoustic analyses of developmental changes and emotional expression in the preverbal vocalizations of infants. *Journal of Voice*, *16*, 509-529.
- Schmitow, C., Kochukhova, O., & Nyström, P. (2016). Social perception: How do 6-month-old infants look at pointing gestures? *Infant Behavioral Development*, *42*, 152-156.
- Shaffer, D. M., Krauchunas, S. M., Eddy, M., & McBeath, M. K. (2004). How dogs navigate to catch frisbees. *Psychological Science*, *15*, 437-441.
- Shapiro, A. D., Janik, V. M., & Slater, P. J. B. (2003). Gray seal (*Halichoerus grypus*) pup responses to experimental-given pointing and directional cues. *Journal of Comparative Psychology*, *117*, 355-362.
- Smet, A. F., & Byrne, R. W. (2013). African elephants can use human pointing cues to find hidden food. *Current Biology*, *23*, 2033-2037.
- Stein, J. F., & Stoodley, C. J. (2006). *Neuroscience: An introduction*. Chichester: John Wiley & Sons.
- Thal, D., & Tobias, S. (1992). Communicative gestures in children with delayed onset of oral expressive vocabulary. *Journal of Speech and Hearing Research*, *35*, 1281-1289.
- Tomasello, M., Call, J., & Hare, B. (1998). Five primate species follow the visual gaze of conspecifics. *Animal Behaviour*, *55*, 1063-1069.
- Tomasello, M., Carpenter, M., & Liszkowski, U. (2007). A new look at infant pointing. *Child Development*, *78*, 705-722.
- Trevarthen, C., & Aitken, K. J. (2001). Infant intersubjectivity: Research, theory, and clinical applications. *Journal of Child Psychology and Psychiatry*, *42*, 3-48.
- Vail, A. L., Manica, A., & Bshary, R. (2013). Referential gestures in fish collaborative hunting. *Nature Communications*, *4*, 1765.
- Vea, J. J., & Sabater-Pi, J. (1998). Spontaneous pointing behaviour in the wild pygmy chimpanzees (*Pan paniscus*). *Folia Primatologica*, *69*, 289-290.
- Vick, S., & Anderson, J. R. (2000). Learning and limits of use of eye gaze by capuchin monkeys (*Cebus apella*) in an object-choice task. *Journal of Comparative Psychology*, *114*, 200-207.
- Xitco, M. J., Gory, J. D., & Kuczaj, S. A. (2001). Spontaneous pointing by bottlenose dolphins (*Tursiops truncatus*). *Animal Cognition*, *4*, 115-123.
- Zuberbühler, K., & Jenny, D. (2002). Leopard predation and primate evolution. *Journal of Human Evolution*, *43*, 873-886.