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Captive gorillas' manual laterality: The impact of gestures, manipulators and interaction specificity

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ABSTRACT

Relationships between humans' manual laterality in non-communicative and communicative functions are still poorly understood. Recently, studies showed that chimpanzees' manual laterality is influenced by functional, interactional and individual factors and their mutual intertwinement. However, what about manual laterality in species living in stable social groups? We tackled this question by studying three groups of captive gorillas (N = 35) and analysed their most frequent manual signals: three manipulators and 16 gesture types. Our multifactorial investigation showed that conspecific-directed gestures were overall more right-lateralized than conspecific-directed manipulators. Furthermore, it revealed a difference between conspecific- and human-directed gestural laterality for signallers living in one of the study groups. Our results support the hypothesis that gestural laterality is a relevant marker of language left-brain specialisation. We suggest that components of communication and of manipulation (not only of an object but also of a conspecific) do not share the same lateralised cerebral system in some primate species.

1. Introduction

Humans' left-hemisphere specialisation for both manipulative and communicative interactions is well documented (e.g. Hecaen & Ajuriaguerra, 1964; Kimura, 1973). However, the relationship between humans' manual laterality in non-communicative and communicative functions is relatively poorly understood (e.g. see Cochet & Byrne, 2013 for a review). To date, so far only Cochet and Vauclair (2012) and Cochet, Jover, Oger, and Vauclair (2014) investigated this aspect by carrying out an experimental study on human adults with a special focus on actions and a specific communicative gesture, POINTING.[1] For example, they reported that individuals used their right hands more frequently for bimanual coordinated manipulations[2] than for POINTING produced without speech. Moreover, the authors found no significant difference in the direction of laterality between bimanual coordinated manipulations and POINTING produced with speech. These findings indicate the ambiguous relationship between the direction of manual asymmetry for manipulations and language left-brain specialisation. Additional studies are, however, crucially needed. A considerable amount of research has focused on the phylogenetic origins and functions of hemispheric specialisation of human laterality by investigating related characteristics in our closest living relatives, the non-human primates (hereafter primates) (e.g. Hopkins, 2007; Hopkins et al., 2012; Vauclair, Fagot, & Dépy, 1999). Many primate species show a right-hand bias at the population-level for manipulation tasks requiring high levels of complexity such as for instance bimanual coordinated actions (e.g. bimanual coordinated tube task for chimpanzees, *Pan troglodytes*: Hopkins, 1995; bimanual feeding for western lowland gorillas, *Gorilla gorilla gorilla*: Meguerditchian, Calcutt, Lonsdorf, Ross, & Hopkins, 2010). On the contrary, recent research showed that manipulation tasks requiring low levels of complexity, such as for example spontaneous uni-manual actions, do not reveal manual laterality at the population-level (e.g. unimanual food reaching for chimpanzees: Hopkins & Rabinowitz, 1997; western lowland gorillas: Meguerditchian, Calcutt, et al., 2010; De Brazza's monkeys, *Cercopithecus neglectus*: Schweitzer, Bec, & Blois-Heulin, 2007). Moreover, an increasing body of work indicates that right hands are used more frequently for gestural communication than for manipulations (e.g. see Meguerditchian, Vauclair, & Hopkins, 2013 for a review). These findings led researchers to postulate that laterality in primates' gestural communication represents a precursor of the left-hemispheric lateralisation for human language (e.g. see

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[1] From here on gestures are depicted in small capitals.

[2] Bimanual coordinated actions require the use of two hands for different but complementary roles (e.g. for bimanual coordinated manipulation of an object, one hand simply holds the object while the other hand is engaged in a more active/complex action).

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Meguerditchian & Vauclair, 2014 for a review). This hypothesis is based on a number of observational and experimental studies of primates' gestural communication (e.g. Arbib, Liebal, & Pika, 2008). For instance, (1) great apes' gestural signalling is more flexible than their vocal production (e.g. Call & Tomasello, 2007; see for different view Schel, Townsend, Machanda, Zuberbühler, & Slocombe, 2013), (2) mirror neurons in the rhesus monkey's premotor cortex (area F5) discharge both when a subject performs a given action and when it observes the same action being performed by an experimenter (see Fabbri-Destro & Rizzolatti, 2008 for a review), and (3) many species of primates, particularly great apes such as chimpanzees and gorillas, present a right gestural laterality (e.g. Prieur, Pika, Barbu, & Blois-Heulin, 2016a, 2016b; see also Hopkins et al., 2012 for a review).

However, most studies investigating primates' gestural laterality have focused on distinct gestures types, such as human-directed gestures (e.g. Hopkins & Leavens, 1998) or gestures used towards both humans and conspecifics (pooled data) (e.g. Meguerditchian, Vauclair, & Hopkins, 2010). Interestingly, recent studies showed that social pressures can affect laterality (e.g. Chapelain et al., 2015; Prieur et al., 2016a; Schaafsma, Riedstra, Pfannkuche, Bouma, & Groothuis, 2009; Prieur, Pika, Barbu, & Blois-Heulin, 2017). For instance, Prieur, Lemasson, Barbu, & Blois-Heulin (submitted for publication-a) showed that social pressures, particularly from the study subjects (conspecifics) but also to a lesser extent from the experimenters, are likely to influence the results of experimental laterality studies. To understand in more detail the factors influencing laterality, it is thus crucial to investigate the spontaneous use of gestures in naturally occurring interactions with conspecifics. So far, only a relatively small number of studies have addressed gestural laterality in naturally occurring interactions between conspecifics although (i) socio-ecological validity is particularly relevant from an evolutionary point of view, and (ii) several researchers have suggested that intraspecific interactions could explain population-level laterality (Ghirlanda, Frasnelli, & Vallortigara, 2009). Furthermore, Prieur, Pika, Barbu, and Blois-Heulin (submitted for publication-b) recently showed that chimpanzees' gestural laterality varied in relation to various aspects such as specificity of recipient (conspecifics vs. humans), spatial position of recipient (in or outside signaller's visual field), and signallers' age. These findings emphasize the necessity to apply multifactorial investigations to study laterality of intentional signals in detail to avoid biases and ambiguous results.

According to Liebal and Call (2012), gestures (mechanically ineffective movements of limbs, head or body movements, which are directed to recipients and result in a voluntary response; Pika, 2008) would originate from actions (mechanically effective) deprived of a communicative function (but see for a different opinion: Pika & Fröhlich, submitted for publication; Prieur et al., submitted for publication-b). Therefore, their function and use can be described along a continuum (see, Scott & Pika, 2012), suggesting that their physical forms are the same, sometimes mechanically effective and sometimes mechanically ineffective, directed or non-directed and eliciting or not a voluntary response. In the evolutionary context of the origin of human right handedness and cerebral specialisation for language, the lively debate concerning the origins of gesture acquisition (see Byrne et al., 2017; Fröhlich, Wittig, & Pika, 2016; Liebal & Call, 2012; Pika & Fröhlich, submitted for publication) raises several issues ranging from the contribution of our ancestors' manual actions directed towards a social partner (from here noted "manipulators") over the emergence of the left-hemisphere language specialisation of modern humans, to the lateralised cerebral structures controlling manipulators and gestures performed in signalling contexts. To address these issues, it is important to investigate the influence of mechanical effectiveness and communication type on manual laterality of the closest phylogenetic species to humans, the great apes.

To date, we know relatively little about the extent of manual laterality with regards to (i) different social structures and dynamics (ii) different spontaneous activities directed towards conspecifics (manipulation actions versus gestures), and (iii) communication types (conspecific- versus human-directed gestures). However, investigations into these aspects are essential to understand relationships between human functional brain specialisation, speech, handedness for gestures and social life. Very recently, Prieur and colleagues (2017, submitted for publication-b) performed for the first time such investigations. First, they compared manual laterality between gorillas and chimpanzees focusing on intraspecific gestures (Prieur et al., 2017). Gorillas are as genetically distant from chimpanzees as they are from humans (Kaessmann, Wiebe, Weiss, & Pääbo, 2001). They show different social structures and dynamics: gorillas live in polygamous and generally stable and cohesive groups (e.g. Bradley, Doran-Sheehy, Lukas, Boesch, & Vigilant, 2004; Schaller, 1963; Watts, 1996) whereas chimpanzees have less stable social structures since they live in fission-fusion societies characterised by a highly variable party membership (e.g. Goodall, 1986; Mitani, 2009). Based on their findings, Prieur and colleagues hypothesized that differences between gestural laterality patterns of the two species may be the consequence of differences in social structure and dynamics.

Second, they investigated the influence of mechanical effectiveness and communication type on chimpanzees' manual laterality (Prieur et al., submitted for publication-b). They found that signallers' right-hand use was more pronounced for conspecific-directed gestures than for manipulations directed towards conspecifics. Furthermore, they showed that conspecific- and human-directed gestural lateralities were modulated differently by the recipient's position with regards to the signaller's visual field and age. However, how do mechanical effectiveness and of recipient specificity impact upon laterality inspecies living in stable social groups? To tackle this central question, the present study adopted a comparative approach and apply the same study design and multifactorial approach used previously (Prieur et al., submitted for publication-b). We assessed manual laterality of gorillas in three different, distinct categories of intentional signals: conspecific-directed manipulators, conspecific-directed gestures and human-directed gestures. Choosing gorillas as model system for the present study and comparing results between both great ape species will enable us to assess the influence of the social-related factors on intraspecific manual signal laterality. We addressed the following three questions:

(1) Do gorillas show a right-hand bias at the population-level for conspecific-directed manipulators (mechanically effective) and for human-directed gestures (mechanically ineffective), as we previously found for conspecific-directed gestures in chimpanzees and gorillas (Prieur et al., 2016a, 2016b)? To investigate this question, we studied the direction of manual laterality at the population level for each behavioural category separately.

Based on recent findings on primates' laterality in both spontaneous gestural interactions and non-communicative actions (e.g. Hopkins et al., 2012; Meguerditchian et al., 2013), we expected to find a right-hand bias at the population-level for human-directed gestures but not for conspecific-directed manipulators (prediction n°1).

(2) Does manual laterality vary depending on mechanical effectiveness? To address this question, we distinguished two functions: communication 'requests' (gestures which involve taking into consideration the recipient's response such as TOUCH BODY) and so-called 'manipulators' (mechanically effective social actions used to get things done such as GRAB BODY) used during interactions with conspecifics. Next, we compared the degree of manual laterality involved in both types of signals in relation to three categories of factors previously found to modulate gestural laterality (e.g. Prieur, 2015). These three categories are as follows: interactional context components (visual fields used by both signaller and recipient