Gorillas are right-handed for their most frequent intraspecific gestures

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Investigations of intraspecific laterality of primates' gestural communication aim to shed light on the evolutionary origins of human handedness and language. Currently, little is known concerning laterality of gestures for purely intraspecific communication. As far as we know, this study is the first to assess laterality of gorillas' purely intraspecific gestures at the population level. We analysed hand use in dyadic interactions in 35 gorillas, Gorilla gorilla gorilla, living in three groups in captivity focusing on their most frequent communication gesture types. We revealed a right-hand bias at the population level for the majority of the most frequent gestures recorded. Our findings support the evolutionary theories predicting that population level asymmetry should be found in fitness-relevant social behaviours and could be explained by an evolutionarily stable strategy based on intraspecific interactions. They also agree with reports evidencing predominant right-hand use for gestural communication by nonhuman primates and suggesting that gestural laterality is a precursor of the left-hemispheric lateralization of language.

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Functional cerebral asymmetry at the population level is not restricted to humans but is widely spread among vertebrates (e.g. see Ocklenburg & Güntürkün, 2012; Rogers, Vallortigara, & Andrew, 2013; Vallortigara, Chiandetti, & Sovrano, 2011 for reviews) and invertebrates (e.g. see Frasnelli, Vallortigara, & Rogers, 2012 for review). The related limb asymmetry has been extensively documented among vertebrates (e.g. Versace and Vallortigara (2015) for a review). However, in spite of a growing and substantial set of reports, the phylogenetic mechanisms that led to overexpression of right-hand use by humans are still poorly understood. Although humans present a strong preference for right-hand use at the population level (e.g. McManus, 2002), nonhumans' limb preference is not obvious and depends on the species (e.g. Ströckens, Güntürkün, & Ocklenburg, 2013). According to the theory of the evolution of laterality at the population level (e.g. Ghirlanda & Vallortigara, 2004; Vallortigara & Rogers, 2005), biases at the individual level would have emerged because they conferred cognitive advantages (e.g. Rogers, Zucca, & Vallortigara, 2004). Thereafter, directional alignment of laterality at the population level would have been favoured by an evolutionarily stable strategy (ESS) for individual asymmetrical organisms to coordinate their behaviour with that of other asymmetrical organisms. This alignment of laterality at the population level would have certain disadvantages, making behaviour more predictable for predators and prey (e.g. Ghirlanda & Vallortigara, 2004), but also advantages, facilitating intraspecific interactions (e.g. Rogers, 2000), as for primates (e.g. chimpanzees, Pan troglodytes: Prieur, Pika, Barbu, & Blois-Heulin, 2016; mangabeys, Cercocebus torquatus torquatus and Lophocebus albigena albigena: Baraud, Buytet, Bec, & Blois-Heulin, 2009). Ghirlanda, Frasnelli, and Vallortigara (2009) recently proposed that the pattern of population level laterality could be explained by an ESS based on a trade-off between competitive and cooperative intraspecific interactions better than by interspecific interactions.

Despite substantial scientific advances concerning laterality of limb use and laterality in social behaviour, further studies are needed to understand better the evolutionary relationship between population level right-handedness and cerebral lateralization of human language. For this, nonhuman primates, particularly great apes, can provide valuable clues (e.g. Corballis, 2002) as they are the species closest phylogenetically to humans (e.g. Scally & Durbin, 2012). Moreover, their hand anatomy (e.g. Aiello & Dean, 1990), manipulation skills (e.g. Byrne, Corp, & Byrne, 2001) and neuroanatomical brain asymmetries (e.g. left-cerebral hemisphere predominance in the homologues of the human Broca's and Wernicke's areas: Cantalupo & Hopkins, 2001; Spocter et al., 2010) present close resemblances to humans. Although numerous studies have investigated nonhuman primates' hand preference for manipulation and gestural communication (e.g. see

Meguerditchian, Vauclair, & Hopkins, 2013 for a review), laterality of gorillas, of all species studied, is still very poorly documented (e.g. Byrne & Byrne, 1991; Forrester, Leavens, Quaresmini, & Vallortigara, 2011; Meguerditchian, Calcutt, Lonsdorf, Ross, & Hopkins, 2010; Quaresmini, Forrester, Spiezio, & Vallortigara, 2014).

Here, the term 'gesture' is restricted to communication and defined as 'movements of the limbs or head and body directed towards a recipient that are goal-directed, mechanically ineffective (that is, they are not designed to act as direct physical agents) and receive a voluntary response' (Pika & Bugnyar, 2011, p 4). From the above-mentioned studies, it appears first that much less is known about laterality of gestures in purely intraspecific communication (chimpanzees: Fletcher & Weghorst, 2005; Meguerditchian, Vauclair, & Hopkins, 2010; Hobaiter & Byrne, 2013; Prieur, 2015; Prieur, Pika, Barbu, et al., 2016; Prieur, Pika, Blois-Heulin, & Barbu, 2016; bonobos, *Pan paniscus*: Chapelain, 2010; gorillas, *Gorilla gorilla gorilla*: Prieur, 2015; olive baboons, *Papio anubis*: Meguerditchian & Vauclair, 2006) than about gestures directed towards humans, or towards both conspecifics and humans (pooled data), although investigations in real-life socially relevant contexts is particularly interesting from an evolutionary point of view because natural selection operates in comparable contexts.

To further our understanding of the evolutionary relationship between direction of handedness and left-cerebral lateralization of language, we followed Prieur's (2015) methodology for chimpanzees to study the intraspecific gestural laterality of gorillas, a species phylogenetically more distant from humans than are chimpanzees. As far as we know, only Shafer (1987) previously investigated gorillas' intraspecific gestural communication. However, she called 'gestures' a category of undistinguished types of hand motions (that do not match our definition of gestures) defined as 'any hand motions interpreted as signalling to another gorilla or that were interpreted as solitary gestures' (Shafer, 1987, p. 51). Moreover, her study raises methodological issues (e.g. sample size, number of data per subject, absence of information about independence of data) that make it difficult to draw conclusions about gorillas' gestural laterality. The present study explored laterality of gorillas' intraspecific gestural communication in depth by analysing their most frequent gestures (e.g. Genty, Breuer, Hobaiter, & Byrne, 2009; Pika, Liebal, & Tomasello, 2003). To evaluate the presence of a gestural laterality bias at the population level we analysed separately 16 gestures. Based on the literature on chimpanzees (e.g. Meguerditchian, Vauclair, et al., 2010; Prieur, 2015; Prieur, Pika, Barbu, et al., 2016), we predicted that a majority of these frequently expressed gestures would be right-lateralized at the population level.

METHODS

Subjects

Thirty-five lowland gorillas, *G. g. gorilla*, raised under semi-natural conditions were observed at three zoos: La Vallée des Singes (France), Apenheul Primate Park and Burgers' Zoo (The Netherlands). Age categories of subjects were based mainly on Breuer, Hockemba, Olejniczak, Parnell, and Stokes (2009) categories for infants (0–3 years), juveniles (4–6 years) and adolescents (7–11 years) and on Stoinski, Lukas, and Kuhar (2013) categories for young adults (12–20 years) and mature adults (>20 years). Our gorillas (23 females and 12 males) were between 0.5 and 42 years old (mean = 13.64, SD = 13.07). All outdoor enclosures offered a seminatural environment surrounded by a water ditch and contained climbing structures (e.g. trees, ropes and platforms) as well as vegetation (e.g. bamboos and various types of

bushes and grass). All indoor enclosures also included climbing structures. Zookeepers fed the study subjects with diverse types of food and enrichments. Water was available ad libitum. As the study was noninvasive and involved only observations of animals in their enclosures, experimental permits or ethical approvals were not required.

Observation Procedures

Observation data were collected in 2012 at La Vallée des Singes (18 May–25 July) and at Apenheul Zoo (14 August–27 October) and in 2013 at Burgers' Zoo (29 April–29 June), respectively, during 196.5 h, 214.5 h and 240 h (total: 651 h observations).

Data were collected during four 1.5 h sessions per day (two in the morning and two in the afternoon) recording 'all occurrences of some behaviours' (Altmann, 1974). Observation data were recorded on paper in real time using a stopwatch and binoculars. Data were mostly collected from above and as close as possible to the subjects. Data were only recorded when a clear view of the subjects was possible.

Coding Procedure

Only intraspecific dyadic interactions were considered. For each interaction, we recorded (1) the type of gesture and the hand (left or right) used by the signaller to communicate (based on Pika and colleagues' repertoire 2003) and (2) the identity of the signaller or recipient.

Following Pika and Bugnyar's (2011) definition of gesture, we considered only intentionally produced gestures that (1) were used to initiate (not continue) a social interaction, (2) were mechanically ineffective (Pollick & de Waal, 2007) and (3) included gazing at the recipient, gaze alternation and/or waiting for a response (e.g. Tomasello, Gust, & Frost, 1989).

We focused on the hand used by the signaller to perform conspecific-directed gestures. A requirement for all records was that both the signaller's hands were free and positioned symmetrically in relation to his/her body midline before the interaction, without any environmental factors potentially influencing the use of a hand (e.g. close to a wall/bush/tree).

Gestures were expressed either singly or in bouts (e.g. Byrne & Byrne, 1991; Marchant & McGrew, 1991). When expressed in bouts, only the first gesture of the sequence was recorded. Criteria employed to determine the termination of a gesture or a bout of gestures were: (1) the signaller's hand returned to its initial position (Meguerditchian, Vauclair, et al., 2010); (2) the signaller's hand switched to another noncommunication activity (e.g. forage); or (3) the movement was influenced by an outside incident (e.g. stumble) (Harrison & Nystrom 2010; Hopkins et al., 2001; Hopkins & de Waal, 1995; McGrew & Marchant, 2001). To ensure statistical independence of data, the minimum required time interval before recording another gesture was 3 s (Hopkins & de Waal, 1995; Morris, Hopkins, & Bolser-Gilmore, 1993).

Gesture Characteristics

Our gesture classification was based on previously described repertoires (when necessary anatomical elements or precisions were added; Tables 1 and 2). We considered 16 specific gestures categorized following Pika et al. (2003), Pika, Liebal, and Tomasello (2005) descriptions as (1) auditory gestures that generate sound while being performed (N = 4), (2) visual gestures that generate a mainly visual component with no physical contact (N = 6) and (3) tactile gestures that include physical contact with the recipient (N = 6).