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HANDEDNESS AND LANGUAGE LATERALIZATION: WHY ARE WE RIGHT-HANDED AND LEFT-BRAINED?

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***Abstract*:** Around 90% of humans prefer their right hand for unimanual actions and are left-hemisphere dominant for language functions; a pattern far from negligible. The phenomena of handedness and cerebral lateralization for language are presented along with the different theories that attempt to explain the presence of these functional asymmetries. The focus is on the adaptive advantages both on the individual and the population level. Most importantly, the intriguing question of why humans are right-handed and left-brained and not the other way around is tackled; a number of evolutionary, cultural, and genetic accounts are presented, along with theories that explain the observed pattern of asymmetries by means of the different properties of the two cerebral hemispheres.

***Key words*:** Handedness, Language, Laterality.

INTRODUCTION

Morphological right-left asymmetry appears to be the rule, rather than the exception in nature, all the way from chiral molecules (Quack, 1989) to the Baryon asymmetry in the universe (Sakharov, 1991). Asymmetry is the rule for biological systems as well (Geschwind & Galaburda, 1987; Kimura, 1973), whereby even single-celled organisms are commonly asymmetric (Nelson, 2003). Human beings are certainly structurally and functionally asymmetric, from the size of their feet and hands to the placement of visceral organs and facial features (Levy & Levy, 1978; Purves, White, & Andrews, 1994). In fact, the two aspects of behavior specific to humans, the use

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of language (Lieberman, 1984) and the strong population-level preference for hand use (Annett, 1985; McManus, 1991), are both asymmetric, lateralized traits. When it comes to language, the majority of humans are left-hemisphere dominant for language functions, while the right hand is the preferred hand for over 9 out of 10 individuals.

One may wonder why these functional asymmetries have emerged. Most importantly, why would this specific pattern be the case? Why are humans right-handed and left-brained and not the other way around? The present review sets out to answer these questions, after defining and discussing the phenomena of handedness and language lateralization. The mere volume of published work in the field of laterality (e.g., under the heading of *handedness* 2,195 articles were cited in PsycINFO only between 1989 and 2006; see Papadatou-Pastou, Martin, Munafó, & Jones, 2008. Between 2007 and September 2011, 746 new papers were cited under the same heading in Psych INFO) makes such an orderly synopsis imperative. This endeavour, apart from its intrinsic interest, gains importance from the fact that the study of handedness and language lateralization contributes to the broader question of individual differences in brain organisation and abilities. Such differences are of key importance to psychiatric, neurological, and neuropsychological research and practice.

WHAT IS HANDEDNESS?

Handedness is the best-known and most studied human asymmetry, and it can be defined as "the individual's preference to use one hand predominately for unimanual tasks and/or the ability to perform these tasks more efficiently with one hand" (Corey, Hurley, & Foundas, 2001). Left-handedness incidence is a point of dispute among different studies; percentages range from 1.6% (Hoosain, 1990) to 32.2% (Gladue & Bailey, 1995), and are usually reported as "around 10%" (Cavill & Bryden, 2003; Holtzen, 1994). An unpublished, large-scale systematic review including 1.8 million participants found that the incidence of left-handedness lies between 7.52% (using the most stringent criterion of extreme left-handedness) and 17.42% (using the most lenient criterion of non-right handedness; Papadatou-Pastou, Martin, Munafó, & Jones, 2010).

Handedness is a uniquely human characteristic; humans appear to be almost alone in exhibiting a strong population-level preference for the use of one limb – the right hand – rather than its mirror limb. While individual members of other species may exhibit preferences for the use of a right or a left limb, there is little or no evidence for a species-wide preference (Annett, 1985; Corballis, 1991; Martin & Jones, 1999). Considering studies in which hand or paw preference has been measured directly, there is no evidence for population-level handedness in mice (Collins, 1985), rats (Kirk, 1935; Uguru-Okorie & Arbuthnott, 1981), cats (Burgess & Villablanca, 1986), and potentially apes (Byrne & Byrne, 1991), although the latter case is controversial (MacNeilage, Studdert-Kennedy, & Lindblom, 1987; Marchant & McGrew, 1991). In non-mammalian species, the parrot may be an unusual exception to the above rule (Harris, 1989).

A wealth of evidence is available supporting the notion that handedness is an early developmental characteristic, both phylogenetically (i.e., in the evolution of the human species) and ontogenetically (i.e., in the development of the individual). As far as phylogenesis is concerned, comparative observations suggest that the event that shaped the evolution of human handedness must have taken place after the split between humans and chimpanzees (Corballis, 1991). The oldest published evidence of human handedness is from the Pleistocene period (Bahn, 1989; deCastro, Bromage, & Jalvo, 1988; Lalueza & Frayer, 1997; Lewin, 1986; Toth, 1985), when incisive marking indicates the existence of right- and left-handed *homo neanderthalensis* for sharp tool manipulation. In the *homo sapiens* taxonomy, the oldest evidence is from the upper Palaeolithic period, when right and left tube holders for blow painting were both present, with a predominance of right tube holders, as indicated by the record of negative hand painting in caves (Groenen, 1988; 1997). Other artefacts such as bone and antler implements from the Neolithic period, about 7000 years ago, also show evidence of a predominance of right-handedness (Spenneman, 1984). The assessment of manual preference from 12,000 works of art from European, Asian, African, and American sources (Coren & Porac, 1977) and rich evidence from anthropological research (Black, Young, Pei, & de Chardin, 1933; Brinton, 1986; Dart, 1949; Mason, 1896) have further shown that the approximated magnitude of this preference does not seem to have undergone any systematic change over the past 50 centuries.

Ontogenetically, handedness also appears quite early in development. In most human embryos, the right hand is more developed than the left at seven weeks post-conception (O'Rahilly & Muller, 1987). Using ultrasonography, Hepper, Shahidullah, and White (1991) observed that 92% of the foetuses who sucked their thumbs tended to choose the right thumb. They further reported that 10-week-old foetuses moved their right arm more often that their left, with 75% of foetuses showing a right arm bias. Goodwin and Michel (1981) studied hand preference among neonates at 19 weeks of age and found that 64% preferred the right hand in a reaching task. Gesell and Ames (1947) found that the tonic neck reflex observed in newborns strongly predicted handedness at the ages of one, five, and ten years.

Other researchers have observed sidedness in hand use (or other motor behaviors associated with handedness) among neonates and infants (Bates, O'Connell, Vaid, Sledge, & Oakes, 1986; Cioni & Pellegrinetti, 1982) and have noted significant stability over time (Archer, Campbell, & Segalowitz, 1988).

WHAT IS LANGUAGE LATERALIZATION?

A brain is considered to be asymmetrical or lateralized if one hemisphere or other brain region is structurally different from the other and/or performs a different set of functions (Bisazza, Rogers, & Vallortigara, 1998). The human brain is typically lateralized with the left hemisphere being the locus of language skills and of analytical processing of stimuli, whereas the right hemisphere is dominant for spatial-constructional skills, for a more global way of processing information, and it is moreover the locus of emotions (McManus & Bryden, 1993). Traditionally, hemispheric asymmetries were considered dichotomous. Today, the generally accepted view is that the two hemispheres show complementary specialization (Bradshaw & Nettleton, 1983).

This critical insight concerning functional lateralization, with language functions being generally located in the left hemisphere was first clearly enunciated by Paul Broca when he said "Nous parlons avec l'hemisphère gauche" ("We speak with the left hemisphere; Broca, 1965)". Broca reached this conclusion when he examined over 25 patients, all of whom suffered from a type of aphasia causing an impairment in language production, and all of whom had suffered lesions to the left side of the brain, in the most anterior part of the frontal lobe (Berker, Berker, & Smith, 1986), in the area now known as Broca's area. In 1874, Carl Wernicke further discovered that damage to a region of the left hemisphere posterior to Broca's area, now known as Wernicke's area, could cause another type of aphasia that resulted in a language comprehension impairment (Wernicke, 1984).

Due to all of Broca's patients being right-handed and having their language areas lateralized to the left hemisphere, it was initially speculated that the reverse, that is right hemisphere language dominance, should be true for left-handers. This claim has been widely accepted as the "Broca rule", although Broca never explicitly postulated such a rule (Harris, 1983). Such explanations would have restored a higher-order symmetry of the brain, in which left-handers simply showed the reverse pattern of language dominance to right-handers (McManus & Bryden, 1993). Luria (1976) was amongst the first to point out that such an association could not be universally true because even in left-handers aphasia usually occurs after a lesion in the left hemisphere.

The relationship between handedness and language lateralization is now known to be much more complex. Knecht et al. (2000), who measured lateralization directly by functional transcranial Doppler ultrasonography (fTCD) in 326 healthy individuals using the Word Generation task, showed that language dominance depends not only on the direction, but also on the degree of handedness. More specifically, they showed that the incidence of right-hemispheric dominance increases linearly with the degree of left-handedness, as measured by the Edinburgh Handedness Inventory (Oldfield, 1971), from 4% in strong right-handers, to 15% in ambidextrous individuals, and 27% in strong left-handers.

Language lateralization patterns are often described as typical (left-hemispheric) or atypical (symmetrical and right-hemispheric), but categorisation schemes of this kind are probably an oversimplification (Szaflarski et al., 2002). Although language-related activation in normal right-handed individuals is predominantly left-hemispheric, almost all individuals activate right hemisphere areas to some extent in language studies with large participant samples using functional magnetic resonance imaging (fMRI), positron emission tomography (PET), and functional transcranial Doppler ultrasonography (fTCD) (Buckner et al., 1995; Frost et al., 1999; Knecht et al., 2000; Pujol et al., 1999; Springer et al., 1999; Tzourio et al., 1998). In other words, there is a continuum of language lateralization patterns ranging from strongly left-dominant to strongly right-dominant. Thus, language is better described as being "actuated by a distributed cerebral network with differences in regional involvement related to specific language subfunctions, with essential regions within this network lateralized to one hemisphere, typically the left" (Frith et al., 1991).

Left Sylvian fissure asymmetry is the best known anatomical asymmetry with regards to language lateralization (for a review see Jäncke & Steinmetz, 1993). Studies mainly focus on the planum temporale (PT), a triangular structure on the supratemporal plane in the depth of the Sylvian fissure, although findings remain inconclusive. A number of studies have shown that individuals with left-hemispheric language representation show a strong leftward asymmetry in the PT, while individuals with right-hemispheric language representation do not exhibit a consistent PT asymmetry (Moffat, Hampson, & Lee, 1998; Ratcliff, Dila, Taylor, & Milner, 1980). Foundas, Leonard, Gilmore, Fennell, and Heilman (1994) reported that asymmetry of the PT correlated to cerebral dominance as assessed with the Wada test in 11 individuals. Tzourio et al. (1998), however, found no correlation between the same measures in 14 individuals. In a much larger sample, Jäncke and Steinmetz (1993) replicated the finding of no significant relationship between dichotic listening scores and PT asymmetry. Similarly, Hellige, Taylor, Lesmes, and Peterson (1998) were not successful in demonstrating this link. Güntürkün and Hausmann (2003) suggested that it might not be the asymmetry of the PT as such, but the absolute size of the left PT that determines language lateralization, as a number of studies, which could not reveal meaningful relationships between language lateralization measures from imaging data and PT asymmetry, showed stronger relations to absolute left PT size (for a review see Habib & Robichon, 2003).

While language, like handedness, is a striking human characteristic, the basic aspects of brain lateralization are common to both birds and mammals (Bradshaw & Nettleton, 1983; Denenberg, 1981). From a phylogenetic point of view this indicates that lateralization emerged early in vertebrate evolution (Vallortigara, Rogers, & Bisazza, 1999). Language-related functional asymmetry also seems to emerge early in ontogenesis. For example, asymmetry in auditory perception exists at or shortly after birth (see Hahn, 1987). Moreover, the left Sylvian fissure asymmetry probably originates during the first trimester of pregnancy (LeMay, 1976).

WHY DO HUMANS EXHIBIT ASYMMETRY OF FUNCTION?

A number of adaptive advantages certainly accompany functional asymmetry. With regards to handedness, Bishop (1990) has put forward two related hypotheses: the motor learning hypothesis and the inference hypothesis. According to the motor learning hypothesis, specializing one hand for unimanual actions can result in advanced performance through practice. In fact, this would also be the case for actions that require bilaterality of movement, where the two hands have complementary roles; instead of both hands learning to execute either role, each hand would specialize in one role in a display of division of labour (Corballis & Beale, 1976). The inference hypothesis builds on the fact that learning a motor movement with one hand facilitates performance of mirror-image movements with the other hand. Therefore, Bishop (1990) claims that for non-mirror reversible activities, such as handwriting, whereby an attempt to switch between hands could interfere with what is learned by each hand, restricting learning to one hand is critical. Lateralization of manual praxis may further convey increased neural capacity, because specializing one hemisphere for a particular function leaves the other hemisphere free to perform other additional functions (Levy, 1977). This would enable brain evolution to avoid useless duplication of functions in the two hemispheres, saving in neural circuitry.

Similarly to handedness, language lateralization may have come about because the segregation of functions of the separate halves of the brain allows for simultaneous parallel processing (Vallortigara & Rogers, 2005). Thus, it represents a solution to the competition for space within the brain and to the problem of functional incompatibility (Vallortigara et al., 1999). Processing and storing information about invariance and variance among experiences are mutually incompatible processes, which might best be handled by functionally separate systems (right and left hemispheres accordingly; ibid.) Moreover, functional neuronal clustering in one hemisphere during language development allows faster linguistic processing because transition times are shorter than in interhemispheric operations (Lieberman, 1984). Language lateralization may thus have an adaptive value and it has even been claimed to present a prerequisite for the full realisation of the linguistic potential (Geschwind & Galaburda, 1985; Hiscock, 1998).

This rationale, useful as it is in explaining lateralization at the individual level, fails to explain the presence of either handedness or brain laterality at the population level. In other words, even though it is clear that asymmetry bears advantages for the individual, it does not address the question of why there are not equal numbers of right- and left-handed humans (and accordingly right- and left-hemisphere dominant humans). Further, it fails to explain why the preference for one of the two sides is not species-universal, as is the case with the position of visceral organs (e.g., the heart is placed to the left of the body). The latter is better explained by genetic models, which typically assume that the genetic variation is preserved through heterozygote advantage (Annett, 1985; Corballis, 1991; McManus & Bryden, 1992). Annett's (1985) theory, for example, postulates a gene for left cerebral dominance that increases the probability of right-handedness (the rs gene) and suggests that the heterozygote advantage is such that those with the rs+- genotype have optimal brain organization. A situation of balanced polymorphism is obtained, as reproductive success of rs+- is higher than both rs- and rs++, thereby maintaining the rs- allele in the gene pool. (A detailed account of the different genetic theories on laterality is beyond the scope of the present paper, but can be found in Papadatou-Pastou et al., 2008.)

WHY ARE HUMANS RIGHT-HANDED AND LEFT-BRAINED?

Solving the riddle of both individual- and population-level preference, still does not explain right hand and left hemisphere preference, as opposed to a possible left hand and right hemisphere preference, or a combination thereof. (Even Annett's genetic theory, which postulates that the right-handedness and left-brainedness gene is the dominant one, does so in an attempt to explain the mechanisms behind humans displaying this observed asymmetry.) Let us begin by asking why the right hand is preferred over the left one. Evolutionary theories claim that right hand preference may have evolved from warriors who were carrying their shields with their left hand, leaving the right hand free for fighting, and who consequently had better survival rates since their hearts were protected (Van Biervleit, 1899). Alternatively, such theories put forward the tendency of human (and presumably pre-human) mothers to hold infants on the left side of their body (Huheey, 1975). This latter practice is ascribed to imprinting and the soothing sound of the mother's heartbeat on the infant. Given the practice of holding the child in this manner, dextral mothers are more skillful in the manipulation of objects and thus selectively favoured. These two theories, interesting as they might be, do not seem plausible. As Bishop (1990) argues, the position of the heart is only slightly biased to the left side of the body. Thus, it is unlikely that a right-handed grip on the sword could significantly improve one's chance of surviving a battle (and indeed there is no evidence that the prevalence of right-handedness has increased since the introduction of the sword) or that it could significantly help mothers soothe their babies.

It could further be the case that right hand preference is merely a learned behavior or a "cultural law" in the early words of Blau (1946). One cannot deny that we live in a right-handed world, all the way from right-handed scissors and door handles to table manners. In other words, social organization forces us to use the right hand in order to share tools and equipment specialized for one hand and to develop social customs based on the conventional use of the right hand, such as in handshakes (Bishop, 1990). Yet, this theory does not explain how this preference originated and took precedence over a possible left one. Even if this were a chance event, or an event shaped by tool use (which should be designed for use by as many individuals in the community as possible) one would expect to find the opposite pattern in at least some isolated communities. Yet, no evidence has emerged to date of communities where there are equal numbers of right- and left-handers or a population-level preference towards left-hand use. Another question that might arise with regards to this account is the following: if right hand preference is merely a learned behavior why aren't all humans right-handed? The persisting minority of left-handers, a minority which is subject to the same cultural pressures as the right-handed majority (or even stronger pressures, as they deviate from the norm) and whose percentage seems to have remained fairly constant throughout history, race, and geographical variation refutes the theory of environmental pressures. Moreover, asymmetry in behavior is evident even before birth, as discussed above (Hepper et al., 1991; O'Rahilly & Muller, 1987). It thus seems fair to conclude that there must be a biological predisposition toward using the right hand rather than the left one.

Previc (1991) claims that asymmetries derive from maternal anatomy in that the intrauterine environment is laterally asymmetric in many different respects (for a review, see Previc, 1991). These asymmetries lead to a leftward bias in foetal positioning (Calkins, 1939), which has been shown to predict later handedness (Churchill, Igna, & Senf, 1962). Handedness is associated with parental hand preference, but Churchill et al. (1962) still found an association between foetal positioning and child handedness, even after excluding children with left-handed parents. However, the associations found were too weak to support this theory as a persuasive explanation for the strong population bias towards right-hand preference. The most compelling theory to date is the one explaining right-hand preference by brain hemisphere division of labour: since both speaking and handiwork require fine motor skills, having one hemisphere of the brain (that would be the left hemisphere for reasons described below) do both would be more efficient than having it divided up. In other words, right hand preference might as well be a secondary characteristic of cerebral lateralization for language.

Therefore, language dominance in one of the two hemispheres is advantageous for the full realisation of language skills, and it may also drive right-hand preference. The question that comes about is why would the left hemisphere be the dominant one, instead of the right. One might argue that this was merely a chance event: out of the two hemispheres, the left one just happened to develop into the dominant one for language functions and fine motor skills. For example, McManus (1991), claims that handedness and language dominance are perhaps a result of a genetic mutation whereby a gene that once influenced the asymmetry of the viscera, caused instead the asymmetric development of the brain. Thus, the hypothesis was put forward (Seddon & McManus, 1993) that right-handedness, along with the capacity to make and use tools, use language, and show functional and anatomical cerebral specialization, are characteristics which are intimately tied together in the divergence of human beings from the apes, an evolutionary event placed at around two and a half million years ago (Calvin, 1982; Frost, 1980; Varney & Vilensky, 1980).

However, evidence points away from left-hemisphere dominance being a chance event, and towards different properties of the two hemispheres that could have led to the segregation of functions. For example, timing differences between the hemispheres have been proposed to explain left-hemispheric dominance for language (Belin, Zilbovicius, Crozier, Thivard, & Fontaine, 1998). More specifically, a prelinguistic advantage of the left-hemisphere for processing information with a high temporal precision has been described (Hammond, 1982; Lackner & Teuber, 1973). The presence of this advantage is supported by psychoacoustic and neuropsychological studies, which have outlined the very rapid acoustic changes of speech and their critical importance for speech perception (Belin et al., 1998; Merzenich et al., 1996; Tallal et al., 1996; Tallal & Piercy, 1973).

Another explanation focuses on action coding. In the left hemisphere, actions are coded through auditory, visual, and motor components, whereas in the right hemisphere action coding seems to occur only via the visual and motor channels (Aziz-Zadeh, Iacoboni, Zaidel, Wilson, & Mazziota, 2004). Therefore, the coding in the left hemisphere encompasses all the contents of an action. This greater number of modalities available selectively to the left hemisphere may have allowed for a more abstract representation of actions that make this hemisphere better suited for facilitating the emergence of language (Hauser, Chomsky, & Fitch, 2002). In addition to the above theories, it has been suggested that the right hemisphere matures before the left (Geschwind & Galaburda, 1987), which means that it is subjected to fewer influences during development. Thus, the right hemisphere is the locus of the processes essential to survival, such as attention and analysis of external space and emotion (Geschwind & Galaburda, 1987).

On a different line of thinking, the hypothesis has been put forward that a gestural system of communication with dominance of the right hand provided the neural architecture for vocal articulation in human evolution (Hewes, 1973; Kimura, 1984). This communication system may be based on "mirror" neurons, that is, premotor neurons that fire when monkeys perform goal-directed actions but also when monkeys observe another monkey making the same actions (Arbib, 2001; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti & Arbibi, 1998). A mirror system for manual actions may have been important in establishing a means of nonverbal communication and it is possible that neural properties supporting language might have evolved from this system (Fadiga, Craighero, Buccino, & Rizzolatti, 2002; Hari et al., 1998; Meister et al., 2003). The critical role of Broca's area in manual imitation (Heiser, Iacoboni, Maeda, Marcus, & Mazziota, 2003; Iacoboni et al., 1999) supports this hypothesis. In fact, Rizzolatti and Arbib (1998) showed that the mirror system in monkeys is the homologue of Broca's area and argued that this observation provides the missing link for the suggestion that primitive forms of communication based on manual gesture preceded speech in the evolution of language (as opposed to previous theories treating right hand preference as a secondary characteristic of left hemisphere dominance). Furthermore, the recent discovery of auditory mirror neurons that fire when monkeys make an action, watch the same action, or hear the sound of the action (e.g., breaking a peanut) in the dark, has tied this system to the auditory modality, which is of crucial importance to human language (Keysers et al., 2003; Kohler et al., 2002). Using transcranial magnetic stimulation (TMS) for measuring motor corticospinal excitability of hand muscles in humans while listening to sounds, Aziz-Zadeh et al. (2004) recently showed that sounds associated with manual actions produced greater corticospinal excitability than sounds associated with leg movements or control sounds. More importantly, they demonstrated that this facilitation was exclusively lateralized to the left hemisphere.

CONCLUSION

Handedness and cerebral laterality for language share an intimate relationship, with around 90% of the population preferring the right hand for unimanual actions, while over 90% of right-handers and around 70-80% of left-handers have their language functions located at their left hemisphere. These functional asymmetries are argued to have emerged due to the adaptive advantages they convey both for the individual, namely advanced performance through practise and increased neural capacity, and the population as a whole through a heterozygote advantage that maintains the genetic variation and which accounts for optimal brain organization.

A number of evolutionary, cultural and genetic theories, as well as theories focusing on maternal anatomy have been developed in order to explain why the right hand/left hemisphere pattern has been established, over a possible left hand/right hemisphere one; they have been unconvincing. The most plausible explanation put forward to date is that certain properties of the left-hemisphere make it more adept for hosting language functions. At the same time, speaking and handiwork both require fine motor skills and should be ideally handled by the same hemisphere, resulting in a right-hand preference. These left-hemisphere properties might include the processing of information with a high temporal precision or the fact that coding in the left hemisphere encompasses all the contents of an action (i.e., auditory, visual, and motor components). Other plausible explanations include maturation differences between the two hemispheres, or the fact that a right-handed gestural system of communication might have preceded the emergence of language, and provided the basis of its neural architecture in the left hemisphere.

In conclusion, asymmetry seems to be a prerequisite for optimal function rather than an epiphenomenon of evolution and critical for an organism's adaptation to the environment. The ever-important functions of manual praxis and communication via language not only exhibit strong asymmetries, but their right hand/left hemisphere pattern is as intriguing as it is a paradigm of the efficiency and adeptness of the human brain.

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