

Review

The origins of non-human primates' manual gestures

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The increasing body of research into human and non-human primates' gestural communication reflects the interest in a comparative approach to human communication, particularly possible scenarios of language evolution. One of the central challenges of this field of research is to identify appropriate criteria to differentiate a gesture from other non-communicative actions. After an introduction to the criteria currently used to define non-human primates' gestures and an overview of ongoing research, we discuss different pathways of how manual actions are transformed into manual gestures in both phylogeny and ontogeny. Currently, the relationship between actions and gestures is not only investigated on a behavioural, but also on a neural level. Here, we focus on recent evidence concerning the differential laterality of manual actions and gestures in apes in the framework of a functional asymmetry of the brain for both hand use and language.

Keywords: gesture; manual; ontogenetic ritualization; phylogenetic ritualization; laterality; great apes

1. INTRODUCTION

Dolphins are one of the most gracile and elegant creatures of the sea. However, before dolphins became what they are today, they underwent a remarkable transformation. The terrestrial ancestor of dolphins was a hippopotamus-like creature that walked on all fours and lacked the stylized forms, and presumably the elegant movements, of its marine descendant. Over the last 50 million years, dolphins have been evolving into what they are today. This remarkable transformation teaches us an important lesson. Complex structures such as legs and snouts can be transmuted over time into equally complex and functionally equivalent structures such as fins and blowholes, respectively.

The relation that exists between gesture and action is in some ways analogous to the relation that exists between fins and legs or between noses and blowholes. A central thesis of this contribution is that many of the gestures displayed by apes began their existence as actions devoid of a communicative function, but over time they became co-opted and transformed into communicative devices that accomplished similar functions [1]. Moreover, just like fins and legs, this change took place over evolutionary time, but in the case of gestures, it can also take place during the

lifetime of one individual. In both cases, however, one can find clues that inform us about their origin. Comparing the communicative repertoires of monkeys and apes with those of humans can play a crucial role in the quest for the roots of human language, and more specifically in the role that gestures might have played in the evolution of language.

The focus of this paper is twofold. First, we will explore the question of how actions are transformed into gestures both from a phylogenetic and an ontogenetic perspective. To this end, we will present the latest advances in ape gestural communication, including some of the controversies in the field. We will begin by defining gestures, briefly presenting some of the features of the apes' gestural repertoires and discussing three ways in which individuals can acquire gestures. Second, having established the connection between actions and gestures, we will turn our attention to the role that gestures may have played in language evolution. First, we will note the increasing interest in gestural communication of our closest living primate relatives in the framework of the proposed close link between action and language in humans. Then we will link recent data on ape laterality in gestural use with language hemispheric specialization.

2. GESTURE ORIGINS (OUT OF ACTIONS)

(a) *Defining a gesture*

Human gestures are usually very broadly referred to as the 'manner of carrying the body' and 'movements of the body or limbs as an expression of feeling' ([2],

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p. 476). According to Kendon [3], a gesture is a form of non-verbal communication in which visible bodily actions communicate particular messages, either in place of speech or together and in parallel with spoken words. Before children start to speak, they use a variety of gestures to communicate with their carers, such as showing objects and pointing to objects, events or persons in their environment [4–7]. Even when they acquire their first words, gestures are not simply replaced but are incorporated in their verbal communication [8,9].

In adults, a substantial body of research addresses the kinds of manual gestures produced by humans while speaking [3,10–12]. If spoken language is not possible, then manual gestures can convey very specific and complex information, even replacing spoken language, thus becoming a form of a highly conventionalized sign system [13,14]. Thus, in humans, gestures can vary in their degree of conventionalization and therefore the degree to which they are linked to or even replace spoken language ([15], pp. 37–40). Therefore, research into human gestures is a highly diverse field, since it covers very different kinds of gestural communication, such as speech-accompanying gestures, gestures of pre-linguistic children or even gestures co-occurring with sign language. The question arising here is whether non-human primate species, which are clearly lacking spoken language but with bodies and particularly forelimbs sharing many characteristics with human beings, use gestures to communicate with conspecifics. To tackle this question and to enable any comparison with humans at all, we need to focus on human gestures not used in combination with language (either spoken or signed) and thus on the gestural communication of pre-linguistic children. By adopting the corresponding criteria, a gesture is defined as a behaviour that unlike an action is motorically ineffective. It requires the active participation of a partner to fulfil its purpose, it is produced in the presence of an audience and is tailored to the attentional state of the audience. Furthermore, it involves gaze alternation or visual checking between social partners and distant objects or events, is characterized by the sender's waiting for the recipient's response and displays persistence and elaboration of communicative behaviour when communicative attempts fail [16–19].

As our previous introduction to the term *gesture* pointed out, gestures are not restricted to the use of hands, but often include movements of limbs and also head and body movements, as well as postures. Some scholars even include facial expressions as gestures [20,21]. However, here we only focus on manual gestures in non-human primates, that is, gestures produced with the whole arm or hands. We also mainly discuss studies of gestural communication in great apes; this is not to neglect gibbons and monkeys, but so far there is still little evidence of hand use for the purpose of communication in non-great ape species ([22], but see [23–25]).

One of the biggest challenges in gestural research lies in determining when an instrumental action has crossed the threshold and becomes a gesture. Some gestures are easy to distinguish from instrumental actions, but there are others that are much more difficult to differentiate. For instance, we would include as

gestures the subtle touches and presses that dancers use to inform their partner about their impending actions or to direct them in a certain way. In contrast, we would not consider as gestures holding an infant when she is beginning to walk because here the main function would be to help the infant to maintain her equilibrium.

The problem of deciding between gestures and actions is further compounded when multiple species are considered. Although the potential for confusing actions and gestures represents a potential analytic weakness, it can become a strength since it tells us something about the origin of gestures. In particular, it suggests that at least some gestures may have begun their existence as actions before they were transformed into a communicative function.

From a more practical point of view, one approach that we find useful in distinguishing actions from gestures is to consider how many of the criteria outlined above are met. Thus, faced with a potential candidate as a gesture, we must ask whether (i) it is motorically ineffective, (ii) there is response waiting, (iii) gaze alternation, and (iv) persistence. The more criteria are met, the more sure we can be that a given behaviour qualifies as a gesture. One cannot be 100 per cent sure but at least this method can help in reducing our uncertainty.

In the next two sections, we present a brief overview of the gestural communication of the great apes (see [18] for a more detailed treatment) and then discuss their potential origins.

(b) *Gestures of non-human primates*

Unlike research into human gestures mostly restricting the focus on the visual channel [3], researchers investigating primate gestures also consider tactile gestures such as *push* or *throw objects* and gestures with an auditory component such as *hand clap* and *chest beat*. Including gestures that transfer information via non-visual channels captures the richness and subtleties of non-vocal communication. However, it also raises potential problems when it comes to distinguishing gestures from instrumental actions. For instance, a gesture called *reach* that consists of extending an arm in the direction of a conspecific is easier to identify as gesture than a gesture called *touch-side* that consists of touching an individual on her side to make her move. The reason for this is simple. The lack of physical contact between the two interacting individuals automatically makes *reach* motorically ineffective, one of the first criteria to identify a gesture as such. After all, it is conceivable that the *touch-side* gesture involved enough force to make the individual move, thus making this action motorically effective and automatically disqualifying it as a gesture. In sum, researchers investigating non-human primates have faced a trade-off between capturing the richness and subtleties of non-vocal communication in primates at the expense of making the distinction between gestures and instrumental actions less clear-cut than in human research.

In a recent summary of a systematic comparison of the four great apes, siamangs and Barbary macaques, Call & Tomasello [18] concluded that those species

differed in repertoire size, composition and function of their gestures. They reported between 20 and 35 different gesture types depending on the species, which meet the above-mentioned criteria of being motorically ineffective and are accompanied by response waiting and/or gaze alternation, as well as persistence in case the recipient did not react. Out of those reported gestural repertoires, at least 50 per cent of each species' repertoire consisted of manual gestures, with the highest proportion found in gorillas (73%). (It is important to note that those numbers refer to the total repertoires found across different groups of one species, not average proportions.) For example, tactile gestures, which included some kind of physical contact with another individual (e.g. *touch, pull or slap*), were used by all great apes, siamangs and Barbary macaques [18]. Auditory gestures often included the individual's own body used to produce that noise, such as *hand clap* in chimpanzees [26], and *chest beat* and *body beat* in gorillas [27]. Alternatively, noise can be produced by using objects while performing gestures such as *ground slap, push objects* or *throw objects*, which are gestures particularly reported for chimpanzees [26]. On the other hand, examples for silent gestures not involving physical contact include gestures like *extend arm (reach), arm raise* and *wave arm* [18]. As opposed to bonobos, siamangs and Barbary macaques, chimpanzees and orangutans often incorporated objects in their gestural displays (15% of the gestures). For example, orangutans offer food to other individuals by extending one arm with food in their hand to another individual [28] and chimpanzees use branches, which they shake vigorously to get the attention of another group member [26]. The higher values for gestures involving objects for chimpanzees and orangutans are interesting in light of their higher propensity to use tools in the wild than the other species and may be indicative of a common neural substrate for tool use and gestural communication.

So far, we have mostly presented the results of our own research project on gestural communication of non-human primates that started with the work by Tomasello *et al.* [29]. Of course, there are many more scholars working on the question of which gestures non-human primates use, how they acquire them and what the underlying socio-cognitive skills are, both in wild and captive settings. The first pioneering field studies report several gestures as parts of ethograms for orangutans [30], gorillas [31], chimpanzees [32] and bonobos [33], but also for gibbons [34,35] and monkeys [36]. Lately, there is an increase in more systematic, mostly observational studies investigating gesture use within social groups of great apes [37,38] and monkeys [22,24,39–41]. This increasing body of research reflects the interest in the role gestures might have played for the evolution of human language [42–45], although studies addressing facial expressions or vocalizations still outnumber studies concerning gestures [46].

However, the reported gestural repertoires for the different species vary considerably between studies. For instance, while Pika *et al.* [27] described 33 gestures for gorillas, Genty *et al.* [37] reported more than 100 gestures for this species. Furthermore, very

different names are often used to categorize the same behaviour, complicating comparisons across studies and species. These discrepancies may be attributed in part to the sampling effort and the differences in the detail of the coding schema across studies [47], but it remains a fact that gestures are, first of all, difficult to differentiate from actions, and second, although the majority of gestures are not gradual signals like in the case of facial expressions, they are difficult to categorize because of the often different criteria used across studies to define a gesture. This is closely related to a third reason, namely that gestures are often defined based on their function or the context they are used in (e.g. *food offer*), resulting in a conflation of form and function rather than referring to form and meaning as separate variables.

However, although the paucity of data in terms of the number of species and groups investigated and also in terms of consistency of definitions used across studies prevents us from concluding that there are any systematic differences between species (yet), at the very least we can say that hands play an important role in gestural communication among primates.

Considering the function of gestural communication, monkeys and apes use the majority of their gestures to request actions like grooming, play or mating. They use their gestures in a dyadic way and usually not to communicate about events or objects outside their dyad, but to request certain actions, expecting an immediate response [48]. In case the recipient is not reacting, they will continue to gesture until they finally receive the appropriate response of their social partner [49–51]. Apes do take into account the visual access of others (see [52] for a review), use visual gestures only if the recipient is attending [18,53], or use other strategies like moving into someone's visual field before starting to gesture [50,54]. In other words, they take into account the behaviour of others and adjust their communicative means accordingly. However, there are inconsistent results as to what extent apes are actually able to alter their gestures if their first gesture was not successful—for chimpanzees and orangutans, it is shown that most often the same gesture is repeated [50,55], while gorillas seem to show more flexibility in alternating the gestures they use to achieve a certain goal [49]. It should be considered that for interactions with a human experimenter, both chimpanzees and orangutans were shown to not only substitute, but also elaborate their gestures depending on the behaviour of a human in case their goal was not met [19,56].

Another much-debated topic is the question of pointing in non-human great apes. In captivity, great apes and also some monkey species point to request food, tools or particular actions from humans [57–61]. Pointing in great apes represents a flexible, intentional behaviour, since the use of this gesture is adjusted to the attentional state of the human and it occurs in combination with other signals such as facial expressions and vocalizations [19,57,62,63]. Pointing is also frequently used by language-trained apes [60,64,65], where it often resembles the form of the pointing gesture of Western cultures with the arm and index finger extended [66].

However, unlike human infants that also point to show objects, to share attention upon things, or even inform others [67], non-human primates usually point to request things or actions in their interactions with humans. The vast majority of great apes' pointing gestures therefore fall within the category of so-called imperative gestures, which consist of the ape using the gesture to obtain something that they want from the human (see [68] for a review). Great apes also inform a human by pointing to the location of a hidden tool, but with the aim that the human can use it to retrieve food for the ape [61]. Unlike humans, however, non-human primates rarely (if ever) use pointing or other gestures aimed at sharing an attitude about the designated referent (expressive declaratives *sensu* Tomasello [69], e.g. [70,71]).

Most importantly, pointing *for* conspecifics and thus the sharing of information is a rather rare event in non-human primates [72]. There is one report about one incidence of pointing in wild bonobos [73], and some studies with language-trained apes mention the use of pointing gestures in interactions with other apes [65]. However, note that the communicative behaviour of those language-trained apes is largely influenced by their raising history and thus their close proximity to the human culture [66,74]. Therefore, pointing for other conspecifics is extremely rare among wild and captive, non-enculturated apes. The flexible and intentional use of this gesture has been only systematically documented for interactions with humans. Gómez [75] argues that captive non-human primates are restricted by cages and therefore use humans as tools to make them do things for them. Interestingly, an uncaged hand-reared gorilla grabbed the hand of the human and took him to the desired object or target of action and therefore preferred contact gestures instead of pointing [70]. Therefore, it seems unlikely that they simply learn to point by trial and error, but it is suggested that they recruit existing cognitive skills into this referential form of communication [75]. For monkeys, the situation seems to be different, since pointing seems to be ritualized from previously reaching for the food [75].

To summarize, great apes and to some extent also gibbons and monkeys use a variety of manual gestures to communicate with other group members, mostly to request immediate actions of their social partner. Thus, they use their gestures mostly in a dyadic, imperative way to get others to do something for them. Interestingly, Bard [76,77] referred to gestural communication as 'social tool use', which is also reflected in the use of pointing gestures in interactions with humans. Unlike humans, non-human primates do not point for conspecifics and their gestures are often derived from functional actions rather than created as arbitrary ones for communicative purposes ([15], pp. 37–40; [78]), although there are single reports about iconic gestures in gorillas and the use of pantomime in orangutans [79,80]. One possible explanation for those observed differences between different groups of great apes may be based on the different ways in which gestures are acquired. In the next section, we turn our attention to this issue.

(c) *Gesture origins*

Since the focus of this paper is on hand-based gestures, we begin this section with a brief description of how hands are used for the purpose of communication by great apes and monkeys. Hands did not evolve as communicative devices in the first place. In fact, the hands of primates are characterized by an extraordinary degree of primitiveness [81], since the basic, five-fingered appearance is shared not only with other mammals, but even other vertebrates. Still, only in primates does the hand serve a variety of functions including locomotion, manipulation and communication [82]. Moreover, each of these functions is represented by a variety of forms. Thus, locomotion can include things like walking, climbing, jumping or brachiating. Manipulation can include actions such as touching, holding or grasping and more complex forms that combine these basic forms with other more elaborate actions that enable primates to engage in a range of fine-grained activities such as grooming and tool use.

From an evolutionary point of view, Napier ([81], p. 14) noted a '...trend ... to emancipate the hands from weight-bearing to sensitive and delicate multipurpose tools'. However, those different functions are not representative for all primate species but very much depend on the differentiation of the hand in the different taxa. While many monkeys and apes have prehensile hands with nails and in some cases even independently movable or opposable thumbs, other primates such as marmosets and tamarins lack those features. Moreover, the gradual shrinkage of the hands' palmar pads in phylogeny correlates with an increase in prehensility and tactile sensitivity [81]. With the emancipation of forelimbs for manipulatory purposes, the stage is set for the development of hands as communicative devices. Indeed, it is not hard to find potential commonalities between manipulative activity and communicative displays. For instance, monkeys and apes touch, push or pull other's fur during communication. Apes beg for food by placing a cupped hand under the chin of a potential food donor as if to catch food that may fall out. Even in the case of locomotor activity, we can find connections between locomotion and communication.

An intriguing and contentious issue refers to the origin of those communicative displays. One possibility is that they evolved over evolutionary time solely for communicative purposes or that they originally evolved for one function (e.g. locomotion) and were co-opted and reused for a communicative function. Alternatively, communicative gestures may have become ritualized not over evolutionary time but in interactions between individuals and thus over a much shorter time span, an individual's lifetime. Next, we turn our attention to the possible changes involved in gesture origin depending on whether changes take place over evolutionary time (phylogenesis) or an individual's lifetime (ontogenesis).

(d) *Phylogenetic origins*

Animal communication can be very complex and highly ritualized. Perhaps the most famous example is the bee 'language' consisting of different dances to indicate

the position of food resources to other members of the hive [83]. Ritualized communication is not only found in invertebrates. There are many examples from vertebrates, including the complex mating display dance of the stickleback or some lek breeding birds [84,85]. In some cases, the communicative displays are composed of a set of discrete actions that follow a fixed sequence, while in other cases they are constituted by single units. Such signals are displayed by all individuals of the species under a set of predetermined conditions and, critically, they appear even if individuals had no opportunity to observe or interact with other individuals to acquire them.

Whereas some communicative displays seem to have evolved for communicative purposes only, other displays appear to have been 'borrowed' from other contexts and thus from movements that previously had no communicative function via a process called phylogenetic ritualization [86]. For instance, dominance signals such as mounting in monkeys are likely to have evolved from mating behaviour, while some courting displays in birds include elements of foraging behaviour. This *principle of derived activities* [87] refers to actions that originally served a different function but were borrowed and modified to some extent to accomplish a communicative function, in some cases even in a different context from its original one.

If we assume that phylogenetic ritualization is the main mechanism underlying gestural communication in non-human primates, then repertoires of each species should be highly uniform and species-specific gestures should be used even if individuals never had contact with another conspecific. Gestures appear fully formed even when subjects have not had a chance to interact with other individuals. Ground-slapping and chest-beating would be examples of these behaviours [88]. However, that they are phylogenetically ritualized does not mean that they are totally inflexible because, at the very least, they are deployed in the right circumstances and the existence of appropriate substrates/elements determines their appearance. A phylogenetic origin of gestures would mean that all members of a given species should inherit their gestural repertoire, as is the case for vocalizations and, provided with the right conditions, all members of the species would display them. However, it is important to consider that some gestures might be limited to certain developmental stages, resulting in species-typical gestures that are restricted to particular age classes.

(e) *Ontogenetic origins*

An alternative mechanism for the origin of gestures entails individuals acquiring them during their interactions with conspecifics during their lifetimes rather than inheriting them as postulated above. One such process that involves two individuals mutually shaping each other's behaviour during the course of repeated interactions is called ontogenetic ritualization [29,89]. Initially, individuals use functional behaviours to affect their partner's behaviour. For instance, when they want to embrace their partner, initially they simply pull their partner towards themselves and when they are within reach, they embrace them.

Over repeated interactions, partners begin to anticipate the individual's goal and react before the individual actually has a chance to pull the partner. Next, the individual (anticipating that their partner will react appropriately) does not actually pull but gives an even more abbreviated version of the pull and their partner reacts. Once this stage is reached, we can say that the instrumental action of pulling has become ritualized into a communicative signal.

Ontogenetic ritualization as the main mechanism of gesture acquisition would result in a high degree of variability of individual repertoires and particularly in the occurrence of idiosyncratic gestures, which are exclusive for single individuals only [27]. Idiosyncratic gestures, which were found in all great ape species (for an overview, see [18]), seem to rule out phylogenetic ritualization and thus a genetic determination of an individual's gestural repertoire, since those instances clearly indicate that new gestures can be acquired during an individual's lifetime. Although we still know very little about how such an individually learned new gesture spreads across other group members, there is some evidence that such a transmission takes place, as was shown for the *grooming handclasp* in a captive group of chimpanzees [90].

Variability between groups is evident in the occurrence of group-specific gestures, which are used by the majority of individuals in one group, but are absent in another group. Although group-specific gestures are infrequent, they are reported for chimpanzees [26], gorillas [27,38] and orangutans [28] in captive settings, but also in wild populations, like the *grooming handclasp* of wild chimpanzees [91].

Two basic kinds of gestures have been described in this context: intention movements and attention-getters [92]. Intention movements result from the abbreviations of full-fledged behaviour. For instance, the gesture *arm raise* has been hypothesized to originate from play hitting, initially a functional behaviour that acquires a value as a signal of impending actions. Intention movements typically convey a clear message and are used in a restricted set of social contexts. Moreover, their meaning and origin can be deduced based on use in those contexts. The second kind of gesture is the so-called attention-getter. It is true that the name attention-getter is not very fortunate because unlike what its name suggests, attention-getters are not just designed to capture attention. In fact, their main function may be to trigger others into action, not to call their attention. That they also serve to capture attention may be a by-product. However, there are inconsistent results in terms of whether great apes actually use their gestures to attract the attention of others. In interactions with conspecifics, chimpanzees use either *poke at* or *throw stuff*—both heavily tactile gestures—to attract the attention of the unattending individual [92]. However, this seems to account only for those particular gestures, since further research found that chimpanzees also use auditory gestures more often towards an attentive recipient and tactile gestures were used regardless of the attentional state of the recipient [26,50]. In other words, tactile and auditory gestures are not used particularly often if the recipient is not attending.

However, in interactions with humans, orangutans, gorillas and chimpanzees do use attention-getting behaviours more when they interact with a human who is facing away compared with situations when the human is facing them [53,93–95]. The different findings for interactions between conspecifics on the one hand and interactions with humans on the other hand might also be explained by the constraints of the captive setting. When apes encountered a human with her back turned and they were given a choice between positioning themselves in front of the human or using an auditory gesture to call the human's attention, all great apes species preferred to walk in front of the human to gesture [54]. Thus, similar to the use of pointing gestures, the use of attention-getters might depend very much on the restraints of captivity.

Compared with intention movements, attention-getters appear to be less context-dependent as they appear in multiple contexts for multiple purposes. Additionally, unlike intention movements, it is not easy to envisage a history of ontogenetic ritualization from pre-existing social behaviours as their origin, so that they are possibly also phylogenetic in origin.

There is a second way in which individuals could acquire gestures during ontogeny without requiring ritualization: learning gestures by observation. One possibility is that the individual would copy the gestures that another individual is directing to her (second-person imitation). Another possibility is that the individual could observe two individuals gesturing to each other and acquires those gestures herself without directly interacting with others (third-person imitation). Interestingly, gestures learned by observation walk an opposite path from those that are ontogenetically ritualized. They are acquired fully formed, the individual does not transform an existing behaviour into a streamlined version that becomes the gesture. The individual copies the streamlined version. The resulting outcome would be a high degree of uniformity within the group, paired with substantial differences between groups because each group may have developed their own idiosyncratic gestures and transmitted them across generations. This is clearly the case in humans but it is unclear whether that is also the case in non-human primates.

(f) *Phylogenetic versus ontogenetic origins of gestures?*

There is currently some debate about what may be the most likely origin of gestures. We have indicated three potential origins for gestures. Historically, observational learning had been proposed as a main mechanism for gesture acquisition. However, there are very little data supporting the idea that apes learn gestures, especially visual gestures, by imitation [26]. Note that the variability in gestural use within groups is as large as between groups. This is not what one would expect based on imitation and cultural transmission since between-group variability should be higher than within-group variability as is the case in humans.

Unlike observational learning, ontogenetic ritualization can explain this pattern of results because the homogeneity within groups would be reduced by

the presence of idiosyncratic gestures developed by some individuals but not others. The reason for idiosyncrasy stems from the fact that certain dyadic interactions between individuals are unique, for instance, mothers and infants may follow different caregiving routines. In fact, according to Tomasello *et al.* [29], the presence of idiosyncratic gestures is a key indicator of ontogenetic ritualization and evidence against a phylogenetic origin of gestures.

Genty *et al.* [37] have recently challenged this idea and proposed that ape gestures are not ontogenetically ritualized but appear fully formed in individuals. This phylogenetic origin of gestures leaves no room for modification over time. They argue that the differences between groups and the idiosyncrasy that has been described are a consequence of the sampling methods that have been used. In particular, not enough hours have been observed to be able to obtain the whole repertoire of gestures. Thus, idiosyncrasy results from a low sampling effort as opposed to individualized experiences with other conspecifics. An increase in the sampling effort showed that all individuals used the same gestures and virtually eliminated idiosyncratic gestures from the sample. This result casts some doubt not only on ontogenetic ritualization but also on observational learning as acquisition mechanisms because there were no differences between groups.

However, one limitation of this and many other studies is that they are not longitudinal and therefore they cannot detect change either within an individual's lifespan or across generations. So, although all individuals use the same gestures, this does not prove that gestures have not undergone an ontogenetic ritualization process. What is needed are long-term studies actually investigating whether the gestures of great apes (and monkeys) change over time. Additionally, studies that have investigated gestural acquisition of apes in contact with humans have described the ritualization process [96]. One could argue that apes in contact with humans would be different, but this is hard to reconcile with the idea that human-reared apes were requesting the same things (e.g. go to another location) as the ones living with their biological mothers. Nevertheless, it is true that the case for ontogenetic ritualization may have been overstated because as Genty *et al.* [37] point out, it is difficult to envisage a history of ontogenetic ritualization for some gestures such as chest beating or ground slapping, although it is also true that ontogenetic ritualization may still be a viable alternative for other gestures such as gentle touch or arm raise.

After discussing the origins of gestures in non-human primates and their close link to actions, we will now briefly refer to some of the current theories on language evolution and the role gestures might have played, before we address the question of laterality in gesture use in non-human primates.

3. LANGUAGE ORIGINS (OUT OF ACTIONS)

(a) *Gestural origin of human language*

The origin of human language is a fiercely debated question, with some scholars favouring a vocal origin (e.g. [97]) and others emphasizing gestures as

precursors to human language (e.g. [43]). To our knowledge, there is no coherent theory currently available that has attempted to reconcile the two opposing sets of theories, which usually see themselves as mutually exclusive [46]. Gestural theories usually refer to the very flexible use of gestures across different contexts and the fact that new gestures can be learned and incorporated into a species repertoire [98]. The discovery of a mirror-neuron system for grasping in monkeys [99] has nourished a variety of evolutionary scenarios focusing on the role of gestures in this process, since mirror neurons represent the link between manual, practical actions and communication.

(b) *From action to language*

Mirror neurons allow macaques to establish a link between performing an action and being able to recognize it [99]. Interestingly, these neurons are located in a brain area that is homologous to Broca's area in the human brain responsible for processing language. Mirror neurons therefore might have played an important role in the evolution of human language, since they were already present in our ancestors representing the neural prerequisite for the development of inter-individual communication and finally of speech [100]. Next, we will give a brief overview of theories suggesting a gestural origin, and second, we will turn to the lateralization of hand use while gesturing and the evidence currently available for non-human primates.

(c) *Gesture and laterality*

Gestural theories of language evolution often refer to the link between lateralization of hand use and language [43]. In humans, the motor systems controlling both manual and oral movements are usually lateralized to the left hemisphere [101]. Therefore, the majority of the human population is right-handed, with the left hemisphere controlling movements of the right hand. Furthermore, both language production and comprehension are located in distinct areas of the left brain hemisphere [102]. The close link between language and manual actions becomes evident in studies showing that while speaking, humans gesture significantly more with their right hand compared with their left hand [103]. This suggests that the functional asymmetry is not specific for one modality only, and that the production of speech apparently also activates motor areas in the left hemisphere, resulting in an increased use of the right hand [104].

Comparable evidence has been found for non-human primates since they show a preference for using their right hand for different manual actions including gestures while vocalizing [105,106]. These findings suggest that the lateralization of manual and oral movements represents a trait shared by both humans and other primates.

However, results for the preference for one hand and particularly the right hand are not completely consistent [107,108]. Although a hand preference is found in many monkey and ape species for different manual actions such as carrying, tool use and locomotion [105,109–111], hand preference is often task-specific and often only evident on an individual, but not

species level [112,113]. So far, there is little evidence that gestures used to communicate with conspecifics—and thus not in interactions with humans when begging for food—are mainly produced with the right hand. To our knowledge, there is only one study showing that baboons use their right hand while they gesture, but not when they perform non-communicative actions [22]. In interactions with humans, however, there is clear evidence that chimpanzees use their right hand preferentially while gesturing [114–116], and they also used their right hand significantly more while producing gestures compared with other manual actions. Hopkins *et al.* [117] therefore concluded that the left-hemisphere specialization for language may have evolved initially from asymmetries in manual gestures in the common ancestor of chimpanzees and humans, rather than from hand use associated with other, non-communicative motor actions such as tool use and bimanual actions. The laterality of hand use in chimpanzees is also reflected in neuroanatomical asymmetries, since chimpanzees that preferably gesture with their right hand also have larger inferior frontal gyri in the left hemisphere than those apes that do not show consistent hand use while gesturing [118].

To summarize, those studies indicate that manual gestures of at least chimpanzees are lateralized, and this functional asymmetry is also associated with asymmetries in the corresponding neural substrate. Hopkins *et al.* [117] therefore suggest that the dominance of the left hemisphere for language has evolved from a gestural communication system already lateralized in the left hemisphere in our common ancestor 5–7 Ma.

4. CONCLUSION

In our contribution, we wanted to highlight that the hands of non-human primates, and particularly those of the great apes, are suitable tools to perform a variety of gestures of different modalities. They are used to achieve a range of different social goals and display a high degree of flexibility as indicated by the possibility of acquiring new gestures often outside of what would be the species-specific repertoire. Still, gestures of non-human primates are different from human gestures in many aspects, since they are mostly used in a dyadic and imperative way, and they also lack the high level of abstraction typical for human gestures. Thus, gestures of non-human primates may emerge from actions via three potential pathways.

The high degree of variability between individual repertoires, the occurrence of idiosyncratic gestures and thus the creation of new gestures support the idea that ontogenetic ritualization may be involved in the origin of some gestures. However, other gestures appear more or less fully formed even in the absence of conspecifics, thus indicating a strong genetic predisposition to develop certain gestures. Finally, some form of social learning might also be implicated either in the form of facilitating the appearance of some gestures or perhaps even the acquisition of novel gestures, although this still needs to be supported by empirical evidence.

After elaborating on the close link between manual actions and gestural communication, we turned to the question of whether gestures of non-human primates are lateralized as many human manual actions including certain gesture types are. There is some evidence for right-handedness at least in captive chimpanzees, and, interestingly, they use their right hand even more while vocalizing, thus suggesting a close link between the manual and oral movements. This fact is often used to support a gestural origin of human language, since the functional asymmetry of hand use while gesturing is also present in the neural substrate of chimpanzees, suggesting some continuity in our phylogenetic history. However, one must keep in mind that the evidence of laterality in chimpanzees and other non-human primate species at the population level is quite mixed. This means that it may be too early to generalize a right-hand preference for gesture use in our closest relatives.

There is much to be done in the future to trace the origins of gestures. Longitudinal studies are especially important as they can throw light on how gestures actually emerge in both monkeys and apes. Some research effort devoted to non-great ape species would be particularly welcome. Otherwise the field runs the risk of underestimating what aspects of gestural communication that are common to human and non-human apes are already present in monkeys. Finally, there is much work to be done in terms of unifying concepts and criteria across the various disciplines that conduct research on gestural communication.

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REFERENCES

- Gómez, J. C. 1990 The emergence of intentional communication as a problem-solving strategy in gorilla. In *'Language' and intelligence in monkeys and apes* (eds S. T. Parker & K. R. Gibson), pp. 333–355. Cambridge, UK: Cambridge University Press.
- Simpson, J. A. & Weiner, E. S. C. (eds) 1998 *The Oxford English Dictionary*, 2nd edn. Oxford, UK: Oxford University Press.
- Kendon, A. 2004 *Gesture: visible action*. Cambridge, UK: Cambridge University Press.
- Liszkowski, U., Carpenter, M., Henning, A., Striano, T. & Tomasello, M. 2004 Twelve-month-olds point to share attention and interest. *Dev. Sci.* **7**, 297–307. (doi:10.1111/j.1467-7687.2004.00349.x)
- Butterworth, G. & Grover, L. 1988 The origins of referential communication in human infancy. In *Thought without language* (ed. L. Weiskrantz), pp. 5–24. Oxford, UK: Clarendon Press.
- Franco, F. & Butterworth, G. 1996 Pointing and social awareness: declaring and requesting in the second year. *J. Child Lang.* **23**, 307–336. (doi:10.1017/S0305000900008813)
- Carpenter, M., Nagell, K. & Tomasello, M. 1998 Social cognition, joint attention, and communicative competence from 9 to 15 months of age. *Monogr. Soc. Res. Child Dev.* **63**, 176. (doi:10.2307/1166214)
- Volterra, V., Caselli, M. C., Caprici, O. & Pizzuto, E. 2005 Gesture and the emergence and development of language. In *Elizabeth Bates: a festschrift* (eds M. Tomasello & D. Slobin). Mahwah, NJ: Lawrence Erlbaum Associates.
- Capirci, O., Montanari, S. & Volterra, V. 1998 Gestures, signs, and words in early language development. *New Dir. Child Dev.* **79**, 45–60.
- Alibali, M. W., Kita, S. & Young, A. J. 2000 Gesture and the process of speech production: we think, therefore we gesture. *Lang. Cogn. Proc.* **15**, 593–613. (doi:10.1080/016909600750040571)
- Goldin-Meadow, S. 2002 Constructing communication by hand. *Cogn. Dev.* **17**, 1385–1405. (doi:10.1016/S0885-2014(02)00122-3)
- McNeill, D. 2000 *Language and gesture*. Cambridge, UK: Cambridge University Press.
- Goldin-Meadow, S. 2003 *The resilience of language: what gesture creation in deaf children can tell us about how all children learn language*. New York, NY: Psychology Press.
- Senghas, A., Kita, S. & Özyürek, A. 2004 Children creating core properties of language: evidence from an emerging sign language in Nicaragua. *Science* **305**, 1779–1782. (doi:10.1126/science.1100199)
- McNeill, D. 1992 *Hand and mind: what gestures reveal about thought*. Chicago, IL: University of Chicago Press.
- Bates, E. 1979 *The emergence of symbols: cognition and communication in infancy*. New York, NY: Academic Press.
- Bates, E., Camaioni, L. & Volterra, V. 1975 The acquisition of performatives prior to speech. *Merrill-Palmer Quart.* **21**, 205–226.
- Call, J. & Tomasello, M. (eds) 2007 *The gestural communication of apes and monkeys*. Mahwah, NJ: Lawrence Erlbaum Associates.
- Leavens, D. A., Russell, J. L. & Hopkins, W. D. 2005 Intentionality as measured in the persistence and elaboration of communication by chimpanzees (*Pan troglodytes*). *Child Dev.* **76**, 291–306. (doi:10.1111/j.1467-8624.2005.00845.x)
- Maestriperi, D. 1999 Primate social organization, gestural repertoire size, and communication dynamics. In *The origins of language: what nonhuman primates can tell us* (ed. B. King), pp. 55–77. Santa Fe, NM: School of American Research Press.
- Paukner, A., Anderson, J. R., Fogassi, L. & Ferrari, P. F. 2006 Do facial gestures, visibility or speed of movement influence gaze following responses in pigtail macaques? *Primates* **48**, 241–244. (doi:10.1007/s10329-006-0024-z)
- Meguerditchian, A. & Vauclair, J. 2006 Baboons communicate with their right hand. *Behav. Brain Res.* **171**, 170–174. (doi:10.1016/j.bbr.2006.03.018)
- Hesler, N. & Fischer, J. 2007 Gestural communication in Barbary macaques (*Macaca sylvanus*): an overview. In *The gestural communication of apes and monkeys* (eds J. Call & M. Tomasello), pp. 159–196. Mahwah, NJ: Lawrence Erlbaum Associates.
- Laidre, M. E. 2008 Do captive mandrills invent new gestures? *Anim. Cogn.* **11**, 179–187. (doi:10.1007/s10071-007-0121-4)
- Liebal, K., Pika, S. & Tomasello, M. 2004 Social communication in siamangs (*Symphalangus syndactylus*): use of gestures and facial expressions. *Primates* **45**, 41–57. (doi:10.1007/s10329-003-0063-7)
- Tomasello, M., Call, J., Warren, J., Frost, G. T., Carpenter, M. & Nagell, K. 1997 The ontogeny of chimpanzee gestural signals: a comparison across groups and generations. *Evol. Commun.* **1**, 223–259. (doi:10.1075/eoc.1.2.04tom)
- 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. (doi:10.1002/ajp.10097)
- 28 Liebal, K., Pika, S. & Tomasello, M. 2006 Gestural communication of orangutans (*Pongo pygmaeus*). *Gesture* **6**, 1–38. (doi:10.1075/gest.6.1.02lie)
- 29 Tomasello, M., George, B., Kruger, A., Farrar, J. & Evans, E. 1985 The development of gestural communication in young chimpanzees. *J. Hum. Evol.* **14**, 175–186. (doi:10.1016/S0047-2484(85)80005-1)
- 30 MacKinnon 1974 The behaviour and ecology of wild orang-utans (*Pongo pygmaeus*). *Anim. Behav.* **22**, 3–74. (doi:10.1016/S0003-3472(74)80054-0)
- 31 Schaller, G. B. 1963 *The mountain gorilla: ecology and behavior*. Chicago, IL: Chicago University Press.
- 32 Goodall, J. 1986 *The chimpanzees of Gombe: patterns of behavior*. Cambridge, MA: Harvard University Press.
- 33 Kuroda, S. J. 1980 Social behavior of the pygmy chimpanzees. *Primates* **21**, 181–197. (doi:10.1007/BF02374032)
- 34 Baldwin, L. A. & Teleki, G. 1976 Patterns of gibbon behavior on Hall's Island, Bermuda: a preliminary ethogram for *Hylobates lar*. In *Gibbon and siamang* (ed. D. Rumbaugh), pp. 21–105. Basel, Switzerland: Karger.
- 35 Chivers, D. 1976 Communication within and between family groups of siamang (*Symphalangus syndactylus*). *Behaviour* **57**, 116–135. (doi:10.1163/156853976X00136)
- 36 Kummer, H. 1968 *Social organization of hamadryas baboons. A field study*. Basel, Switzerland: Karger.
- 37 Genty, E., Breuer, T., Hobaiter, C. & Byrne, R. 2009 Gestural communication of the gorilla (*Gorilla gorilla*): repertoire, intentionality and possible origins. *Anim. Cogn.* **12**, 527–546. (doi:10.1007/s10071-009-0213-4)
- 38 Tanner, J. & Byrne, R. 1999 The development of spontaneous gestural communication in a group of zoo-living lowland gorillas. In *The mentalities of gorillas and orangutans* (eds T. Parker, S. Milks & R. Mitchell), pp. 211–239. Cambridge, UK: Cambridge University Press.
- 39 Maestripiéri, D. 1996 Gestural communication and its cognitive implications in pigtail macaques (*Macaca nemestrina*). *Behaviour* **133**, 997–1022. (doi:10.1163/156853996X00576)
- 40 Maestripiéri, D. 1996 Social communication among captive stump-tailed macaques (*Macaca arctoides*). *Int. J. Primatol.* **17**, 785–802. (doi:10.1007/BF02735264)
- 41 Maestripiéri, D. 1997 Gestural communication in macaques: usage and meaning of nonvocal signals. *Evol. Commun.* **1**, 193–222. (doi:10.1075/eoc.1.2.03mae)
- 42 Arbib, M. A., Liebal, K. & Pika, S. 2008 Primate vocalization, gesture, and the evolution of human language. *Curr. Anthropol.* **49**, 1053–1076. (doi:10.1086/593015)
- 43 Corballis, M. C. 2003 From mouth to hand: gesture, speech, and the evolution of right-handedness. *Behav. Brain Sci.* **26**, 199–260. (doi:10.1017/S0140525X03000050)
- 44 Hewes, G. W. 1973 Primate communication and the gestural origin of language. *Curr. Anthropol.* **12**, 5–24. (doi:10.1086/201401)
- 45 Pollick, A. S. & de Waal, F. 2007 Ape gestures and language evolution. *Proc. Natl Acad. Sci. USA* **104**, 8184–8189. (doi:10.1073/pnas.0702624104)
- 46 Slocombe, K., Waller, B. & Liebal, K. 2011 The language void: the need for multimodality. *Anim. Behav.* **81**, 919–924. (doi:10.1016/j.anbehav.2011.02.002)
- 47 Cartmill, E. A. & Byrne, R. W. 2010 Semantics of primate gestures: intentional meanings of orangutan gestures. *Anim. Cogn.* **13**, 793–804. (doi:10.1007/s10071-010-0328-7)
- 48 Pika, S. 2008 What is the nature of the gestural communication of great apes? In *The shared mind: perspectives on intersubjectivity* (eds J. Zlatev, T. P. Racine, C. Sinha & E. Itkonen), pp. 165–186. Amsterdam, The Netherlands: John Benjamins Publishing Company.
- 49 Genty, E. & Byrne, R. 2010 Why do gorillas make sequences of gestures? *Anim. Cogn.* **13**, 287–301. (doi:10.1007/s10071-009-0266-4)
- 50 Liebal, K., Call, J. & Tomasello, M. 2004 Use of gesture sequences in chimpanzees (*Pan troglodytes*). *Am. J. Primatol.* **64**, 377–396. (doi:10.1002/ajp.20087)
- 51 Tanner, J. 2004 Gestural phrases and gestural exchanges by a pair of zoo-living lowland gorillas. *Gesture* **4**, 1–24. (doi:10.1075/gest.4.1.02tan)
- 52 Rosati, A. G. & Hare, B. 2009 Looking past the model species: diversity in gaze-following skills across primates. *Curr. Opin. Neurobiol.* **19**, 45–51. (doi:10.1016/J.Conb.2009.03.002)
- 53 Hostetter, A. B., Cantero, M. & Hopkins, W. D. 2001 Differential use of vocal and gestural communication by chimpanzees (*Pan troglodytes*) in response to the attentional status of a human (*Homo sapiens*). *J. Comp. Psychol.* **115**, 337–343. (doi:10.1037//0735-7036.115.4.337)
- 54 Liebal, K., Pika, S., Call, J. & Tomasello, M. 2004 To move or not to move: how great apes adjust to the attentional state of others. *Interact. Stud.* **5**, 199–219. (doi:10.1075/is.5.2.03lie)
- 55 Tempelmann, S. & Liebal, K. In press. Spontaneous use of gesture sequences in orangutans. A case for strategy? *Gesture*.
- 56 Cartmill, E. A. & Byrne, R. W. 2007 Orangutans modify their gestural signaling according to their audience's comprehension. *Curr. Biol.* **17**, 1345–1348. (doi:10.1016/j.cub.2007.06.069)
- 57 Leavens, D. A., Hopkins, W. D. & Bard, K. A. 1996 Indexical and referential pointing in chimpanzees (*Pan troglodytes*). *J. Comp. Psychol.* **110**, 346–353. (doi:10.1037/0735-7036.110.4.346)
- 58 Mitchell, R. & Anderson, J. 1997 Pointing, withholding information, and deception in capuchin monkeys (*Cebus apella*). *J. Comp. Psychol.* **111**, 351. (doi:10.1037/0735-7036.111.4.351)
- 59 Anderson, J., Kuwahata, H. & Fujita, K. 2007 Gaze alternation during 'pointing' by squirrel monkeys (*Saimiri sciureus*)? *Anim. Cogn.* **10**, 267–271. (doi:10.1007/s10071-006-0065-0)
- 60 Call, J. & Tomasello, M. 1994 The production and comprehension of referential pointing by orangutans (*Pongo pygmaeus*). *J. Comp. Psychol.* **108**, 307–317. (doi:10.1037/0735-7036.108.4.307)
- 61 Zimmermann, F., Zemke, F., Call, J. & Gómez, J. C. 2009 Orangutans (*Pongo pygmaeus*) and bonobos (*Pan paniscus*) point to inform a human about the location of a tool. *Anim. Cogn.* **12**, 347–358. (doi:10.1007/s10071-008-0194-8)
- 62 Leavens, D. A. & Hopkins, W. D. 1998 Intentional communication by chimpanzees (*Pan troglodytes*): a cross-sectional study of the use of referential gestures. *Dev. Psychol.* **34**, 813–822. (doi:10.1037/0012-1649.34.5.813)
- 63 Leavens, D. A., Hopkins, W. D. & Thomas, R. K. 2004 Referential communication by chimpanzees (*Pan troglodytes*). *J. Comp. Psychol.* **118**, 48–57. (doi:10.1037/0735-7036.118.1.48)
- 64 Pedersen, J. & Fields, W. M. 2009 Aspects of repetition in bonobo–human conversation: creating cohesion in a conversation between species. *Integr. Psychol. Behav.* **43**, 22–41. (doi:10.1007/s12124-008-9067-6)
- 65 Savage-Rumbaugh, E. S. 1986 *Ape language: from conditioned response to symbol*. New York, NY: Columbia University Press.
- 66 Leavens, D. A., Hopkins, W. D. & Bard, K. A. 2005 Understanding the point of chimpanzee pointing.

- Curr. Dir. Psychol. Sci.* **14**, 185–189. (doi:10.1111/j.0963-7214.2005.00361.x)
- 67 Liszkowski, U., Carpenter, M., Striano, T. & Tomasello, M. 2006 Twelve and 18-month-olds point to provide information for others. *J. Cogn. Dev.* **7**, 297–307.
- 68 Call, J. 2011 How artificial communication affects the communication and cognition of the great apes. *Mind Lang.* **26**, 1–20. (doi:10.1111/j.1468-0017.2010.01408.x)
- 69 Tomasello, M. 2008 *Origins of human communication*. Cambridge, MA: MIT Press.
- 70 Gómez, J. C., Sarria, E. & Tamarit, J. 1993 The comparative study of early communication and theories of mind: ontogeny, phylogeny, and pathology. In *Understanding other minds: perspectives from autism* (eds S. Baron-Cohen & H. Tager-Flusberg), pp. 397–426. Oxford, UK: Oxford University Press.
- 71 Tomonaga, M., Tanaka, M., Matsuzawa, T., Myowa-Yamakoshi, M., Kosugi, D., Mizuno, Y., Okamoto, S., Yamaguchi, M. K. & Bard, K. 2004 Development of social cognition in infant chimpanzees (*Pan troglodytes*): face recognition, smiling, gaze, and the lack of triadic interactions. *Jpn Psychol. Res.* **46**, 227–235. (doi:10.1111/j.1468-5584.2004.00254.x)
- 72 Gómez, J. C. 2007 Pointing behaviors in apes and human infants: a balanced interpretation. *Child Dev.* **78**, 729–734. (doi:10.1111/j.1467-8624.2007.01027.x)
- 73 Veà, J. J. & Sabater-Pi, J. 1998 Spontaneous pointing behaviour in the wild pygmy chimpanzee (*Pan paniscus*). *Folia Primatol. (Basel)* **69**, 289–290. (doi:10.1159/000021640)
- 74 Cartmill, E. A. & Maestriper, D. 2012 Socio-cognitive specializations of nonhuman primates: evidence from gestural communication. In *The Oxford handbook of comparative evolutionary psychology* (eds J. Vonk & T. Shackelford). Oxford, UK: Oxford University Press.
- 75 Blaschke, M. & Ettliger, G. 1987 Pointing as an act of social communication by monkeys. *Anim. Behav.* **35**, 1520–1523. (doi:10.1016/S0003-3472(87)80023-4)
- 76 Bard, K. 1990 'Social tool use' by free-ranging orangutans: a Piagetian and developmental perspective on the manipulation of an animate object. In *'Language' and intelligence in monkeys and apes: comparative developmental perspectives* (eds S. T. Parker & K. R. Gibson), pp. 356–378. New York, NY: Cambridge University Press.
- 77 Bard, K. 1992 Intentional behaviour and intentional communication in young free-ranging orangutans. *Child Dev.* **63**, 1186–1197. (doi:10.1111/1467-8624.ep9301210043)
- 78 Kendon, A. 1988 How gestures can become like words. In *Cross-cultural perspectives in nonverbal communication* (ed. F. Poyatos), pp. 131–141. Toronto, ON: Hogrefe & Huber.
- 79 Russon, A. & Andrews, K. 2010 Orangutan pantomime: elaborating the message. *Biol. Lett.* (doi:10.1098/rsbl.2010.0564)
- 80 Tanner, J. & Byrne, R. 1996 Representation of action through iconic gesture in a captive lowland gorilla. *Curr. Anthropol.* **37**, 162–173. (doi:10.1086/204484)
- 81 Napier, J. R. 1976 *The Human hand*. Burlington, NC: Carolina Biological Supply Company.
- 82 Schultz, A. H. 1968 Form und Funktion der Primatenhände. In *Handgebrauch und Verständigung bei Affen und Frühmenschen* (ed. B. Rentsch), pp. 9–30. Bern, Switzerland: Hans Huber.
- 83 Frisch, K. V. 1973 Honeybees: do they use direction and distance information provided by their dancers? In *Perception: an adaptive process* (ed. T. L. Bennett), pp. 84–91. New York, NY: MSS Information Corp.
- 84 Kirkpatrick, M. & Ryan, M. 1991 The evolution of mating preferences and the paradox of the lek. *Nature* **350**, 33–38. (doi:10.1038/350033a0)
- 85 Tinbergen, N. 1954 The origin and evolution of courtship and threat display. In *Evolution as a process* (eds A. C. Hardy, J. S. Huxley & E. B. Ford), pp. 233–250. London, UK: Allen and Unwin.
- 86 Krebs, J. R. & Dawkins, R. 1984 Animal signals: mind-reading and manipulation. In *Behavioral ecology: an evolutionary approach* (eds J. R. Krebs & N. B. Davies), pp. 380–402. Oxford, UK: Blackwell Scientific Publications.
- 87 Tinbergen, N. 1952 'Derived' activities; their causation, biological significance, origin, and emancipation during evolution. *Q. Rev. Biol.* **27**, 1–32. (doi:10.1086/398642)
- 88 Redshaw, M. & Locke, K. 1976 The development of play and social behaviour in two lowland gorilla infants. *Dodo J. Jersey Wildlife Preserv. Trust* **13**, 71–86.
- 89 Plooij, F. X. 1978 Some basic traits of language in wild chimpanzees? In *Action, gesture and symbol: the emergence of language* (ed. A. Lock), pp. 111–131. London, UK: Academic Press.
- 90 Bonnie, K. & de Waal, F. 2006 Affiliation promotes the transmission of a social custom: handclasp grooming among captive chimpanzees. *Primates* **47**, 27–34. (doi:10.1007/s10329-005-0141-0)
- 91 McGrew, W. C. & Tutin, C. E. G. 1978 Evidence for a social custom in wild chimpanzees? *Man* **13**, 234–251. (doi:10.2307/2800247)
- 92 Tomasello, M., Gust, D. & Frost, G. 1989 A longitudinal investigation of gestural communication in young chimpanzees. *Primates* **30**, 35–50. (doi:10.1007/BF02381209)
- 93 Poss, S., Kuhar, C., Stoinski, T. S. & Hopkins, W. D. 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. *Am. J. Primatol.* **68**, 978–992. (doi:10.1002/ajp.20304)
- 94 Hopkins, W. D., Tagliabata, J. P. & Leavens, D. A. 2007 Chimpanzees differentially produce novel vocalizations to capture the attention of a human. *Anim. Behav.* **73**, 281–286. (doi:10.1016/j.anbehav.2006.08.004)
- 95 Leavens, D. A., Hostetter, A. B., Wesley, M. J. & Hopkins, W. D. 2004 Tactical use of unimodal and bimodal communication by chimpanzees *Pan troglodytes*. *Anim. Behav.* **67**, 467–476. (doi:10.1016/j.anbehav.2003.04.007)
- 96 Gómez, J. C. 1990 The emergence of intentional communication as a problem-solving strategy in the gorilla. In *'Language' and intelligence in monkeys and apes: comparative developmental perspectives* (eds S. T. Parker & K. R. Gibson), pp. 333–355. Cambridge, UK: Cambridge University Press.
- 97 Zuberbühler, K. 2005 The phylogenetic roots of language: evidence from primate communication and cognition. *Curr. Dir. Psychol. Sci.* **14**, 126–130. (doi:10.1111/j.0963-7214.2005.00357.x)
- 98 Tomasello, M. 2007 Ape gestures and the origins of language. In *Gestural communication in apes and monkeys* (eds J. Call & M. Tomasello), pp. 221–239. Hillsdale, NJ: Lawrence Erlbaum Associates.
- 99 Rizzolatti, G. & Arbib, M. A. 1998 Language within our grasp. *Trends Neurosci.* **21**, 188–194. (doi:10.1016/S0166-2236(98)01260-0)
- 100 Arbib, M. A. 2005 From monkey-like action recognition to human language: an evolutionary framework for neurolinguistics. *Behav. Brain Sci.* **28**, 105–124. (doi:10.1017/S0140525X05000038)
- 101 Kimura, D. 1993 *Neuromotor mechanisms in human communication*. New York, NY: Oxford University Press.
- 102 Corballis, M. C. 1992 *The lopsided brain: evolution of the generative mind*. New York, NY: Oxford University Press.

- 103 Kimura, D. 1973 Manual activity during speaking—I. Right-handers. *Neuropsychologia* **11**, 45–50. (doi:10.1016/0028-3932(73)90063-8)
- 104 Kinsbourne, M. & Hicks, R. E. 1978 Functional cerebral space: a model for overflow, transfer, and interference effects in human performance. In *Attention and performance* (ed. J. Requin), pp. 54–68. Hillsdale, NJ: Erlbaum.
- 105 Stafford, D. K., Milliken, G. W. & Ward, J. P. 1990 Lateral bias in feeding and brachiation in *Hylobates*. *Primates* **31**, 407–414. (doi:10.1007/BF02381111)
- 106 Hopkins, W. D. & Cantero, M. 2003 From hand to mouth in the evolution of language: the influence of vocal behavior on lateralized hand use in manual gestures by chimpanzees (*Pan troglodytes*). *Dev. Sci.* **6**, 55–61. (doi:10.1111/1467-7687.00254)
- 107 McGrew, W. C. & Marchandt, L. F. 1992 Chimpanzees, tools, and termites: hand preference or handedness. *Curr. Anthropol.* **33**, 114–119. (doi:10.1086/204041)
- 108 Cashmore, L., Uomini, N. & Chapelain, A. 2008 The evolution of handedness in humans and great apes: a review and current issues. *J. Anthropol. Sci.* **86**, 7–35.
- 109 Westergaard, G. & Suomi, S. 1993 Hand preference in capuchin monkeys varies with age. *Primates* **34**, 295–299. (doi:10.1007/BF02382624)
- 110 Hopkins, W. D., Bennett, A. J. & Bales, S. L. 1993 Behavioural laterality in captive bonobos (*Pan paniscus*). *J. Comp. Psychol.* **107**, 403–410. (doi:10.1037/0735-7036.107.4.403)
- 111 Hopkins, W. D., Bard, K. A., Jones, A. & Bales, S. L. 1993 Chimpanzee hand preference in throwing and infant cradling: implications for the origin of human handedness. *Curr. Anthropol.* **34**, 786–790. (doi:10.1086/204224)
- 112 Sugiyama, Y., Fushimi, T., Sakura, O. & Matsuzawa, T. 1993 Hand preference and tool use in wild chimpanzees. *Primates* **34**, 151–159. (doi:10.1007/BF02381386)
- 113 Anderson, J., Degiorgio, C., Lamarque, C. & Fagot, J. 1996 A multi-task assessment of hand lateralization in capuchin monkeys (*Cebus apella*). *Primates* **37**, 97–103. (doi:10.1007/BF02382926)
- 114 Hopkins, W. D. & Cantalupo, C. 2005 Individual and setting differences in the hand preferences of chimpanzees *Pan troglodytes*: a critical analysis and some alternative explanations. *Laterality* **10**, 65–80.
- 115 Hopkins, W. D. 1996 Chimpanzee handedness: causes and consequences. *Int. J. Primatol.* **31**, 3665–3665.
- 116 Hopkins, W. D. & Leavens, D. A. 1998 Hand use and gestural communication in chimpanzees (*Pan troglodytes*). *J. Comp. Psychol.* **112**, 95–99. (doi:10.1037/0735-7036.112.1.95)
- 117 Hopkins, W. D., Russell, J., Freeman, H. D., Buehler, N., Reynolds, E. & Schapiro, S. J. 2005 The distribution and development of handedness for manual gestures in captive chimpanzees (*Pan troglodytes*). *Psychol. Sci.* **16**, 487–493(487). (doi:10.1111/j.0956-7976.2005.01561.x)
- 118 Tagliabata, J. P., Cantalupo, C. & Hopkins, W. D. 2006 Gesture handedness predicts asymmetry in the chimpanzee inferior frontal gyrus. *Neuroreport* **17**, 923–927. (doi:10.1097/01.wnr.0000221835.26093.5e)