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On the Origins of Human Handedness and Language: A Comparative Review of Hand Preferences for Bimanual Coordinated Actions and Gestural Communication in Nonhuman Primates

ABSTRACT: Within the evolutionary framework about the origin of human handedness and hemispheric specialization for language, the question of expression of population-level manual biases in nonhuman primates and their potential continuities with humans remains controversial. Nevertheless, there is a growing body of evidence showing consistent population-level handedness particularly for complex manual behaviors in both monkeys and apes. In the present article, within a large comparative approach among primates, we will review our contribution to the field and the handedness literature related to two particular sophisticated manual behaviors regarding their potential and specific implications for the origins of hemispheric specialization in humans: bimanual coordinated actions and gestural communication. Whereas bimanual coordinated actions seem to elicit predominance of left-handedness in arboreal primates and of right-handedness in terrestrial primates, all handedness studies that have investigated gestural communication in several primate species have reported stronger degree of population-level right-handedness compared to noncommunicative actions. Communicative gestures and bimanual actions seem to affect differently manual asymmetries in both human and nonhuman primates and to be related to different lateralized brain substrates. We will discuss (1) how the data of hand preferences for bimanual coordinated actions highlight the role of ecological factors in the evolution of handedness and provide additional support the postural origin theory of handedness proposed by MacNeilage [MacNeilage [2007]. Present status of the postural origins theory. In W. D. Hopkins (Ed.), *The evolution of hemispheric specialization in primates* (pp. 59–91). London: Elsevier/Academic Press] and (2) the hypothesis that the emergence of gestural communication might have affected lateralization in our ancestor and may constitute the precursors of the hemispheric specialization for language. © 2013 Wiley Periodicals, Inc. *Dev Psychobiol* 55: 637–650, 2013.

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INTRODUCTION

Almost 90% of humans are right-handed for manipulative actions and this bias remains quite consistent across cultures (Annett, 1985; Marchant, McGrew, & Eibl-Eibesfeldt, 1995; Porac & Coren, 1981; Raymond & Pontier, 2004). In addition, a large majority of humans (including both right-handed and left-handed for manipulation) shows a left-hemispheric dominance for the control of linguistic functions (e.g., Knecht et al., 2000). Hand preferences for gestural communication (including signing in deaf people, co-speech gestures or pointing gestures in children) may constitute a better predictor than hand preferences for manipulative functions of the location of the dominant (contralateral) hemisphere for language (Bellugi, 1991; Kimura, 1993); i.e., the left hemisphere for the right-hand bias for gestures, and the right hemisphere for a left-hand bias.

In contrast to humans, a considerable number of studies in animals has reported a lack of limb preference for motor actions at a population level in many species (see Hook, 2004 for a review) including nonprimate mammals (e.g., tree shrews: Joly, Scheumann, & Zimmermann, 2012), prosimians (e.g., mouse lemur: Leliveld, Scheumann, & Zimmermann, 2008) and other nonhuman primates (see Papademetriou, Sheu, & Michel, 2005 for a review). Handedness and hemispheric specialization at a population-level have then been historically considered as one of the hallmarks of human evolution (e.g., Crow, 2004; Ettlinger, 1988; Warren, 1980). This latter view is now challenged by a growing body of evidence of limb and neuroanatomical population-level asymmetries in a host of vertebrates. For example, population-level limb preferences for motor actions have been found in chickens, mice, rats, cats, dogs, some species of toads, of African parrots and of Australian birds (see for reviews: Joly et al., 2012; Rogers & Andrew, 2002; Hook, 2004; Vallortigara, Cinzia, & Sovrano, 2011; Vallortigara & Rogers, 2005) as well as some species of prosimians including Senegal bushbaby and several species of Lemur (reviewed in Watson & Hanbury, 2007). Given the closer phylogenetical proximity of nonhuman primates with humans, monkeys and great apes are models that have preferentially been considered for investigating the factors that drive the expression and the evolution of handedness and its potential continuity with humans (e.g., Hopkins, 2007). There were some reports of predominance of right-handedness particularly in large samples of captive chimpanzees—our closest relative—for specific complex tasks such as bimanual feeding, coordinated bimanual actions, bipedal reaching, throwing, gestural communication, and so forth (for review, see Hopkins, 2006a,

2007). The rest of the literature revealed various patterns of handedness that can differ within and between the species, but showed also a large variability concerning the method of data collection, the environment of the subjects (e.g., captive vs. wild subjects), the manual behaviors observed or the experimental manual tasks used for assessing hand preferences (see Hopkins, 2007; McGrew & Marchant, 1997; Papademetriou et al., 2005 for reviews). It remains then quite difficult to identify which factors drive the expression of handedness and how to interpret these inconsistent results with respect to evolutionary models of handedness (e.g., Crow, 2004; Hopkins, 2004; MacNeilage, Studdert-Kennedy, & Lindblom, 1987).

In this present article, through a large comparative approach among primates, we will try to identify these potential factors and thus to reconcile these divergent findings in focusing on specific relevant manual behaviors. We will first present some consistencies of finding across the literature that underline the critical effect of the type of tasks on the patterns of hand preferences in primates. In a second and a third section, we will then focus on the comparison of findings found in various primate species for two distinct sophisticated manual behaviors - bimanual coordinated actions and gestural communication—and thus demonstrate how these particular behaviors might have specific and differential significance in terms of expression and evolution of hemispheric specialization. These comparative reviews will allow us discussing the potential prerequisites of the predominance of right-handedness in humans and hemispheric specialization for language from our common ancestor.

Effect of the Task Demand on Hand Preferences

There is a large set of published studies showing that the variations of the task demands and task complexity have an effect on the direction, strength, or consistency of hand preferences in almost all primate species including New World monkeys, Old World monkeys, Great apes and even humans (see Tab. 1 for some examples of reference per species). Regarding this task effect, investigating potential continuities/discontinuities between primate species (including humans) within a comparative approach on handedness requires standardizing procedures of data collection across studies focusing on similar relevant manual tasks. In most of the studies summarized in Table 1, the distinction between unimanual and bimanual coordinated behaviors has been critical for underlying such task complexity effects on handedness at both individual and population-level. Indeed some of these studies have investigated hand preferences for both unimanual and bimanual behaviors in the same samples

Table 1. Examples of Studies Reporting Effect of the Complexity of the Task on the Expression of Hand Preference

	Scientific Name	Habitat	Manual Tasks	Effect on Handedness	Refs.
Prosimians					
Sifaka	<i>Propithecus</i> species	Captive	Postural support, leaf eating	Direction	Milliken, Ferra, Kraiter, and Ross (2005)
Aye-aye	<i>Daubentonia madagascariensis</i>	Captive	Holding food, tap, digit feed	Strength	Feistner, Price, and Milliken (1994)
Indri	<i>Indri indri</i>	Wild	Postural support, leaf eating	Direction	Rigamonti, Spiezio, Poli, and Fazio (2005)
Ruffed lemur	<i>Varecia variegata variegata</i>	Captive	Multi-postural unimanual reach	Strength	Forsythe, Milliken, Stafford, and Ward (1988)
New World Monkeys					
Squirrel monkey	<i>Saimiri sciureus</i>	Captive	Multi-postural unimanual reach, catch Multi-postural unimanual reach	Direction Strength and direction	King and Landau (1993) Laska (1996)
Tufted capuchin monkey	<i>Cebus apella</i>	Captive	Unimanual reach, bimanual tube Multi-unimanual actions, bimanual task	Direction Strength and direction	Meguerritchian et al. (2012a) Fragaszy and Mitchell (1990)
White-faced capuchin monkey	<i>Cebus capucinus</i>	Captive	Unimanual reach, sponging tool Multi-unimanual tasks, probing tools	Strength Strength	Westergaard and Suomi (1993) Anderson, Degiorgio, Lamarque, and Fagot (1996)
Old World Monkeys					
Guinea baboon	<i>Papio Papio</i>	Captive	Multi-unimanual reach, bimanual tube	Strength	Spinozzi et al. (1998)
Olive baboon	<i>Papio anubis</i>	Captive	Multi-unimanual reach, bimanual tube	Strength	Lilak and Phillips (2008)
Rhesus macaque	<i>Macaca mulatta</i>	Captive	Unimanual reach, bimanual tube	Strength	Meunier and Vauclair (2007)
Japanese macaque	<i>Macaca fuscata</i>	Wild	Unimanual reach, multi-bimanual tasks	Direction	Fagot and Vauclair (1988b)
Sichuan snub-nosed monkey	<i>Rhinopithecus roxellana</i>	Wild	Unimanual reach, bimanual tube Quadrupedal and bipedal reaching	Strength and direction Strength and direction	Vauclair et al. (2005) Westergaard, Kuhn, and Suomi (1998a)
Vervet monkey	<i>Chlorocebus pygerythrus</i>	Wild	Unimanual and bimanual stone handling Unimanual and bimanual grooming	Strength Strength and direction	Leca et al. (2010) Zhao et al. (2010)
Red-capped mangabey	<i>Cercocebus torquatus</i>	Captive	Unimanual and bimanual food processing Multi-unimanual and bimanual tasks	Strength Strength	Harrison and Byrne (2000) Blois-Heulin et al. (2006)
Grey-cheeked mangabey	<i>Lophocebus albigena</i>	Captive	Multi-unimanual and bimanual tasks Multi-unimanual and bimanual tasks	Strength and direction Strength and direction	Laurence et al. (2011) Blois-Heulin et al. (2007)
De Brazza's monkey	<i>Cercopithecus neglectus</i>	Captive	Multi-unimanual and bimanual tasks	Strength	Trouillard and Blois-Heulin (2005)

(Continued)

Table 1. (Continued)

	Scientific Name	Habitat	Manual Tasks	Effect on Handedness	Refs.
Campbell's monkey	<i>Cercopithecus campbelli</i>	Captive	Multi-unimanual and bimanual tasks Multi-unimanual and bimanual tasks	Strength and direction Strength	Schwitzer et al. (2007) Chapelain, Bec, and Blois-Heulin (2006)
Great apes					
Orangutan	<i>Pongo pygmaeus</i>	Captive	Uni- and bimanual eating, self-touch Uni- and bimanual eating, multi-tool use	Strength and direction Strength	Rogers and Kaplan (1996) O'Malley and McGrew (2006)
Mountain gorilla	<i>Gorilla beringei beringei</i>	Wild	Unimanual and bimanual food processing	Strength and direction	Byrne and Byrne (1991)
Western lowland gorilla	<i>Gorilla gorilla gorilla</i>	Captive	Unimanual reach, multi-bimanual tasks Unimanual reach, bimanual feeding	Strength and direction Strength and direction Strength	Fagot and Vauclair (1988a) Meguerditchian et al. (2010a) Lambert (2012)
Bonobo	<i>Pan paniscus</i>	Captive	Multi-unimanual tasks, bimanual feeding	Direction	Hopkins and De Waal (1995)
Chimpanzee	<i>Pan troglodytes</i>	Wild captive Wild	Multi-unimanual actions, tool anvil use Multi-unimanual and bimanual tasks	Strength Strength and direction	Boesch (1991) Colell, Segarra, and Sabater-Pi (1995)
		Captive	Tool anvil use	Strength	McGrew, Marchant, Wrangham, and Kleinm (1999)
		Captive	Unimanual and bimanual tool termite fish	Direction	Hopkins and Rabinowitz (1997)
		Captive	Multi-unimanual and bimanual tasks	Strength and direction	Wesley et al. (2002)
			Unimanual and bimanual grooming	Direction	Hopkins et al. (2007)
			Unimanual reach, bimanual tube	Strength	Llorente et al. (2009)
Human	<i>Homo sapiens sapiens</i>	/	Questionnaires—multi-tasks Multi-tasks, tool use Multi-unimanual and bimanual tasks Multi-unimanual and bimanual tasks	Strength Strength Strength Strength and direction	Steenhuis and Bryden (1989) Marchant et al. (1995) Fagard and Marks (2000) Potier et al. (in press)

of subjects. It turned out that, in humans (Fagard & Marks, 2000), in wild and captive gorillas (Byrne & Byrne, 1991; Meguerditchian, Calcutt, Lonsdorf, Ross, & Hopkins, 2010a), in captive chimpanzees (Hopkins & Rabinowitz, 1997; Hopkins, Russell, Remkus, Freeman, & Schapiro, 2007; Llorente, Mosquera, & Fabre, 2009; Wesley et al., 2002), in captive baboons (Vauclair, Meguerditchian, & Hopkins, 2005), in captive De Brazza's monkeys (Schweitzer, Bec, & Blois-Heulin, 2007), in wild Sichuan snub-nosed monkeys (Zhao, Gao, & Li, 2010), simple unimanual behaviors showed an absence or a lower degree of population-level handedness than bimanual behaviors which elicited significant manual biases at a population-level. These collective findings might suggest that bimanual coordinated behaviors are more reliable tasks than unimanual tasks to investigate and measure hand preferences in primates. In fact, according to "the task complexity" model proposed by Fagot & Vauclair (1991), low-level tasks such as simple unimanual reaching are less sensitive to detect individual handedness and thus poor measures for evaluating manual biases at a population-level, whereas high-level tasks such as bimanual coordination would be a better predictor of hemispheric specialization of the brain (see Rogers, 2009). The efforts for homogenizing the methodology and the manual tasks used for assessing hand preferences across human and nonhuman primates have been pursued, especially with respect to the distinction between unimanual (e.g., Meunier, Blois-Heulin, & Vauclair, 2011) versus bimanual tasks (e.g., Hopkins et al., 2011; Potier, Meguerditchian, & Fagard, in press) and also between noncommunicative actions versus gestural communication (e.g., Cochet & Vauclair, 2010b; Meguerditchian, Cochet, & Vauclair, 2011a; Meunier, Fagard, & Vauclair, 2012). Other complex motor tasks showing also an effect on hand preferences have been investigated particularly in chimpanzees such as throwing, using a variety of tools, bipedal reaching or bipedal tool use (see Hopkins, Tagliabata, Leavens, Russell, & Schapiro, 2010, for a recent review) but have not been included in the present comparative review. Indeed, the specificity of these tasks did not favor generalization of data collection in other species and reduced thus the related comparative framework in contrast to bimanual coordinated actions and communicative gestures. In the next sections, we will then focus on these latter specific tasks that have been investigated and generalized in many primate species.

Hand Preferences for Bimanual Coordinated Actions

Bimanual coordination consists of engaging the two hands in an asymmetrical and coordinated manner: while

one hand holds or maintains an item, the other hand (the "dominant" hand, considered as the most active) is used to manipulate the item (see Fig. 1). In some studies, bimanual behaviors have been experimentally induced by the introduction of "the tube task," initially designed by Hopkins (1995) for testing chimpanzees. This task consists, for the subject, of holding a PVC tube with one hand and removing the food inside the tube (e.g., peanut butter) with the fingers of the other "dominant" hand. The bimanual tube task has been successfully replicated in many captive primate species such as capuchin monkeys, squirrel monkeys, baboons, De Brazza's monkeys, mangabeys, Sichuan snub-nosed monkeys, rhesus macaques, bonobos, gorillas, orangutans, and chimpanzees (Bennett, Suomi, & Hopkins, 2008; Blois-Heulin, Guitton, Nedellec-Bienvenue, Ropars, & Vallet, 2006; Blois-Heulin, Bernard, & Bec, 2007; Chapelain & Hogervorst, 2009; Chapelain, Hogervorst, Mbonzo, & Hopkins, 2011; Hopkins, Stoinski, Lukas, Ross, & Wesley, 2003; Hopkins, Wesley, Izard, Hook, & Schapiro, 2004; Hopkins et al., 2011; Laurence, Wallez, & Blois-Heulin, 2011; Lilak & Phillips, 2008; Llorente et al., 2009, 2011; Meguerditchian, Donnot, Molesti, & Vauclair, 2012a; Meunier & Vauclair, 2007; Schweitzer et al., 2007; Spinozzi, Castorina, & Truppa, 1998; Vauclair et al., 2005; Westergaard & Suomi, 1996; Westergaard, Chamoux, & Suomi, 1997; Zhao, Hopkins, & Li, 2012).

Interestingly, contrary to simple unimanual reaching, such a bimanual coordinated tube task has been shown to elicit hand preferences that are related to neuroanatomical asymmetries within the primary motor cortex in both captive chimpanzees (Hopkins & Cantalupo, 2004) and capuchin monkeys (Phillips & Sherwood, 2005). Other researchers have used a naturalistic approach on hand preferences for bimanual actions in focusing on the spontaneous expression of similar bimanual coordinated behaviors such as bimanual feeding, bimanual grooming, bimanual food processing, bimanual tool use, or bimanual stone handling (e.g., Byrne & Byrne, 1991; Corp & Byrne, 2004; Harrison & Byrne, 2000; Hopkins & Rabinowitz, 1997; Hopkins et al., 2007; Lambert, 2012; Leca, Gunst, & Huffman, 2010; Meguerditchian et al., 2010a; Zhao et al., 2010).

Within an evolutionary framework on human handedness, some studies on bimanual coordinated actions in Old world monkeys, great apes and humans, using consistent methods of data collection, might suggest a continuity with human handedness. These studies have found significant and similar predominance of right-handedness for bimanual behaviors in captive baboons (Vauclair et al., 2005), in captive mother-reared female rhesus macaques (Bennett et al., 2008), in different large groups of captive chimpanzees (Hopkins, 1995;

Hopkins et al., 2004, 2011; Llorente et al., 2011), in captive adult bonobos (Chapelain et al., 2011), in both wild and captive gorillas (Byrne & Byrne, 1991; Hopkins et al., 2003, 2011; Meguerditchian et al., 2010a) and in human infants (Fagard & Marks, 2000; Potier et al., in press). Thus, it has been proposed that bimanual coordinated activities in our ancestors may have played a major role for the evolution of human handedness (e.g., Hopkins, 2006a,b; Meguerditchian et al., 2010a). Specifically, right-lateralization of hand use may have been selected in our ancestors for such bimanual actions rather than exclusively for tool use (Bradshaw & Rogers, 1993) and may thus constitute an ideal prerequisite for human hemispheric specialization.

However, this view has been challenged by some reports of predominance of left-handedness for similar bimanual coordinated behaviors in other primate species including great apes, Old World and New world monkeys: captive orangutans (Hopkins et al., 2003, 2011), captive Brazza's monkeys (Schweitzer et al., 2007), captive male red-capped mangabeys (Laurence et al., 2011), wild Sichuan snub-nosed monkeys (Zhao et al., 2010, 2012), and captive male squirrel monkeys (Meguerditchian et al., 2012a). Such divergent directions of population-level handedness across primate species might be reconciled if we consider the variations of the postural and biomechanical factors related to the ecology of the species (i.e., arboreal vs. terrestrial species). Indeed, according to the postural origins theory of handedness proposed by MacNeilage et al. (1987); see also MacNeilage (2007) for a recent review, whether primate species are arboreal or terrestrial may constitute another major factor in addition to the complexity of the

manual behaviors for explaining the phylogenetic distribution of population-level handedness among primate lineages. Then, in an updated view of this theory, arboreal species (such as orangutans, De Brazza's, squirrel and Sichuan snub-nosed monkeys) preferentially developed right-handedness for supporting the body in the trees while the left hand has been favored for manipulative actions, which can be detected by bimanual coordinated activities. By contrast, due to the liberation of the hands from the biomechanical constraints of living in the trees, more terrestrial primates such as chimpanzees (semi-terrestrial), bonobos, baboons, macaques, and gorillas, would have developed a right-handedness predominance for bimanual manipulative tasks (see Fig. 2).

Nevertheless, some studies that investigated hand preferences for bimanual coordinated tasks in other primate species revealed no manual bias at a population-level and are then not strictly consistent with this theory (in vervet monkeys: Harrison & Byrne, 2000; in bonobos: Chapelain & Hogervorst, 2009; Chapelain et al., 2011; Hopkins et al., 2011; in Rhesus macaques: Bennett et al., 2008; in capuchin monkeys: Lilak & Phillips, 2008; Meunier & Vauclair, 2007; Phillips & Sherwood, 2005, 2007; Westergaard & Suomi, 1996, but see Spinozzi et al., 1998 for a report of a predominance of right-handedness). However, those studies have revealed the involvement of complementary factors (e.g., sample-size, sex, rearing history effects, age-effect), other than the task-complexity factor, for reconciling the divergent findings in the primate handedness literature. For instance in bonobos and macaques, only adult bonobos (Chapelain et al., 2011) and female mother-reared rhesus macaques (Bennett et al., 2008) showed significant degree of right-hand



FIGURE 1 Examples of bimanual coordinated behaviors in primates: bimanual tube task in squirrel monkeys (Meguerditchian et al., 2012a), in olive baboons (Vauclair et al., 2005), bimanual coordinated fine grip feeding in gorillas (Meguerditchian et al., 2010a), a bimanual coordinated fine grip task in human infants (Potier et al., in press).

bias for the bimanual tube task and thus consistency with the postural origin theory of handedness. In another example, there are some consistent findings of a sex effect on the pattern of hand preferences for bimanual coordinated actions. A similar difference of direction and/or degree of group-level handedness have been reported between males and females in wild chimpanzees (Corp & Byrne, 2004), in rehabilitated orangutans (Rogers & Kaplan, 1996), somewhat in captive gorillas (Meguerditchian et al., 2010a), in Brazza's monkeys (Schweitzer et al., 2007), in capuchins monkeys (Spinozzi et al., 1998; Meunier & Vauclair, 2007; Phillips & Sherwood, 2007) and in squirrel monkeys (Meguerditchian et al., 2012a). In all these latter studies, females turned out to be more right-handed than males at a group-level. The reasons of the sex difference for bimanual handedness are unclear. However, the sex effect on hand preference is inconsistent across the remaining literature. A large set of data in various primate species failed to show any

sex effect on the patterns of handedness (see for a review: McGrew & Marchant, 1997).

Right-Handedness for Gestural Communication

Right-hand dominance in humans is not only associated with manipulation but also with communicative gestures, including signing in deaf people (Grossi, Semenza, Corazza, & Volterra, 1996; Vaid, Bellugi, & Poizner, 1989), manual movements when people are talking (Kimura, 1973), and pointing gestures by infants (e.g., Blake, O'Rourke, & Borzellino, 1994). In these latter studies, the authors have reported that the degree of predominance of right-handedness for pointing tends to increase during speech development (see also Cochet & Vauclair, 2010a). Interestingly, signing, pointing or symbolic actions have not only been shown to play a role in the development of language (Iverson & Goldin-Meadow, 2005) but also elicited a stronger

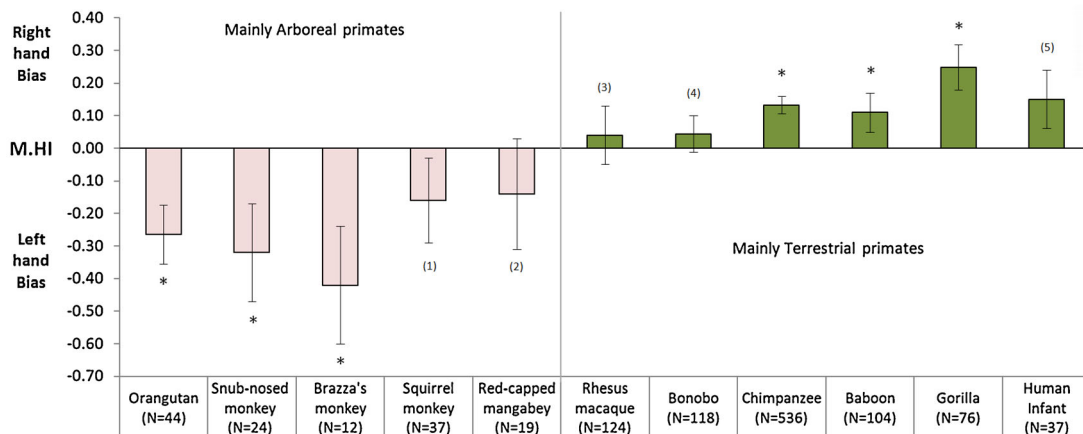


FIGURE 2 Comparison of the degrees of population-level handedness (MHI) for the bimanual coordinated tube task between arboreal and terrestrial primates. Mainly arboreal primates: Orangutans (Hopkins et al., 2011); Snub-nosed monkeys (Zhao et al., 2010); De Brazza's monkeys (Schweitzer et al., 2007); Squirrel monkeys (Meguerditchian et al., 2012a); and Red-Capped Mangabeys (Laurence et al., 2011). Mainly terrestrial primates: Rhesus macaques (Bennett et al., 2008); Baboons (Vauclair et al., 2005); Bonobos, Chimpanzees and gorillas (Hopkins et al., 2011) and human infants from 12-months to 20-months-olds (Potier et al., in press). MHI scores \pm SE. The error bar represents the SE around the MHI score. Asterisks indicate that the MHI score differed significantly from zero. $*p < 0.05$. (1) Only male squirrel monkeys showed population-level left-handedness that approaches conventional level of significance ($p = 0.068$), (2) a left bias which is significant only in male red-capped mangabeys; (3) Mother-reared female rhesus macaques and (4) adult bonobos showed significant predominance of right-handedness (Chapelain et al., 2011); (5) human infants (aged from 12 to 20 months) showed significant predominance of right-handedness for bimanual coordinated actions related to fine precision grip only. Note that capuchin monkeys *Cebus* (arboreal New World primates) showed generally no population-level handedness in the literature for the tube task. This species is not represented in this figure since its results are dispersed in different studies and are then difficult to combine and represent into a single MHI of the overall sample without having the raw data.

degree of predominance of right-handedness than noncommunicative manual actions in young children (Bates, O'Connell, Vaid, Sledge, & Oakes, 1986; Blake et al., 1994; Bonvillian, Richards, & Dooley, 1997; Cochet & Vauclair, 2010b; Jacquet, Esseily, Rider, & Fagard, 2012; Vauclair & Imbault, 2009). These findings might indicate that hand preferences for communicative gestures and noncommunicative actions might develop relatively independently (see Jacquet et al., 2012) and might favor a greater involvement of the left hemisphere for communicative signaling. This hypothesis is consistent (1) with the report of "speech-like" brain activations of Broca's area in the left hemisphere for sign production in deaf people (Corina, San Jose-Robertson, Guillemin, High, & Braun, 2003; Emmorey, Mehta, & Grabowski, 2007) and (2) with the notion of a single integrated communication system within the left cerebral hemisphere for both vocal articulated language and gestural communication (e.g., Bernardis, Bello, Pettenati, Stefanini, & Gentilucci, 2008; Bernardis & Gentilucci, 2006; Gentilucci & Dalla Volta, 2008; Kimura, 1993; McNeill, 1992; Willems, Özyürek, & Hagoort, 2007).

Regarding these links between gestures, language and brain specialization in humans, studying hand preferences for gestural communication in our primate cousins within a comparative framework might potentially have a great interest for investigating the prerequisites of left-hemispheric specialization for language. It is well known that nonhuman primates and particularly great apes produce intentional manual gestures to communicate with social partners in various social contexts (e.g., Call & Tomasello, 2007). In other words, are nonhuman primates predominantly right-handed for gestural communication?

The first studies of this domain have only concerned few subjects of great apes that were trained to sign such as the gorilla Koko (Shafer, 1988), the orangutan Chantek (Miles, 1990) and several chimpanzees (Krause & Fouts, 1997; Morris, Hopkins, & Bolser-Gilmore, 1993; Steiner, 1990). However, these latter samples were way too small to infer representative population level hand preferences. To our knowledge, investigations of hand preferences for gestures in larger samples size have only been investigated in captive chimpanzees, bonobos, gorillas and baboons (see Hopkins et al., 2012 for a recent review). All of these studies have reported similar and pronounced degree of population-level right-handedness for different categories of gestures, including (1) communicative clapping in a sample of 94 captive chimpanzees (Meguerditchian, Gardner, Schapiro, & Hopkins, 2012b) and both intraspecific (e.g., hand slap, extended arm) and human-directed gestures (e.g., food begging extended arm) in both

chimpanzees (sample-size from 70 to 227 subjects: Hopkins & Cantero, 2003; Hopkins et al., 2005; Meguerditchian, Vauclair, & Hopkins, 2010b) and olive baboons (from 33 to 162 subjects: Meguerditchian, Molesti, & Vauclair, 2011b; Meguerditchian & Vauclair, 2006, 2009). Similar, though less well documented, evidence of asymmetries in undistinguished types of gestures have also been reported in a sample of 18 gorillas (Shafer, 1987, see also Shafer, 1993) and in 51 captive bonobos (Hopkins & Vauclair, 2012, resulting from the combined samples of three different studies: Harrison & Nystrom, 2008; Hopkins & De Waal, 1995; Shafer, 1997). Moreover, in baboons and chimpanzees, these patterns of hand preferences for gestural communication have been shown to be very consistent across time in test-retested subjects but also across different samples of subjects (Meguerditchian et al., 2010b, 2011b, 2012b).

Interestingly, as demonstrated in many human infants' studies (see first paragraph of the Right-Handedness for Gestural Communication Section), the degree of right-handedness for gestural communication in these primate species, except in gorillas (see Fig. 3), turns out to be much more pronounced than for noncommunicative motor actions, such as the bimanual coordinated tube task that have also revealed a predominance of right-handedness in baboons, gorillas, chimpanzees and in adult bonobos (see the Hand Preferences

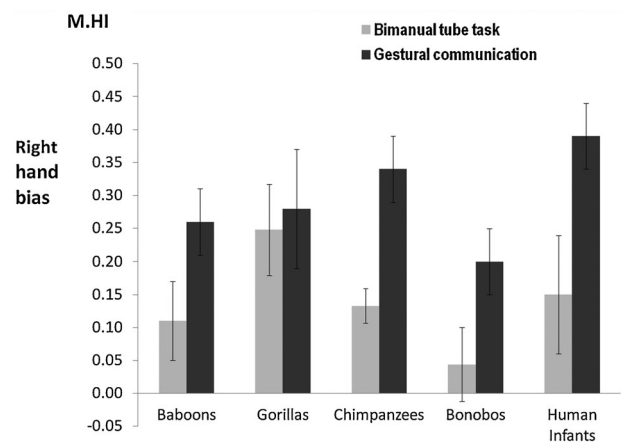


FIGURE 3 Degrees of population-level right-handedness (MHI) for species-typical communicative gestures in 162 baboons (Meguerditchian et al., 2011b), in 18 gorillas (Shafer, 1987), in 70 chimpanzees (Meguerditchian et al., 2010b), in 51 bonobos (Hopkins & Vauclair, 2012) and whole-hand pointing in 37 human infants (Cochet & Vauclair, 2010b) compared with the bimanual coordinated task. MHI scores \pm SE. The error bar represents the SE around the MHI score. Asterisks indicate that the MHI score differed significantly from zero. $*p < 0.05$. The positive MHI values all indicate bias toward right-handedness.

for Bimanual Coordinated Actions Section). In addition, among test and re-tested subjects in both baboons and chimpanzees, whereas individual hand preferences are consistent across different types of gestures, no correlation of individual hand preferences was found between bimanual coordinated actions and any types of communicative gestures (Meguerditchian & Vauclair, 2006, 2009; Meguerditchian et al., 2010b, 2012b). To sum up, different communicative gestures in both baboons and chimpanzees showed a similar pattern of hand preferences with each other and may thus share partially the same cerebral system, whereas noncommunicative actions exhibited different patterns of handedness in comparison with manual communication.

Collectively, these findings support the hypothesis of a continuity between baboons, gorillas, bonobos, and chimpanzees concerning left hemispheric specialization for gestural communication. Within an evolutionary perspective, we might suggest the existence of a specific left-hemispheric lateralized system involved in the production of communicative gestures that may differ from the system involved in purely motor functions. It might then be hypothesized that such a communicative lateralized system in nonhuman primates constitutes an ideal prerequisite of the cerebral substrate for human language in the common ancestor of these species at least 30–40 million years ago (Meguerditchian & Vauclair, 2008; Meguerditchian et al., 2011a).

Anatomical brain imaging studies in chimpanzees are consistent with this hypothesis. Being left- or right-handed for food begging gestures (Hopkins & Nir, 2010; Tagliabata, Cantalupo, & Hopkins, 2006) or communicative clapping (Meguerditchian et al., 2012b) has been shown to affect the neuroanatomical asymmetries in cerebral regions (the inferior frontal gyrus and the planum temporale) that are known to overlap key cerebral regions of language in humans (i.e., Broca and Wernicke areas respectively). In contrast, hand preferences for bimanual coordinated actions in chimpanzees are related only to neuroanatomical asymmetries in the primary motor cortex but not to any of the homologous language areas (Hopkins & Cantalupo, 2004).

DISCUSSION

The reviewed collective findings in primates highlight the special but different significance of both bimanual coordinated actions and gestural communication in terms of handedness and potentially its related hemispheric specialization. This comparative approach clearly suggests some continuities between humans and some nonhuman primate species concerning handed-

ness and hemispheric specialization of the brain. However, the origin of human handedness might result from two different and independent evolutionary paths if we consider the distinction between gestural communication and bimanual coordinated actions. Specifically, for bimanual behaviors, in agreement with the postural origins of handedness proposed by MacNeilage (2007), a continuity of predominance of right-handedness for manipulation with humans seems to extend in all terrestrial primates only, but not in arboreal species. As suggested by Wundrum (1986), the ability to coordinate the hands in an asymmetric manner may be an important requisite skill for the emergence of right-handedness in early hominids and in our terrestrial ancestors. From this view, right-lateralization of hand use may have been selected in our terrestrial ancestors for such bimanual actions rather than tool use exclusively (Bradshaw & Rogers, 1993) and may constitute an ideal prerequisite for human hemispheric specialization related to motor actions. It is important to emphasize that an efficient asymmetric coordination of the hands to perform complex manipulations is not a necessary condition for the emergence of population-level handedness (see Hopkins, 2007; Vallortigara & Rogers, 2005). Indeed, asymmetric coordination of the hands can provide the needed adaptive functions to individual subjects without the need for all the individuals to have the same hand preference.

Concerning gestural communication, evidence of specific and pronounced patterns of right-handedness in different terrestrial primates species might be related to a specific left-hemispheric communicative system, that is different from the one involved in bimanual coordinated actions. Given the links between gestures and language in the human brain, these data in congruence with brain imaging studies in chimpanzees support the idea that the manual asymmetries for communicative behaviors might be specifically related to the origins of left-hemispheric specialization for language. We have argued that lateralization for language may have thus evolved from a gestural system of communication, lateralized in the left cerebral hemisphere in the common ancestor of baboons, gorillas, bonobos and chimpanzees at least 30–40 million years ago (e.g., Meguerditchian & Vauclair, 2006).

However, some authors remain skeptical concerning the claims of population-level handedness in nonhuman primates on both methodological and theoretical grounds (Cashmore, Uomini, & Chapelain, 2008; Crow, 2004; McGrew & Marchant, 1997; Palmer, 2002, 2003; Uomini, 2009). For instance, some authors have suggested that population-level right-handedness in chimpanzees is only found in captive conditions but is absent in wild apes, suggesting that right-handedness in

captive chimpanzees is an artifact of being raised in a human right-handed environment rather than a species-typical trait (e.g., McGrew & Marchant, 1997). When looking closer to the sets of data, it turns out that most of the available studies in wild populations of chimpanzees that have failed to report population-level manual biases have largely focused on simple measures of hand use, such as unimanual reaching for food (Marchant & McGrew, 1996; McGrew & Marchant, 1997, 2001). We have seen in the Effect of the Task Demand on Hand Preferences Section that unimanual tasks have been shown to elicit inconsistent findings across the literature and to be a poor detector of hand preferences (see the Effect of the Task Demand on Hand Preferences Section and Papademetriou et al., 2005), even in captive or “highly humanized” chimpanzees (e.g., Hopkins, 1993; Llorente et al., 2009). Given the effect of the type of task on hand preferences and the reports of population-level handedness in the only two available studies that have investigated bimanual coordinated behaviors in wild great apes (gorillas: Byrne & Byrne, 1991; chimpanzees: Corp & Byrne, 2004), we have some reasons to believe that the distinction between low level tasks (e.g., unimanual reaching) versus high-level tasks (e.g., bimanual coordinated action) may be a better factor for reconciling the variations of findings in the handedness literature rather than the distinction between wild and captive populations of primates (Hopkins, 2006b). However, there is unfortunately very little research of hand preferences for both bimanual coordinated and gestural communication in wild nonhuman primates. This research field is critical to investigate the potential continuities/discontinuities of handedness between human and nonhuman primates, and these two specific behaviors might be a fruitful area of future handedness investigations in populations of primates living in their natural environment.

In conclusion, these joint findings still highlight how difficult it is to determine the factors that would explain the phylogeny of the distribution of hand preferences among primate lineages. Whether the effects of sex, of rearing history and of age on manual biases are not entirely consistent across the studies in nonhuman primates and might depend on the species, the contrasts of hand preferences (1) between terrestrial versus arboreal primates, (2) between unimanual versus bimanual coordinated behaviors, and (3) between non-communicative versus communicative gestures seem to be consistent across the literature for explaining the divergent patterns of handedness reported between and within nonhuman primate species. Within a large comparative approach, this kind of investigations including large samples of monkeys and apes is still

needed for understanding the expression of handedness in primates, the origins of human handedness and hemispheric specialization for language.

NOTES

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