Animal Behaviour 116 (2016) 31–43

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

A multifactorial investigation of captive chimpanzees' intraspecific gestural laterality

Jacques Prieur [a, *], Simone Pika [b], Stéphanie Barbu [a], Catherine Blois-Heulin [a]

[a] Ethos 'Ethologie Animale et Humaine', Université de Rennes 1–CNRS UMR 6552, Station biologique de Paimpont, France
[b] Max Planck Institute for Ornithology, Humboldt Research Group 'Comparative Gestural Signalling', Seewiesen, Germany

ARTICLE INFO

Article history:
Received 19 May 2015
Initial acceptance 7 July 2015
Final acceptance 2 March 2016

MS. number: 15-00425R

Keywords:
brain asymmetry
chimpanzee
communication
gesture
social laterality

Social laterality is the core of two major theories: one concerns the evolution of laterality at the population level and the other the evolution of human language. However, few studies have investigated gestural laterality in communication between conspecifics. To our knowledge, the present study is the first to investigate the production of intraspecific gestures taking into account the influence of multiple factors on gestural laterality: first, gestural characteristics (sensory modality, use of a communication tool, sharing degree in the population and duration); second, the interactional context (visual field and body sides of signaller and recipient, and emotional context); and third, individual sociodemographic characteristics of signaller and recipient (age, sex, group, hierarchy, affiliation and kinship). We questioned, first, whether gestural laterality differed with gesture at the population level and second, whether some factors influenced gestural laterality. To do so, we evaluated social laterality in dyadic interactions in 39 chimpanzees, *Pan troglodytes*, living in three groups in captivity. We found that, at the population level, 13 of the 21 gestures we observed were performed predominantly with the right hand. Gestural laterality of signallers was influenced mainly by interactional context, gesture characteristics (except gesture duration) and signallers' hierarchical rank and age. Signallers used their hand ipsilateral to recipients for tactile and visual gestures and their contralateral hand for gestures involving auditory communication and a communication tool. Moreover, signallers' use of their right hand was more important for subordinates. This was also true in negative contexts for gestures common to most of the subjects. Our results further support the hypothesis that laterality in gestural communication might represent a precursor of the left-hemispheric lateralization of language. We discuss our results in relation to theories concerning the origins of cerebral hemispheric lateralization and their consistency with previous studies.

Laterality in social behaviour is becoming an important research area as it is the core of two major theories: the first concerns the evolution of laterality at the population level (ELP) and the second the origin of human language (OHL). The ELP theory (e.g. Ghirlanda, Frasnelli, & Vallortigara, 2009; Ghirlanda & Vallortigara, 2004; Vallortigara & Rogers, 2005) hypothesizes that the evolution of population level asymmetries is influenced by social behaviour. It suggests that behavioural laterality at the population level emerged in species subject to selection pressures imposed by social interactions rather than in solitary species. The gestural OHL theory (e.g. Arbib, Liebal, & Pika, 2008; Corballis, 2002; McNeill, 2012) hypothesizes an evolutionary relationship between the roots of human language and handedness. It postulates that the left-cerebral lateralization of language evolved from gestural communication.

According to the ELP theory, brain lateralization may have evolved in two steps. First, biases at the individual level would have been selected because they increase brain efficiency (e.g. see Rogers, Zucca, & Vallortigara, 2004 for review). Second, biases at the population level could have emerged from an evolutionarily stable strategy (ESS)/frequency-dependent selection based on interspecific prey–predator interactions. More recently, Ghirlanda et al. (2009) proposed that the pattern of population level laterality could be better explained by an ESS based on a trade-off between competitive and cooperative intraspecific interactions than by interspecific interactions. Social laterality could have appeared at the population level through social pressures (e.g. Vallortigara & Rogers, 2005) and because it facilitated intraspecific interactions

* Correspondence: J. Prieur, UMR 6552, Station Biologique, Université de Rennes 1–CNRS, 35380 Paimpont, France.
E-mail address: jac.prieur@yahoo.fr (J. Prieur).

http://dx.doi.org/10.1016/j.anbehav.2016.03.024
0003-3472/

(Rogers, 2000). This view is supported by empirical data on fish (e.g. Bisazza, Cantalupo, Capocchiano, & Vallortigara, 2000) and tadpoles (e.g. Bisazza, De Santi, Bonso, & Sovrano, 2002) showing that population level laterality is more likely to be exhibited by social than solitary species.

Among laterality expressed in social interactions, laterality of gestural communication of our closest living relatives, the great apes, is the focus of an ever-growing body of research (e.g. see Hopkins et al., 2012 for review) participating in the perennially vivid scientific debates on the origins of language by providing recent arguments in favour of a gestural origin. Below, we refer to gestures 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). All the properties underlying the production and use of sophisticated gestural communication (e.g. intentionality and flexibility) are crucial prerequisites for human language (e.g. see Hopkins et al., 2012; Meguerditchian, Vauclair, & Hopkins, 2013 for reviews). However, despite the challenges, intraspecific data remain sparse in the literature (Forrester, Quaresmini, Leavens, Spiezio, & Vallortigara, 2012), and this is all the more the case for gestures for which laterality has been more extensively investigated, in captive conditions, in communication directed towards humans. Therefore, whether most frequent spontaneous gestures directed towards conspecifics are lateralized at the population level remains open.

In addition, many factors have been found to modulate laterality expressed in gestural communication (e.g. gesture type, relative positions of subjects during an interaction, emotional valence and sociodemographic components). For instance, Hobaiter and Byrne (2013) showed that chimpanzees, *Pan troglodytes*, in the wild use their right hands significantly more for object manipulation gestures than for nonobject manipulation gestures. Moreover, captive chimpanzees used their right hands more for begging to humans than for pointing at them (Hopkins & Leavens, 1998; Hopkins & Wesley, 2002). Therefore, the type of chimpanzees' gestures seems to have a crucial impact on the direction and strength of hand use during communication. This factor could explain discrepancies within studies focusing on different gestures (e.g. Hopkins & Leavens, 1998; Hopkins & Wesley, 2002). Investigating the effect of gesture type on laterality requires considering various elementary gestural characteristics (e.g. sensory modality: tactile, visual and auditory; with or without use of a communication tool; degree of sharing among the population: rare or common; duration: short or long). However, which factors could explain why observational studies of behavioural laterality focusing on the same gesture have provided different results (e.g. Fletcher's (2006) and Meguerditchian, Gardner, Schapiro, and Hopkins (2012) studies of chimpanzees for Clap hand directed towards humans)?

Taking into account multiple elementary factors related to social interactions (e.g. interactional context components and sociodemographic factors) should help us to explain heterogeneous results between studies. This multifactorial approach could also be particularly relevant to investigate possible effects of social pressures on laterality. Surprisingly, relatively little is known about the impact of the position of the recipient (most often a human) on primates' hand preference. To date, authors have reported the influence of the experimenter's position on hand preference for Food beg and Pointing (pooled data) by chimpanzees (Hopkins & Wesley, 2002), but not for Food beg by olive baboons, *Papio anubis* (Bourjade, Meunier, Blois-Heulin, & Vauclair, 2013). Concerning the emotional valence of the context, intraspecific agonistic interactions generally induce a preferential use of the left visual field by many vertebrates (e.g. gelada baboons, *Theropithecus gelada*: Casperd & Dunbar, 1996). In contrast, Chapelain, Hogervorst, and Blois-Heulin (n.d.) found a left visual field bias for bonobos, *Pan paniscus*, during positive interactions. These studies highlight complex interactions between the respective positions of signaller and recipient (for both body side and visual field) and the emotional context, interactions that require further investigations to understand better their influence on primates' gestural communication with conspecifics.

Concerning sociodemographic factors that may be particularly associated with social pressure acting on laterality, a few studies have investigated the effect of age on gestural laterality. For example, chimpanzees' right direction in hand preference increased with age in the wild (Hobaiter & Byrne, 2013) and in captive environments (Hopkins & Leavens, 1998). However, age effects have not been consistently found across studies (e.g. chimpanzees: Hopkins et al., 2005a). Regarding a sex effect, as far as we know, only two studies have reported such an effect, but with opposite results: Hopkins and Leavens (1998) found that male chimpanzees tended to be less right-handed than females, whereas Hopkins and de Waal (1995) found that male bonobos were more right-handed than females. Other studies did not find an influence of sex on nonhuman primates' laterality in gestures (e.g. chimpanzees: Hopkins et al., 2005a). Studying a group effect can also help us shed light on possible effects of social pressures on gestural laterality. To date, an absence of a group effect on gestural laterality has been found for captive chimpanzees for human-directed Clapping (Meguerditchian et al., 2012) and for Throwing directed towards both humans and conspecifics (pooled data; Hopkins, Russell, Cantalupo, Freeman, & Schapiro, 2005b) as well as for captive olive baboons for Hand slap directed towards both humans and conspecifics (pooled data; Meguerditchian, Molesti, & Vauclair, 2011). Concerning social factors, to our knowledge, only one study has investigated a kinship effect: Hopkins et al. (2005b) study of captive chimpanzees' hand preference for Throwing did not show an influence of kinship. Hierarchical rank effects have been investigated only in visual laterality of two species of mangabeys, *Cercocebus torquatus torquatus* and *Lophocebus albigena albigena*: Baraud, Buytet, Bec, & Blois-Heulin (2009) showed that high-ranking mangabeys were approached more often from their left than from their right. Although the quality of relationships (i.e. affiliation) may also represent a possible source of social pressure acting on laterality, the influence of affiliation so far remains undocumented. Therefore the full range of individual sociodemographic characteristics remains to be taken into consideration simultaneously to assess as rigorously as possible their relative weights and possible influences on primates' gestural communication.

To date, most studies have focused on some particular factors in isolation providing a fragmented picture of the issue and contradictory results. This emphasizes the importance of investigating further nonhuman primates' gestural communication to improve our understanding of the origin and evolution of both social laterality at a population level and of language. To our knowledge, no previous study has assessed gestural laterality using a comprehensive approach simultaneously taking into account multiple influential factors and their interactions as well as considering sociodemographic characteristics and narrow categories of age (e.g. immature, adolescent, young and mature adult and elder) and hierarchy (e.g. dominant, intermediate and subordinate) of both signaller and recipient, essential requirements to avoid biases and to yield unambiguous results. Although socioecologically relevant conditions close to conditions in which natural selection has acted are of particular interest to study gestural laterality in an evolutionary perspective, many studies have investigated nonhuman primates' gestural communication