

CHAPTER 10

Human Handedness

“It seems that humans routinely use a single ‘preferred’ hand to play the leading role in tool use, and that nearly nine times out of ten the choice is of the right hand”
[Steele and Uomini, 2005, p. 234].

“The exact mechanisms that selected for increased preferential use of one hand or another remain unclear”
[Hopkins, 2006, p. 554].

Introduction. If the bipedal use of weapons provided advantages to early hominins who used this behavior in conflicts over scarce resources, natural selection would have acted to incorporate into the hominin genome inherited variations that led to its improvement. Handedness, which means one of the two hands is preferably used, may be an example of this effect. About 90% of modern humans are right-handed and the remaining 10% are left-handed [Coren, 1993; McGrew and Marchant, 1997]. There are some geographical differences in this ratio; these may be cultural or genetic in origin [Raymond and Pontier 2004, Faurie, et al., 2005]. Ethological studies also reveal variability [Marchant, et al., 1995, Marchant and McGrew, 1998]. However, all human societies, whatever the method of investigation, show right-hand predominance. There are no populations with anything close to a majority of left-handers.

Is human handedness inherited or learned? There is a genetic component, but it is complex and no simple genetic model seems possible [Annett, 1973; McManus, 1991; Corballis, 1991; Coren, 1993; Raymond and Pontier, 2004]. Right- or left-handedness runs in families, it develops in all children without teaching, and in all ethnic and geographically dispersed populations where it has been studied. Prehistoric populations also show a dominance of right-handed individuals. Nevertheless, a minority of left-handers persists. Natural selection must be maintaining this lateral bias; otherwise, selection for right-handedness would have eliminated it [Llaurens, et al., 2009].

Handedness emerges from asymmetrical neural organization of human motor systems [Sainberg, 2002, 2005; Bagesteiro and Sainburg 2002]. It appears early in childhood, with a tendency to use a preferred hand beginning to appear by about two years of age. After four years, right-handedness predominates [Halverson, 1940; Gesell and Ames, 1947; Annett, 1970; Rat-Fischer, et al., 2012]. During development of over- hand throwing, the preferred arm always outperforms the other one [Teixeira and Gasparetto, 2002].

Is handedness a unique human characteristic? “Historically, population-level handedness has been considered a hallmark of human evolution” [Hopkins, 2006, p. 538]. This is the received view—that handedness is a unique trait which developed in the hominin lineage [Wile, 1934; Annett, 1970; Corballis, 1991; Coren, 1993]. According to McGrew and Marchant [1997, p. 226] “the biggest, simplest conclusion is that there is yet no compelling evidence that nonhuman primates are lateralized at the population level” for any species, task or setting. Nonhuman primate hand function therefore seemed unable to provide a model for the evolution of the pronounced handedness of modern humans.

Some recent studies have reported evidence that certain anthropoid ape populations lack a preferred hand, lending support to the view that humans alone exhibit this property. Corp and Byrne [2004] found no population-level hand preference in wild chimpanzees. Fletcher and Weghorst [2005], who studied 28 captive chimpanzees, found little evidence of hand specialization. The subjects mainly used either hand for tool use (yoghurt fishing). They observed either left-handedness or no preference. Humle and Matsuzawa [2009] studied four tool-using behaviors in wild chimpanzees. Nut-cracking, the most cognitively challenging, yielded the greatest incidence of handedness, but no directional preference. Chapelain and Hogervorts [2009] used the “tube task” to study handedness in 29 captive bonobos. (In this task the ape must use one hand to hold a tube so that a tasty treat can be retrieved by the fingers of the other, preferred hand). The frequency of unilaterality was 11 right-handed, 15 left-handed and 3 no preference. The authors conjectured that hand preferences in non-human primates are about equally right and left handed. Harrison and Nystrom [2010] examined handedness in 22 captive gorillas by noting their preferences in a range of behaviors in their daily routine. Ten showed no hand preferences and most of the others were handed for only a single behavior. For tool use, two showed a left-hand bias, two a right-hand bias and six showed no preference.

Other reports indicate that there is population-level handedness in ape populations, but the bias toward one side or the other (more often to the right) is much less than in human populations and many individuals show no preference. No one has been more assiduous than Hopkins in researching this topic of population-level handedness in apes. Together with his colleagues, he has amassed evidence demonstrating that the received view of human uniqueness in possessing this property needs to be revised.

In 2004 Hopkins and coworkers reviewed their earlier studies in captive chimpanzees which revealed population-level right-handedness for throwing, gestural communication, and coordinated bimanual actions. To this they added a new study of 467 captive chimpanzees in three separate colonies. A bias toward right-handedness was found that was unrelated to whether the subjects were raised by humans or not [Hopkins, et al., 2004]. They used the “tube task” which revealed that in this large sample, the animals displayed an approximate 2:1 ratio

of right-handed to left-handed individuals and many animals were ambidextrous. Lonsdorf and Hopkins [2005] found a 2:1 ratio of dominant to non-dominant handed individuals within captive and wild communities of chimpanzees, depending on the task: termite-fishing elicited left-handedness; nut-cracking was mainly right-handed. Hopkins and coauthors [2005] reported that right-handed throwing was more pronounced than other measures of handedness in captive chimpanzees. Such throwing (which involves only the arm) was observed in about half of the apes in two captive colonies. Among the most active throwers (n=89) 56 threw right-handed, 23 left-handed, and 16 were ambiguous. Throws were underhanded (25), mixed posture (27) and overhand (38). Most of the overhand throws were from an erect stance.

In 2006 Hopkins summarized all the published data on handedness in great apes then available. Comparative analysis indicated that chimpanzees (n = 1,044) and bonobos (97) show population-level right-handedness, whereas gorillas (n = 280) and orangutans (n = 103) do not. In the genus *Pan*, throwing and hand gestures were the two most lateralized behaviors, and both the strength and direction of hand preferences ran in families [Hopkins, 2006]. Handedness was more pronounced for some measures than for others, suggesting that hand preferences in apes are task specific [Hopkins, 2006]. “At a minimum, the evidence of population level handedness in *Pan* suggests that hemispheric specialization for motor skill can be dated back to 6 or 7 million years ago when the *Pan* and *Homo* genuses split” [Hopkins, 2006, p. 554].

Later, in 2011, Hopkins and his coworkers examined investigations of 536 chimpanzees, 76 gorillas, 118 bonobos and 47 orangutans by means of the “tube task”. Table 2 of this publication shows that among 324 adult chimpanzees, 50% used their right hand to retrieve the treat, 29% used their left hand, and 20% had no preferred hand; thus 80% were handed, and the ratio of right-to-left preference was 1.7 to 1 (compared to ~9 to 1 in humans). Smaller groups of gorillas and bonobos also favored use of the right hand for retrieving the treat, but orangutans did the reverse. The authors conclude that apes show population-level handedness, but the magnitude of expression is lower than in humans, and handedness varies in direction between species. They suggest that “the antecedents to human right-handedness developed in African apes, after they split from the common ancestor with orangutans” (p. 609).

Forrester and colleagues [2011, 2012, 2013] studied three small groups (12 gorillas, 9 chimpanzees, and 10 human children) using the same video sample approach in each case. They found a slight right-hand bias for hand movements from a position of rest directed towards inanimate objects and a lack of bias of similar movements to animate targets (self or social partners). Although the sample sizes were small, the investigators agreed they supported Hopkins’ conclusion that human handedness is not a new or unique human characteristic.

Nevertheless, there is something about human handedness that is unique. No other primates show frequencies even close to the right bias typical of modern

humans [Fruyer, et al., 2011]. What is also unique is that not only are we more strongly handed, we are essentially *all* handed. There are exceedingly few ambidextrous individuals. Essentially everyone has a preferred hand, the vast majority of us being right-handed (~90%) and the remainder are left-handed (~10%). Something unprecedented must have happened in the hominin lineage [Chapelain and Hogervorts, 2009] which activated natural selection to exaggerate markedly the weak right-handed bias that was present in our ape ancestors—something that also preserved a modicum of left-handedness. How can this be explained? What was the reproductive advantage? No attempt has been made so far to account for the tendency toward right-handed bias in apes, but some writers have attempted to explain this phenomenon in hominins.
