



Manual asymmetries and hemispheric specialization: Insight from developmental studies



Hélène Cochet

Laboratory CLLE-LTC (UMR 5263), University of Toulouse Jean Jaurès, Department of Psychology, 5 allées Antonio Machado, 31058 Toulouse Cedex 9, France

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ABSTRACT

The objective of this review is to obtain a better understanding of the relationship between manual asymmetries and hemispheric specialization by focusing on the development of hand preference and cerebral lateralization of language. We first sought to describe the development of manual asymmetries for different activities (*i.e.*, grasping and manipulating objects vs. communicating through gestures), and the development of cerebral asymmetries, before examining available data on the association between hand preference and HS for language. We also analyzed behavioral studies on the relation between hand preference and language development, as well as more specific studies on the relation between the cerebral control of gestures and language. Finally, we aimed at providing a wider view on functional asymmetries by emphasizing the need to study hemispheric specialization for functions other than language, and in particular for visual attention.

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1. Introduction: on the importance of asking relevant questions

Hemispheric specialization (HS) has evolved as a defining characteristic of humans because it may have provided them with some adaptive advantages, allowing the development of new competences by splitting functions between cerebral hemispheres (Gazzaniga, 2000). Studies on HS have long been concerned with the question of the relationship between handedness and hemispheric dominance for language, first because of the high prevalence of left HS at the population level for these two functional asymmetries (representing approximately 90% of individuals), and second because atypical HS for language in adults is more frequent in left-handers than in right-handers (Knecht *et al.*, 2000). Focusing on the emergence of HS, especially as children acquire language and develop manual skills, has been regarded as an efficient way to further understand the relationship between these asymmetries. During the course of development, one of the objectives has thus been to find out whether children develop left HS for language as a consequence of predominantly using their right hand, or conversely.

However, the majority of left-handers present typical HS (Knecht *et al.*, 2000) and the association between language lateralization and manual asymmetries was recently refuted in adults (Mazoyer *et al.*, 2014), thus providing an opportunity to redefine questions on the

development of behavioral and anatomo-functional asymmetries. HS for language does appear as a key feature of human cerebral organization, but such a close focus on verbal language, as a uniquely human capacity, may have relegated to the background HS for other functions, such as attention and spatial skills. As a result, relations between HS for attention and manual asymmetries have for example never been explored during development, and scarcely ever in adults. Moreover, there is now growing evidence showing that the development of handedness is a complex question that requires longitudinal measures from infancy to childhood and involving different activities, to be properly examined. The links between behavioral and cerebral asymmetries may indeed depend on some functional characteristics of the manual actions considered.

By presenting recent data, first, on the development of hand preference and second, on the development of HS, the aim of this review is to unravel the nature of the relation between manual asymmetries and language lateralization and to identify other functional asymmetries that may be of key importance for analyzing this relation.

2. Development of handedness

2.1. Methodological questions

Handedness does not entirely stabilize until adulthood, but early signs of manual asymmetries are manifest from infancy, even

E-mail address: helene.cochet@univ-tlse2.fr

to some extent before birth, as revealed by some lateralized motor behaviors of the fetus (e.g., from 15 to 18 weeks for thumb sucking; Hepper et al., 2005). Environmental and cultural factors have been argued to strongly reinforce the initial influence of genetic and hormonal factors on the development of handedness (e.g., Fagard and Dahmen, 2004; Provins, 1992). However, one source of confusion in assessing manual asymmetries lies in the nature and the complexity of the actions observed. Rather than analyzing the causal origins of handedness, the aim of the present review is therefore to describe the development of handedness by taking into account different types of manual activities. We will focus on hand preference measures rather than on performance measures (in terms of speed and/or precision), as they may enable more relevant comparisons between infants, children and adults.

In addition to inherent difficulties in defining manual asymmetries, it is also necessary to consider methodological discrepancies across studies in the conditions under which handedness is measured and in the criteria used to categorize individuals as left-handers, right-handers or ambidextrous. In young children, direct observation of hand preference in ecological contexts (e.g., home, nursery, school) is usually preferred over the use of questionnaires assessing hand preference for daily activities (either self-report or parental questionnaires) or experimental tasks that can sometimes seem purposeless or arbitrary. Even though the two latter methods are frequently used in adults (e.g., peg-moving tasks; Annett, 1985), it is important to compare similar situations across all age ranges to analyze the development of handedness. Laterality biases in the posture of the participants and in the position of the objects involved also need to be identified to make sure that the asymmetries recorded do reflect individuals' actual preferences (e.g., Leconte and Fagard, 2004). Moreover, differences in the way of characterizing these asymmetries can constitute another obstacle to the comparisons across studies and across development: although most researchers now agree that a simple dichotomy between left- and right-handers is too limited, some choose to define intermediate categories (i.e., moderate vs. strong left- and right-handers) whereas others use handedness indices to examine both the strength and the direction of asymmetries. One of the most widely used handedness index, calculated with the formula $(R-L)/(R+L)$, where R and L stand for the total number of right- and left-hand responses, varies from -1 to 1 , with the sign indicating the direction of handedness and the absolute value reflecting its degree. Handedness indexes, thus reflecting the continuous distribution of hand preference, can also be used to compare the strength of manual asymmetries for different activities, independently of their direction.

2.2. Grasping and manipulating objects

With these methodological elements in mind, longitudinal observations over several months in infants and children have allowed researchers to identify different pathways in the development of handedness, depending on the activities considered and on individuals' patterns of HS (Cochet, 2012; Nelson et al., 2013). A first distinction has been highlighted between unimanual preference for grasping objects, which can be assessed from approximately 6 months of age, and bimanual preference for manipulating objects, with differentiated roles of the two hands: the hand regarded as non-dominant stabilizes the object for the manipulatory actions of the dominant hand (e.g., grasping a receptacle while picking up an object inserted in it). Bimanual activities usually elicit stronger degree of handedness than unimanual activities (e.g., Fagard and Marks, 2000), which may reflect the association between the emergence of new manual skills (infants become able to perform such bimanual activities by one year of age) and the need for functional specialization. However, hand

preferences for unimanual and bimanual actions are not independent from each other: a longitudinal study in 6–24 month-olds has shown that hand preferences for grasping objects are stable in most infants and persist across more complex manual skills acquired a few months later (Nelson et al., 2013). Other infants had no preference, but were found to shift to left or right lateralized hand use as toddlers. The majority of children were thus categorized as right-handers by 2 years of age, despite a weaker degree of preference compared to adults and a higher incidence of left-handedness. Handedness for bimanual manipulation of objects thus seems influenced by handedness for unimanual manipulation. Hand-preference strength for object manipulation has been reported to increase until 7 years of age (McManus et al., 1988), in concert with an increase in the complexity of the actions children come to perform, although preferences are less consistent and stabilize later in left-handers than in right-handers (Michel et al., 2014).

Another study, confirming consistency in hand preference from childhood to older adulthood, has also emphasized the influence of end-goal and spatial demands of the task by showing stronger right-hand preference when the objective of unimanual grasp is to eat, rather than place or manipulate the target (Gonzalez et al., 2015). Similar results have been described in 1- to 5-year-old children: right-hand preference for grasp-to-eat movement was present earlier (from 1 year of age) and was then stronger than hand preference for grasp-to-build movement (Sacrey et al., 2013). However, although mechanical requirements of the different types of grasp do seem identical, investigations of hand kinematics have shown smaller grip apertures during the pre-shaping phase of right-hand grasp-to-eat action, compared to other grasping movements (Flindall and Gonzalez, 2014). Smaller grip apertures are typically associated with greater precision, in relation with increased need for visual and somatosensory guidance of the hand, which might explain the greater right-hand bias for reach-to-eat behavior. This right-hand advantage for grasp-to-eat actions has been argued to stem from selective pressures favoring more efficient food retrieval and consumption, thus maximizing individual fitness (e.g., Flindall and Gonzalez, 2013). Altogether, these results highlight the importance of defining end-state goals of actions for the analysis of hand preference, as they may be supported by several distinct neural networks (Gonzalez et al., 2015).

2.3. Communicating through gestures

Moreover, the distinction based on the nature of the activities considered has led researchers, especially in the last 15 years, to compare asymmetries for non-communicative activities (unimanual and bimanual manipulative activities) and for communicative gestures. Infants start using their hands to communicate intentionally around the end of their first year, for example by pointing toward a specific object, person or event to direct the attention of the adult. Even if the development of handedness for communicative gestures also involves a high degree of inter-individual variability, preferential use of the right hand to produce such gestures has been observed from infancy. At least before 3 years of age, these right-sided asymmetries were shown to be stronger than asymmetries characterizing unimanual or bimanual manipulative activities (Jacquet et al., 2012; Vauclair and Imbault, 2009), just like signed gestures produced by children born to deaf parents are more right-handed than other manual activities (Bonvillian et al., 1997). Moreover, several studies have shown a lack of correlation (e.g., Cochet and Vauclair, 2010b; Esseily et al., 2011), and even negative correlations (Cochet, 2012), between handedness for manipulative activities and handedness for communicative gestures. From 3 years of age, as children are more and

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