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Handedness Development: A model for investigating the development of hemispheric specialization and interhemispheric coordination.

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Abstract

The author presents his perspective on the character of science, development, and handedness and relates these to his investigations of the early development of handedness. After presenting some ideas on what hemispheric specialization of function might mean for neural processing and how handedness should be assessed, the neuroscience of control of the arms/hands and interhemispheric communication and coordination are examined for how developmental processes can affect these mechanisms. The author's work on the development of early handedness is reviewed and placed within a context of cascading events in which different forms of handedness emerge from earlier forms but not in a deterministic manner. This approach supports a continuous rather than categorical distribution of handedness and accounts for the predominance of right-handedness while maintaining a minority of left-handedness. Finally, the relation of the development of handedness to the development of several language and cognitive skills is examined.

Key Words: Development, handedness, lateralization, hemispheric specialization, interhemispheric coordination, embodiment

Introduction

There is a general consensus among neuroscientists that the human left and right hemispheres of the brain have different perceptual, motor, emotional, and cognitive functions with the most distinctive difference of a left hemisphere predominance in praxis (e.g., gestures and tool-use) and language (speech and comprehension) functions (Prieur, Lemasson, Barbu, & Blois-Heulin, 2019). However, many have argued that the phenomenon of hemispheric specialization of function is poorly specified as to what functions are separated between hemispheres and how functions interrelate both within a hemisphere and across hemispheres (e.g., de Haan, Corballis, Hillyard, Marzi, Seth, Lamme, … Pinto, 2020; Vingerhoets, 2019). Also, the mechanisms that underlie these hemispheric differences in function are unclear (cf., Jasper, Christman, & Clarkson, 2021). Finally, there is little research focused on describing how the functional specialization of the hemispheres develops (Gunturkun & Ocklenburg, 2017) or what role interhemispheric communication plays in that development. Thus, there is much opportunity for research.

When I began my investigations of the development of handedness more than 45 years ago, I did so because I thought that the development of handedness could be a good model for how other forms of hemispheric specialization of function might be investigated developmentally. In 1970, as a graduate student, I had spent a week in Roger Sperry’s lab testing the inter-manual transfer of haptic weight and size perception in patients with callosotomies (some work that I did as an undergraduate student revealed hand differences in haptic perception and that had prompted my invitation). Although the results were inconclusive, I became fascinated with the issue of hemispheric specialization. At the time (and still today), the assumption was that hemispheric specialization of function derived from hemispheric specialization of neuroanatomical circuits supposedly controlled by genes during development.

I was trained by comparative psychologists, who, contrary to most Ethologists, argued that the development of species-typical behaviors required systematic investigations of individual-environment coactions (Beer, 1973; Lehrman, 1953, 1970) and not the interaction between genetic and environmental processes. I was trained to seek explanations that account for those phase transitions during development that result in a species-typical trait and to expect that the explanation would involve a complex array of reciprocal coactions between the individual's physiology and its environment. To study development of a trait required: 1) detailed descriptions of the trait; 2) description of the course of its manifestation during the lifespan (or at least the period of focus for the research); 3) specification of the physiological processes related to its manifestation; 4) specification of the social/physical environmental characteristics that are the context of development; and 5) identification of how those physiological processes and contextual characteristics create the experiences involved in the individual's developmental expression of that trait (Michel, 2010). The discipline of developmental psychobiology provides research strategies for examining how the dynamic bidirectional relationships between the individual's biological processes and the individual's social and physical environment operate to construct the developmental pathways of species-typical behaviors (Michel & Moore, 1995).

For example, as part of Lehrman's (e.g., 1965) programmatic investigations of the development of the ring dove reproductive cycle, my dissertation research focused on the role of experience for the initiation and maintenance of the incubation phase. The dove's cycle is a species-typical sequential pattern of courtship, nest-building, incubation, and brooding behavioral with concomitant physiological phases (both hormonal and neural). My work demonstrated the importance of the conditions established during the earlier nestbuilding phase of the dove's **first cycle** (pair-bonding, nest building, and their concomitant hormonal changes) which prepared the dove’s nervous system and general physiology (e.g., formation of a “brood patch”) and which helped create those experiences (the production of a nest and the presence of a nesting mate) that facilitated the transition to the subsequent incubation and brooding phases. The actual experience of engaging with eggs (the defining focus of incubation) is irrelevant for the initiation of incubation but is relevant for the maintenance of incubation and the initiation of brooding (cf., Michel, 1986 for details).

Thus, the transition to, and maintenance of, each phase of the dove’s first reproductive cycle requires concurrent social (mate and colony behaviors) and physical (nesting material and nest-site) and experience-elicited modulation of hormones (specific to each phase) that operate on a nervous system prepared by both the effects of the immediately previous and past experiences and previous and concurrent hormonal condition of the dove. For **subsequent cycles**, the neural and hormonal physiology of reproductively experienced doves function somewhat differently from that of reproductively naïve doves but they still require much of the web of reciprocal causality among physiological condition, social and physical conditions plus the experiences operative during the first cycle.

Working out the details of the individual-environment transactions during the development of species-typical behaviors constitutes part of the discipline of developmental psychobiology (Michel, 2007; Michel & Moore, 1995; Michel & Tyler, 2007). What appears to be an innate, instinctive, relatively rigid, pattern of reproduction in the dove is highly dependent upon the reciprocal coaction of a complex array of previous experience and hormonal conditions and concurrent social and physical stimuli. The alteration of any aspect of this array can have formative influences on the pattern and even interfere with reproduction. These factors become autogenously choreographed into a web of causation that exhibits extensive feedback and reciprocal influences but ensures the manifestation of the species-typical behavior appropriate for the species-typical ecological conditions. Adherence to a linear causal explanatory process (e.g., the interaction of nature and nurture in which the proportion of influence of each and the interaction may be separately estimated) distorts the complex transactions among multiple levels of influence in the development of any trait. Developmental psychobiological research provides examples of how several common species-typical behaviors develop (Michel, 2010; Michel & Moore, 1995).

In the mid-1970s, I sought to transfer my graduate training to the study of the development of hemispheric specialization for language (a human-typical trait). However, the category "language" involves a wide range of characteristics with different abilities and skills that are typically grouped together based on little more than convention. Moreover, with the exception of the production/comprehension distinction, these different characters are often substituted for one another when investigating hemispheric functioning on the assumption that they all represented the same underlying neurobiological process. Since most research focused on the language abilities involved in the production and comprehension of speech, this meant that broad inferences had to be made about what constituted language production or comprehension during infant development.

Since handedness (another species-typical trait exhibiting hemispheric specialization) could be defined by the actual actions of the infant, without extensive inference on the part of the investigator, I thought that it would be more suitable for study of the development of hemispheric specialization during infancy. Handedness ought to be more readily identified and its developmental changes could be measured more precisely than language. Also, at that time, the mechanisms responsible for lateralization of handedness and language functions were thought to be related.

Recently, there has been a growing consensus that the handedness and language functions of the left hemisphere are not causally related (Badzakova-Trajkov, Corballis, Häberling, 2016; Mazoyer, Zago, Jobard, Crivello, Joliot, et al., 2014; but see Michel, Babik, Nelson, Campbell, & Marcinowski, 2013). In part, this is because we lack good models of the distribution of each and therefore have no way of assessing whether their joint probability occurs by chance. Of course, no matter the relation of handedness and language laterality, demonstrating how to use a developmental psychobiological perspective to investigate the developmental processes involved in handedness could encourage other researchers to use this perspective to discover the development processes involved in other lateralized functions (Michel, 1983, 1988, 2001, 2002).

During my investigations of the development of handedness, I discovered that I had a somewhat atypical way of conceptualizing 1) development; 2) the character of science; and 3) human handedness (Michel, 2001; Michel & Tyler, 2007; Michel, Babik, Nelson, Campbell, Marcinowski, 2018; Michel, Marcinowski, Babik, Campbell, Nelson, 2015). My conceptions derived from my background training in comparative psychology and developmental psychobiology (cf., Michel, 2010, 2014). To understand the difference in developmental conceptions, consider this conclusion from a recent review of the neuroimaging work on adults who had been forced to use their right hand for acquiring the skill of writing. “Together, the functional and structural neuroimaging studies on forced right-handedness show that the adult brain holds an accumulated record of both innate biases of preferred hand use (nature) and early developmental experience (nurture)” (Andersen & Siebner, 2018, p. 125).

Thus, without examining the literature on the early development of handedness, the authors consider the acquisition of writing skills (in school-aged children) to be the only "early" developmental experience that could have affected the structure and functioning of the adult brain. Moreover, they assume that development is a process of the interaction between nature and nurture factors in which the influences of each can be readily identified by specific neural structural and functional consequences. Therefore, before presenting my evidence of how the development of handedness might serve as a model for investigating the development of other aspects of hemispheric specialization and interhemispheric communication, I must describe how I conceive of the character of science, human handedness, and development.

I present my conceptions only to contextualize my own research and not to provide a comprehensive account of handedness and lateralization. There are several excellent comprehensive accounts available (e.g., Annett, 2002, McManus, 2002, Gerald Young, 2020) that I highly recommend.

Character of Science.

Since Ethologists frequently challenged the research of my mentors (cf., Lorenz, 1965), my doctoral training involved strict adherence to Popper's (1959) falsifiability approach when designing research studies. That is, the research project had to be designed to challenge my hypothesis; that is, the design had to have the potential of producing results that were counter to those predicted. Too many researchers believe that the presence of a control group and a statistical test of the null hypothesis prevent the occurrence of confirmation bias in their experimental designs. Unfortunately, the null hypothesis simply assumes no differences between groups – it does not reveal the falsifiability of the hypothesis.

For example, showing statistically significant similarities among right handers across age and revealing that the similarities are unlikely to occur by chance is a confirmation bias. A developmental explanation for why right-handedness prevails in the population could only be falsified if left-handers exhibited the same developmental factors as those who develop right-handedness. If, as I hypothesized (Michel, 1981), a neonate's preference to orient the head rightward is a developmental precursor to the later development of a right hand-use preference, only the development of those infants with a left head orientation could challenge this hypothesis. Infants with leftward head orientation preferences must develop left hand-use preferences, which they do (Michel & Harkins, 1986).

Recently, Strevens (2020) argued that science has come to alter the course of civilization during the past 400 years, not because of its adherence to some fictional notion of a scientific method that scientists employ in an objective, non-passionate manner. On the contrary, he notes that scientists pursue their questions about the nature of reality with the same human biases of personal proclivities, attitudes, opinions, desires, experiences, group affiliation, popular fashions and fancies as anyone else. According to Strevens, what makes science unique is that scientists have agreed to use an "**Iron Rule of Explanation**" in their discourse. This Iron Rule requires that all scientific disputes be conducted with reference to empirical evidence.

To be sure, previous to the institution of science, arguments were supported by rhetorical "evidence" – usually in the form of personal anecdotes, testimonials, case studies, casual observations, thought experiments, etc. - selected to support the argument. However, modern science eschewed such evidence in favor of that acquired via systematic observation, especially when variables could be manipulated by the researchers so as to observe the effect of the manipulation on other variables. This method became the gold standard of evidence required by the Iron Rule. Adherence to the Iron Rule forces scientists to uncover and generate new data to support their arguments. This rule channels the scientist's passions (hope, envy, ambition, anger, resentment) and ideology into the production of empirical evidence.

According to Strevens, the Iron Rule of Explanation created a new manner of human communication with arguments based upon the presentation of empirical evidence, rather than upon techniques of rhetorical persuasion (still characteristic of modern non-scientific debates and marketing techniques). Thus, although individual scientists are fallible and have their own values and goals and, occasionally, axes to grind, the iron rule permits science to progress. Since scientists gather data for the purpose of disputation, progress can be made empirically, even when there is a lack of conceptual clarity. This data gathering process gradually builds a consensus about which research paths should be abandoned and which should be supported. Consequently, consensual understanding (a conventional wisdom) is achieved.

Because of the Iron Rule, the scientist has a limited number of options to engage in scientific communication: 1) The scientist can lie about the collected data; 2) the data may be distorted inadvertently; 3) the collection of the data may be conducted in a sloppy manner via insufficient attention to the structure of the research design (e.g., poor selection of subjects for observation, confounding in the manipulation of the variables tested, inadequate or inappropriate statistical analyses); 4) data can be cherry-picked to support the argument (this can happen, either deliberately or not, when the data collection enterprise becomes so vast that it is difficult for any one scientist to be cognizant of all of the data); 5) contradictory data simply can be ignored; 6) finally, scientists can pay extraordinary attention to the details when designing and conducting of their research and when analyzing and interpreting data. It is because most scientists adhere to this last option that ensures progress in the scientific enterprise and the reason why science has been able to transform the trajectory of civilization (Strevens, 2020).

For Strevens, science is not self-correcting; rather, the collection of evidence on a vast scale eventually swamps bad data and incorrect arguments. Although there is much that I admire in Strevens' account of science, I believe that he fails to adequately incorporate the contributions of Kuhn (1962, 2012) and Popper (1959). Kuhn correctly noted the "fashionable" aspect of what he called "normative science". Scientists readily add empirical evidence to a popular hypothesis or theory by conducting studies designed to confirm the hypothesis (demonstrate an effect that is unlikely to occur by chance). This confirmatory process creates a conventional wisdom in each of the various disciplines of science. It is this confirmatory process that prompted Popper to argue that science can only progress via a process of conjecture and refutation. Popper argued that scientific studies should be designed to challenge the tested hypothesis (conjecture), not seek evidence in its support. By deliberately seeking the occurrence of data that a hypothesis claims cannot occur, only then can the hypothesis be evaluated. If contradictory evidence begins to accumulate, then the hypothesis must be reevaluated.

Unfortunately, it may not be possible to always design a "refutation" study. My own research has been constrained by the contingencies of working with human infants and the pressures of academic publication requirements. However, I have tried to include in my research designs the ability to collect data which would contradict my hypotheses. I have done so because if the results do not match those predicted, they still reveal something about the phenomenon of study, unlike simply failing to reject the null hypothesis.

Since most tested hypotheses in lateralization research derive from the conventional wisdom of the discipline, any failure of the data to support the hypothesis can be interpreted as resulting from a weak design and the results may go unreported. Also, any difference from a control group is taken as support for the hypothesis. Thus, it is possible for the confirmation bias of normative science to result in an accumulation of evidence that can swamp not just “bad data” but also data and/or interpretations that otherwise conflict with the conventional wisdom. Moreover, the research enterprise can become so vast that any many researchers (myself included) may fail to be aware of all of the relevant data – Google Scholar search on April 2021 lists over 402,000 articles on handedness. Hence, reviews, hypotheses, and theoretical accounts often suffer from missed or ignored data (the present paper included).

It is my contention that much of the study of hemispheric specialization and interhemispheric communication (HS/HC) is constrained by a conventional wisdom that inhibits discovery of the developmental processes involved. Indeed, many critical reviews of HS/HC note problems of inadequate statistical power, missing details on proportion of those showing atypical lateralization, selection of tasks whose lateralization bias is insufficiently validated, and the use of many different and inconsistent methods to ascertain functional lateralization (Johnstone, Karlsson, & Carey, 2020; Vingerhoets, 2019; Vul, Harris, Winkielman, & Pashler, 2009). Thus, there are too many instances of failures of replication (Bradshaw, Bishop, & Woodhead, 2017), poor research designs (Paszulewicz, Wolski, & Gajdek, 2020), and the accumulation of conflicting evidence that fails to support any explanation of the character of HS/HC (e.g., Flevaris & Robertson, 2016; Guenther & Hickok, 2016) or for the mechanisms responsible for the specialization (Vuoksimma, Koskenvuo, Rose, & Kaprio, 2009).

Please note that I am not advocating for a rejection of the conventional wisdom; I am only noting that too many studies are not designed to challenge it and hence, we cannot know whether the consensus adequately represents the reality of HS/HC. However, I do advocate that there is much to be obtained by adopting a developmental psychobiological perspective to the issues of HS/HC (Michel, 2018). That perspective starts with some theoretical notion about the mechanisms underlying hemispheric specialization

Some Speculations about the Mechanism Underlying Hemispheric Specialization.

The typical functional labels for those processes that differ between hemispheres (e.g., language, spatial ability, positive emotions) hide a myriad of many different simpler neural processes and circuits (Michel, 2018). Only by identifying the precise differences in the processing circuitry between the hemispheres can we discover how particular functions come to be distinct aspects of hemispheric specialization. Although currently there are only a few hypotheses about such processing circuits, it is not unreasonable to presume that hemispheric differences reflect forms of information processing (Albouy, Benjamin, Morillon, & Zatorre, 2020) and/or neural network architecture-function which affect pattern perception and motor organization (Deco, Tononi, Boly, & Kringelbach, 2015) rather than complex functional categories.

One theoretical notion is that complex visual, auditory, and haptic stimuli are composed of many spatial and temporal patterns of transitions in their activation of the sensory/perceptual systems and that these are hierarchically organized according to the relative frequency of the transitions (from low to high). Decades ago, Sergent (1984) proposed a ***frequency hypothesis of hemisphere processing*** which proposed that identifying, comparing and remembering the characteristics of any complex hierarchically structured visual, auditory, or haptic stimulus depends upon **two** neuronal systems. One system is more effective at processing higher frequency transitions in temporal and spatial patterns and, hence, it is better at distinguishing the sort of subtle details that enable discrimination of speech sounds, individual faces, printed letters, etc. The other system is more effective at processing lower frequency transitions and would be better at extracting the more global, or Gestalt, aspects of any stimulus (e.g., prosody, melody, emotional tone, relative position in space).

According to Sergent’s hypothesis, analysis of high-frequency transitions is the typical processing ability of the left hemisphere; whereas, the analysis of low-frequency transitions is the typical processing ability of the right hemisphere (see also, Flevaris & Robertson, 2016 for a more modern perspective). Thus, the prosodic characteristics of speech sounds would be processed by the right hemisphere because they reflect low frequency transitions (Godfrey & Grimshaw, 2016).

This differential processing, however, does not mean that the hemispheres must be distinctly different in their information processing ability. Both hemispheres might be capable of processing information that is in their non-preferred range, but not as proficiently (Sergent, 1982). Developmental experience of success in the usual processing mode, in combination with interhemispheric inhibition (via the corpus callosum among other mechanisms), would likely constrain the ability of the hemispheres to readily shift from their typical processing modes. Since frequency and temporal characteristics of stimuli do not always align with clear distinctions of functional organization (e.g., language vs. spatial), it is not always the case that verbal visual information or speech sounds would reveal a left hemisphere processing advantage or that visuo-spatial stimuli would reveal a right hemisphere advantage. For example, the right vs. left ear advantage in dichotic listening tasks might depend on the *relative* frequency of the presented stimulus (Previc, 1991) among other factors. The right ear (left hemisphere) advantage would be recorded for the higher frequency of two tones, irrespective of whether they represent speech or noise (e.g., Deutsch, 1985; Efron, Koss, & Yund, 1983). Similarly, the right

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hemisphere exhibits an advantage in processing of low frequency information regardless of the stimulus type (Thatcher, 1980). However, developmental events might modulate this difference.

In tonal languages, correct detection of tonal qualities of speech sounds (usually associated with prosody) is necessary for understanding the meaning of those sounds. Therefore, native Mandarin speakers demonstrated right-ear advantage (left hemisphere) for tonal inflection, whereas English speakers tested on the same stimuli exhibited no asymmetry (Wang, Jongman, & Sereno, 2001; Wang, Behne, Jongman, & Sereno, 2004). Although the Norwegian language is also tonal, Norwegian speakers exhibited a right-ear advantage for tonal qualities of their language, but not for tonal sounds typical for Mandarin (Moen, 1993; Wang et al., 2004). This demonstrates a developmental dependency for the lateralization. Also, Zulu language speakers exhibited right-ear advantage for processing of click consonants of Zulu language, whereas English speakers did not show this pattern (Best & Avery, 1999). Thus, as a result of developmental experience, the degree of activation in the left-hemisphere temporal cortex depends on experience in a language-based context, rather than just the characteristics of sounds (Shtyrov, Pihko, & Pulvermuller, 2005).

Hypothesizing a difference between hemispheres in frequency analysis helped clarify the confusing observation of a right hemisphere advantage at discriminating a face from non-face stimulus (Levine, Banich, & Koch-Weser, 1988) and a left hemisphere advantage for discriminating two faces that differ in just one feature; the latter requires a higher spatial frequency analysis (e.g., Patterson & Bradshaw, 1975; Sergent, 1982). Thus, neither functional categories nor simple notions about processing strategies (spatial and temporal frequency analysis) characterize the differences between the hemispheres because developmental experiences (with faces, native language sounds, etc.) contribute to the shaping of hemispheric differences. Developmental psychobiological research frequently shows that the developmental origins of species-typical traits often begin with nonintuitively obvious patterns quite distinct from the species-typical forms manifested later (Michel & Moore, 1995). For example, face-selective neural activity in the right hemisphere of four-month-old infants is mediated by the presence of a maternal body odor (Leleu et al., 2020). Thus, early exposure to the mother's face during feeding and close-contact permitted the maternal odor to enhance right-hemisphere face processing and this enhancement was not a consequent of arousal or visual attention in the maternal odor context.

What is frequently missing from spatial and temporal frequency notions of hemisphere differences in processing hierarchically structured stimulus patterns is that the hemispheres also differ for the construction of actions. Data from animals (Forrester & Todd, 2018) and humans (Pflug, et al., 2019) show that the left and right hemispheres of the brain confer asymmetric contributions to the organization and manifestation of sensorimotor processes and manual actions. Therefore, motor behaviors can be informative behavioral markers of asymmetric brain function and organization.

The left hemisphere is typically involved in the production of precisely-timed, serially-ordered fast movement patterns that contribute to the articulation of speech sounds, as well as sophisticated manual actions manifested in object manipulation, artifact construction, tool-use, imitating actions, and communicative pantomiming. In contrast, the right hemisphere seems to provide the postural and contextual support for the manual actions produced by the left hemisphere. Trajectory control and visual feedback for movement of the preferred right arm is processed more accurately whereas positional control and proprioceptive feedback is processed more accurately with the non-preferred left arm (e.g., Goble and Brown, 2008). Indeed, there are complementary specializations of each hemisphere for different aspects of the manual control involved in a role-differentiated bimanual manipulation (RDBM – the preferred hand holds the needle in sewing or the lid when unscrewing a jar, etc.) task (Woytowicz, Westlake, Whitall, & Sainburg, 2018). Again, these differences are relative, not absolute.

Moreover, human motor cortical organization of control of arm and hand muscles is influenced by handedness (as measured by the Edinburgh Handedness Index - Nicolini, Harasym, Turco, & Nelson, 2019). The cortical representation of the muscles for the preferred limb of both left- and right-handers is larger. Changing handedness through practice, either willingly or if obliged by injury, is not easy. However, a review of the studies examining brain activation and hand skills after such handedness shifts reveals that practice seems to play a significant role in the formation and consolidation of both neural and behavioral asymmetries **(**Marcori, Monteiro, & Okazaki, 2019). Since the motor cortex has extensive interconnections which can permit experience-based potential for functional reorganization (e.g., Hammond, 2002), any asymmetry of use would lead to increased practice of the preferred hand, and further enhance the skill of that hand. Living in a society, which strongly favors the use of right hand, could encourage enhanced use of right hand for trajectory and left hand for positional control during development, even for those developing a left-hand-use preference. Thus, left-handedness would not be the mirror of right-handedness in neural structure or function.

Both hemispheres potentially appear to be capable of processing any type of information, whereas, the relative spatial or temporal frequency pattern of the information, its complexity, and socio-cultural experiences and practice aspects would influence which hemisphere might cope with a particular task more effectively. Both hemispheres may be capable of controlling precisely timed, sequentially organized muscle contractions and relaxations that underlie the ability to manifest serially ordered speech and manual skills. However, the skill differences that come from experience and the influence of interhemispheric communication (both inhibition and facilitation) likely contribute to how the hemispheres become functionally lateralized during development. Therefore, it is not correct to state that there is a distinct division of processing ability between the two hemispheres or that the left hemisphere controls language functions while the right hemisphere controls visuo-spatial skills.

There are two important caveats for understanding hemispheric specialization. *First*, the division of labor between the hemispheres has a relative rather than absolute character that seems to be established during development. This means that the type of information processing, or action programming, is more important for the distribution of work between the two hemispheres than our linguistic labels for such phenomena. *Second*, although the two hemispheres become structurally and functionally distinct during development, they are still deeply connected via the corpus callosum and other integrating networks: they have access to and can potentially process any type of information needed for the manifestation of any skill. Therefore, the development of callosal functioning ought to be a major concern of developmental studies of hemispheric specialization. How and when different forms of processing control can be shared across hemispheres will greatly affect the development of specialization.

Character of Human Handedness.

Laterality refers to asymmetries of bilateral structures (including neural structures) and left-right biases in function and behavior. Laterality has been demonstrated in species from all major vertebrate classes, and in many invertebrates (cf., Wiper 2017). Some have considered this evidence of evolutionary conservation (cf., Gunturkun & Ocklenburg, 2017) which suggests strong evolutionary pressure (something akin to the pressure responsible for the rostral-caudal and dorsal-ventral asymmetries). In humans, laterality typically refers to a division of functional processing between the two cerebral hemispheres. This pattern of functional asymmetry is explained in terms of preventing conflict between duplicate functional regions, enhancement of parallel processing, and increased neural capacity by eliminating redundant duplication (cf., Gonzalez, Rootslaar, & Gibb, 2018).

Although most of the reviews (cf., Rogers, 2014) and theorizing (cf., Rogers, Vallortigara, & Andrew, 2013) focus more on the advantages and potential evolutionary adaptiveness of lateral asymmetry than on its phylogeny (evolutionary history), it is difficult to specify the benefits (vs. costs) for many lateral asymmetries (Gunturkun & Ocklenburg, 2017). Laterality at the individual level supposedly provides advantages by increasing efficiency in neural organization (Gonzalez, Rootslaar, & Gibb, 2018), for foraging (Fragaszy and Mitchell 1990), for monitoring predators (Rogers 2000), for numerical abilities (Dadda, Agrillo, Bisazza, & Brown, 2015), etc. Laterality at the population level supposedly provides advantages by facilitating behavioral coordination between asymmetrical individuals of the same or different species (e.g., Baraud, Buytet, Bec, & Blois-Heulin, 2009; Chapelain et al. 2015; Vallortigara and Rogers 2005).

However, consider human handedness: it is likely that handedness reduces the decision time for the initiation of unimanual tasks (putting food in mouth, throwing or swinging a stick) and for the selection of the different actions in role-differentiated bimanual manipulations (RDBM). During RDBM, the preference efficiently dictates the sequence of the actions of each hand and the practice of manual actions improves their skill of execution. It is possible that a population-level hand preference may facilitate the acquisition of manual skills via imitation (Michel & Harkins, 1985; but see Uomini, & Lawson, R., 2017). However, it is more difficult to specify benefits and costs for the population to have a prevalence for a particular form of handedness (e.g., right handedness) unless it is an artifact of some other form of lateral asymmetry (e.g., hemispheric control of language functions, Annett, 2002). If the latter, then there must be benefits to maintaining a minority form (left-handedness, e.g., Mebert & Michel, 1980; Michel, Nelson, Babik, Campbell, & Marcinowski, 2013) or an atypical hemispheric separation of functions (Vingerhoets, 2019).

The human population-level laterality is left hemisphere specialization for language and praxis and right hemisphere for spatial attention, face recognition, and prosody of speech. However, there is some evidence that atypical functional segregation in the hemispheres may not be very rare in the general population (Vingerhoets, 2019). Therefore, investigation of those individuals with atypical functional segregation ought to be a priority for understanding notions of “neural crowding” and the value of “complementarity” in theories about the benefits of HS/HC. As yet, any distinct disadvantages for individuals who fail to exhibit the typical pattern of lateralization has not been demonstrated (Bishop, 2013). Moreover, there are many aspects of both cortical and sub-cortical neural functioning for which there appears to be neither evidence of any lateral asymmetry nor evidence of inefficiency or disruption as a consequence of their symmetry.

Although five non-mutually exclusive theories have been proposed to account for the population predominance of human right-handedness (cf., Prieur, Lemasson, Barbu, & Blois-Heulin**,** 2018), the postural theory (MacNeilage, 2007; MacNeilage, et al. 1987) seems to be the most popular. This theory proposes that manual laterality evolved in primates from structural and functional adaptations for unimanual feeding (initially arboreal and requiring three limb support for acquiring food with the free limb that shifted when terrestrial species evolved).

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Unfortunately, none of the five theories adequately accounts for the predominance of right-handedness in humans or for the consistent minority of left-handers (cf., Papademetriou, Sheu & Michel, 2005).

Indeed, one problem with accounting for the evolution of human handedness is the assumption that all aspects of handedness are derived from the same underlying mechanisms and reflect the same phylogenetic history. When explanations for population-level asymmetries of hand-use preference are made, they fail to distinguish between homologous and convergent laterality (Michel, 2013). The issue of underlying identity is an important feature of character specification in taxonomy and phylogeny. Are traits similar across species or across ontogenetic phases within a species because of homologous (derived from the same ancestral character) or convergent (adapted to similar ecological conditions) evolution?

Handedness exhibits similarities across species (in the form of preferred limb-use) and similarities across development within an individual. In order to pursue the developmental psychobiology of handedness, I depend on the concept of homology to extrapolate from experimental research on the neural mechanisms involved in the control of limb use in certain model mammals to my explanations of the differences in how the preferred and nonpreferred hands are controlled in humans (see section The Neuroscience of Arm/Hand Control).

Thus, I infer, from experiments involved in controlling hand use in specific primate species, that differences in visual, haptic, and proprioceptive experiences between the hands results in differences in their neuromotor control mechanisms. In turn, these differences in control concatenate through continued use into distinct differences in neural circuitry between the left and right hemispheres of the brain (Volkmann, Schnitzler, Witte, & Freund, 1997). However, I do not assume homology of hand-use preferences among primates. Throwing a stick or rock to hit a target relies on the same homologous structures (skeletal musculature, visual-motor neural pathways, and likely sensorimotor coding processes) as hurling a javelin or pitching a baseball but that does make them homologous actions. It is more likely that they are related via functionally prompted transfer of skills (Bavelier, Bediou, & Green, 2018).

There are five criteria for identifying homology (Atz, 1970; Michel, 2013); three concern morphological structures and two concern behavioral functions, specifically. The latter two include movements employing homologous structures (defined by any of the three morphological criteria) in similar ways may be considered homologous. Behaviors dependent on homologous regions of the brain may be considered homologous (Pribram, 1958). Unfortunately, since structure constrains function, behavioral similarities can be biomechanically induced without reflecting homology. Also, although there are homologous regions of the brains of vertebrates, strikingly dissimilar behaviors often depend on these homologous brain regions (Atz, 1970).

Therefore, caution must be exercised in identifying a behavior as homologous based on similarity of movement pattern, the employment of homologous structures for the movement, or when relying on homologous aspects of the nervous system. Throwing sticks and rocks are unlikely to be homologous across ape species but rather simply transferred skills prompted by functional goals of hitting a target with an object and constrained by the characteristics of the object (e.g., aerodynamics, manual affordances, and physical mechanics), the conditions of the context (e.g., wind, speed of action, distance to target, relative positions of subject and target), and the constraints from the biomechanics of the limb (Kutch & Valero-Cuevas, 2012).

Atz (1970) argued that using the construct of homology in behavior research requires: (i) robust descriptions of the behavioral repertoire of an organism; (ii) extensive comparative work on both morphology of structures and the structure–function relation in neural processes across a wide range of species; and (iii) detailed descriptions of developmental processes, especially in closely related species. All of these requirements are missing from the investigation of hemispheric specialization of function, including handedness (Michel, 2013). There was no evidence to support the notion that the hand preferences (however defined) exhibited at different phases of development (prenatally, infancy, toddlerhood, preschool, preadolescent, adolescent and adult) represent different manifestations of the same underlying trait in the manner of a serial homology. Therefore, human handedness is likely a convergent trait which evolved independently among different species and which emerges across developmental phases as ontogenetic adaptations to the ecological conditions specific to each different phase (Oppenheim, 1984). However, if handedness does represent ontogenetic adaptations, then any account of its development must address how can it exhibit the same preference (e.g., right-hand) across different phases of ontogeny (see section "My Perspective on the Development of Handedness").

The lack of homology of hand preferences during development requires that each type of preference must be examined in relation to both concomitant developmental changes in brain structures/functioning and developmental changes in cognitive, emotional and social abilities. Also, each of these abilities must be carefully described according to their sensorimotor character and not just by their functional consequences. For example, careful description reveals patterns of infant facial expression that evoke perceptions of infant emotions by observing adults (Camras, Sullivan, & Michel, 1993) but these patterns really reflect coordinative structures of movement synergies (Michel, Camras, & Sullivan, 1992). How those coordinative structures develop into expressions of emotion has not been systematically investigated but should be (cf., Camras & Witherington, 2005).

Of course, a "deep homology" could be identified if the same DNA information relates to the different forms of handedness. Since hemispheric specialization is considered to be the result of genetically determined processes of neural circuit formation, it is not surprising that handedness also would be considered to be genetically determined. Studies of large populations have been disconcerting because they have failed to reveal any Mendelian character to handedness. Moreover, these studies have shown that genes account for only a minor proportion of the variance of handedness in the population. Indeed, heritability estimates for handedness are in the range of 0.23–0.45 (Annett, 1985; McManus and Bryden, 1992; Medland et al., 2006; Porac and Coren, 1981; Risch and Pringle, 1985; Warren et al., 2006). Elsewhere (Michel & Moore, 1995; Michel, 2013; Michel, et al., 2013), I have noted that **heritability estimates** do not reveal the degree of genetic influence on a trait. Rather, heritability estimates only identify the relative ease by which controlled breeding manipulations could change the distribution of a trait in the population. Moreover, such heritability estimates for breeding require that there be no changes in the environmental conditions; otherwise, the estimates can change.

In a study of over 12,000 subjects, using their own non-psychometrically evaluated questionnaire (Granville, Ehrman, & Perelle, 1979), but not using heritability estimates, Perelle and Ehrman (1994) reported that 76% of right-handed and 61% of left-handed subjects had reported no left-handed first-degree relatives. A recent meta-analysis of 35 samples from studies of twins that employed techniques for estimating heritability, found that additive genetic effects account for 25% (95% Confidence Intervals = 16–30%) of the variance in handedness with the remainder associated with unique non-shared environmental effects (Medland et al., 2006). Similarly, a large study of twins and their family members from Australia and the Netherlands estimates that only 25% of the variance in handedness is attributable to additive genetic effects

(Medland et al., 2008). In a sample of 30,161 adults in Finland (Vuoksimaa, Koskenvuo, Rose, & Kaprio, 2009), unique environmental effects accounted for most of the observed variability of handedness, both in childhood (92–100%) and adulthood (74–86%).

Based on self-reported handedness from over 72,000 offspring, McManus and Bryden (1992) found that the prevalence of left-handed offspring with two left-handed parents was 26% and about 20% with one right-handed and one left-handed parent (only 10% with two right-handed parents). A higher proportion of left-handedness has been observed in children from right-handed fathers and left-handed mothers (R-L pair) than from left-handed fathers and right-handed mothers (L-R pair - Annett, 1975; Harkins & Michel, 1988; McKeever, 2000; McManus, 1991). McManus (1991) estimated an increase frequency of only 0.4% of left-handedness in children of R-L pairs as compared with an increased frequency of 2.9% in children of L-R pairs, with higher left-handedness rates reported in male offspring in both sets (see also, Harkins & Michel, 1988). Michel (1992; Michel et al., 2013) provided evidence of some of the social interactive influences on offspring handedness, which derive from maternal-infant engagement with objects, that likely accounts for the greater left-handedness in offspring of R-L parents.

A recent meta-analysis of genome-wide association studies (McManus et al., 2013) estimated the number of genetic loci that relate to handedness differences is likely to be between 40 and 100. However, it is more likely that the 40-100 loci are more related to specifying the receptors for specific neurotransmitters, their location within the neural cell membrane, the enzymes and proteins for the production, transport, storage, and release of the neurotransmitters involved with sensorimotor control of the actions of the hand and arm. Moreover, these molecular mechanisms may operate at different levels of the nervous system (e.g., spinal, brain-stem, and cortical, Gunturkun & Ocklenburg, 2017). And they may have effects on other organ systems as well as other functions. It would seem to be a fool's errand to try to specify the genetics of handedness, much less to use it to distinguish homologous from convergent evolution. This is not to deny the necessary role of molecular neurobiological processes, in which DNA plays a part, in the manifestation of handedness; rather, I do not expect that there is a DNA contribution that is sufficient to explain the unique character of handedness. Thus, the studies of the genetics of handedness force me (Michel, 2013, see also Gunturkun & Ocklenburg, 2017) to conclude that: 1) handedness emerges from a developmental process in which genes play, at best, a very limited and indirect role; 2) there is unlikely to be any deep homology in ontogenetic or phylogenetic handedness.

Assessing Handedness

As McManus, Van Horn, and Bryden (2016) note, handedness is "…that difference between the hands of which every right-hander and left-hander is **entirely aware** from their own behaviour, but for which we have almost no adequate scientific explanation" (p. 394, emphasis added). For me, this definition of handedness aligns with only one method of handedness assessment, of which I count four. The **first** handedness assessment method is the most familiar and is associated with human narrative identity ("I'm right-handed"). For most societies, handedness becomes a part of the person's identity similar to their gender, geographic locale (e.g., British, Parisian, Australian, Bostonian), familial ethnicity (e.g., Irish, Scandinavian, German, Italian, Persian, Thai, Taiwanese), etc. Like most forms of our narrative identity, the developmental precursors become observable during the second and third postnatal year and are marked by the production of such statements as "I am", "like me", etc. Therefore, the acquisition of symbolic language seems to be an important characteristic in the development of an individual's narrative or self-identified handedness. Once established, this handedness identity likely plays a role in the subsequent development of manual skills as children seek to make their skills concordant with their narrative identity.

Oddly, some societies have separate words for the right- and left-hand use (as in English), but they do not have a way of expressing a hand-use preference as part of their narrative identity (cf., Cavanagh, Berbesque, Wood, & Marlowe, 2016; Perelle & Ehrman, 2005). Members can describe a preference for which hand they use for various manual activities (hammering, throwing, sewing with a needle, pulling the flesh while skinning an animal, etc.). Interestingly, the hand-use descriptive pattern that these societies use is very similar to a **second** method of assessing handedness: the self-report of the hand preferred for various manual actions (both unimanual and RDBM). This assessment method is represented by the 3 or 4 different questionnaires frequently used in neuropsychological research (e.g., the Edinburgh Handedness Index-EHI (Oldfield, 1971), the Waterloo Handedness Questionnaire-WHQ (Bryden, 1977), Annett Questionnaire-AQ (Annett, 1970), Home Handedness Questionnaire-HHQ (Nelson, Gonzalez, El-Asmar, Ziade, & Abu-Rustum, 2019)).

Interestingly, the self-identity handedness fails to capture the individual variability that emerges when large samples of people are assessed via questionnaires. Indeed, the classification distribution for questionnaires is not as clearly categorical as that of self-identity (but see, Dragovic, Milenkovic & Hammond, 2008) and the more varied the manual tasks addressed by the questions (usually 10-15 tasks but can be as many as 60+), the more individual variability that can be expressed. Of course, there are statistical procedures that can reveal latent categories of people by identifying the associative patterns among the answers to the questions (Dragovic et al., 2008). There may be three or more dimensions of handedness on which people may differ (Healey, Liederman, & Geschwind, 1986, but see Steenhuis & Bryden, 1989) or as many as eight handedness types (Annett, 1970) depending on the type of analysis used and the number of questions in the questionnaire (Bishop, 1990).

The answers on a questionnaire are typically reduced to a single score, a Laterality Index (LI - (often (R-L)/(R+L) answers)). Interestingly, this LI can be used for various measures of hemispheric specialization of function from fMRI (Bradshaw et al., 2017) to observational measures of handedness (McManus, et al., 2016). All too often, researchers choose an arbitrary cut-off score for the index in order to create most often 2, but sometimes 3 categories (to capture ambilateral individuals) of people's handedness. These categories provide some consistency between the questionnaire and the narrative identity pattern. Unfortunately, problems arise because arbitrary cut-off scores can vary across studies making the categories established less reliable.

For example, although the typical LI ratio does not indicate whether the difference between the hands (or hemispheres) is significant, a categorical dominance classification is often imposed. A standard method of dominance classification for fMRI (Bradshaw, et al., 2017) uses cut-offs at +0.2 and -0.2, to divide left dominance (LI > +0.2) from bilaterality (-0.2</= LI </=+0.2) and right dominance (LI <-0.2). However, since such cut-offs are arbitrary, and Bradshaw, et al. (2017) found multiple studies that chose their own cut-offs values, including 0.1, 0.33, 0.4, 0.5 and 0.6. Using statistical classification techniques could provide some estimate of the reliability of the classification (e. g., for handedness, Michel, 1981; Michel, Shue & Bromley, 2002; for fMRI, Baciu, Juphard, Cousin, & Le Bas, 2005), but these techniques are seldom used (cf., Campbell, Marcinowski, Latta, & Michel, 2015).

Indeed, variability in how handedness is assessed (e.g., parental report or measured hand-use preference), the type of handedness assessed (e.g., reaching or manipulation), methodology (ages of assessment, frequency of assessments, and time between assessments), and how the differences between the hands are defined (Ferre, Babik, & Michel, 2010; Michel, Sheu, & Brumley, 2002) is likely to have contributed to the conventional notion that handedness is unreliable and unstable before 6–10 years of age (Schaafsma, Riedstra, Pfannkuche, Bouma, & Groothuis, 2009). However, defining a hand-use preference by a simple difference between hands (a "handedness index", Ramsay, 1980) may create the impression that hand preferences are unstable across assessment ages. Whereas, defining a preference by statistical estimates of whether the intermanual differences are likely to have occurred by chance (Michel et al., 2002; Michel, Tyler, Ferre, & Sheu, 2006) can reveal consistent patterns (Ferre, et al., 2010; Marcinowski, Campbell, Faldowski, & Michel, 2016). Also, Ferre et al. (2010) found that four bimonthly longitudinal assessments during the period from 6 to 14 months of age show a different pattern of handedness development (no significant trend in hand-use preference) than nine monthly assessments (a significant quadratic trend for right hand-use preference). Infant handedness reflects the consequences of an immature but rapidly developing nervous system and appears to be sensitive to various assessment procedures and conditions. Nevertheless, this does not mean that infant handedness is unreliable or even unstable or cannot be characterized.

Although questionnaires often show poor test-retest reliability (Flindall & Gonzalez, 2019), this can be improved psychometrically (Tran & Voracek, 2019). Indeed, using a psychometrically enhanced version of the EHI (and comparing it to a speed of finger-tapping performance task) and two taxometric procedures, Dragovic, et al. (2008) provided evidence that the distribution of hand preferences is discrete, not continuous. They found three categories of hand preference in large samples from two different geographic and demographic populations (Serbian teenagers and Australian adults): ~64% with consistent right-handedness, ~29% with inconsistent right handedness, and ~7% with consistent left handedness. Hand preference was assessed using a shortened (only seven questions – drawing hand, upper hand on broom, and hand for lifting lid of a box were removed) but psychometrically enhanced EHI with better measurement properties (Dragovic, 2004).

Interestingly, one criticism of the EHI is that it is composed of actions, the majority of which are culturally dependent on Westernized tools (Perelle & Ehrman, 2005). Even a sample from a population in France had to have the broom question removed because so few participants had experience with a broom (Mazoyer et al., 2014). Nevertheless, the EHI is the most commonly used handedness assessment method in neuroscience research (Edlin, Leppanen, Fain, Hackländer, Hanaver-Torrez, & Lyle, 2015). Also, when used, it is often modified according to the purposes of the researcher, which can change its psychometric properties (Edlin, et al., 2015).

For example, Christman and colleagues (e.g., Prichard, Proper, & Christman 2013; Jasper et al., 2021) used neither a statistical nor a taxometric method with EHI scores to create a three-group classification procedure that distinguished “consistent right-handed”, “consistent left-handed” and “inconsistent handed” (or “mixed-handed”) individuals. They note that mixed-handed individuals are not ambilateral. Indeed, a “mixed-handed” individual could be someone who reports “always” using their right-hand for 8 of the 10 EHI questions and “usually” using their right hand for 1 activity and “always” using their left hand for the one remaining question. Thus, the “mixed handed” groups is likely to be more heterogeneous than the “consistent handed” group (a dodgy problem for statistical analysis). Then, they examined different relations of mixed-handed vs. consistent-handed individuals for many psychological functions (e.g., eating disorders and body image, gullibility, false memory, framing effects in cognitive decisions, Foreign language learning, episodic memory, paranormal beliefs). Some of these functions are measured by questionnaire but some by empirical manipulations (Jasper, et al., 2021).

Since mixed-handedness (albeit not defined as in the Christman studies) is reported to be associated with a larger corpus callosum and presumably facilitates interhemispheric communication, Christman and colleagues posed a particular hypothesis about hemispheric specialization of function and interhemispheric communication to account for the observed relation of handedness to so many psychological functions. Their hypothesis (Jasper, et al., 2021) proposes a dual process pattern of hemispheric specialization with some psychological functions requiring mutually exclusive separation between hemispheres (e.g., left hemisphere efficiently processes prototyped/abstract visual forms whereas right hemisphere efficiently processes exemplar/specific visual forms) and other functions require interhemispheric integration for effective functioning.

By re-examining several of their experiments, they (Jasper, et al., 2021) discovered that when dual processes must be integrated, mixed-handers are more affected by the experimental manipulations; whereas, if the processes are mutually exclusive (independent), then it is the consistent right-handers who are more affected by the experimental manipulations. Christman and colleagues do note that the hemispheric specialization of some functions for consistent left-handed individuals is distinctly different from that of consistent right-handed individuals but since consistent left-handers are such a small proportion of the population (~2-3% by their method of classifying handedness), they are considered too difficult to study and were ignored (Jasper, et al., 2021, footnote p 3).

So, in order to reveal a relation of handedness to a very large variety of psychological functions, Christman and colleagues propose an elaborate theory about the relation of types of handedness (consistent vs. mixed) to hemispheric specialization and interhemispheric communication. To derive the consistent verses mixed handedness groups, they manipulate the EHI by using the absolute value of the LI scores, identifying the median (supposedly a score of 80), and then classifying individuals with absolute value scores of 75 or less as mixed-handed and those with higher scores as "consistent-handed". Using the median to construct groups is statistically troublesome, at best. At least, the classification technique of Dragovic, et al. (2008) might have been a more defensible procedure for specifying handedness groups. Even so, I would argue that the Christman method is not an adequate means of defining handedness groups, especially from the EHI scores. Therefore, the relation of handedness to such a variety of psychological functions needs replication and evaluation using more defensible ways of characterizing types of handedness. Indeed, I would apply this concern to nearly all studies that use questionnaire data to relate handedness to other psychological functions.

A **third** method of assessing handedness derives from observing preferred hand use during various manual actions. This reveals even more individual variability than the questionnaire assessment, probably because the self-report is biased by the individual's narrative identity and their desire to create cognitive consistency. Also, the questionnaire may miss some aspects of manipulation that commonly occur in daily activities (self-grooming, gesturing, pulling/pushing oneself up from squatting, etc.). Observed handedness ought to bear some relation to hand differences in the gestural actions of infants and children (but see Esseily, Jacquet, & Fagard, 2011; Jacquet, Esseily, Rider, & Fagard, 2012). Also, unless statistical procedures are used to reveal underlying groups of individuals with different patterns of hand-use expression (Michel, Babik, Sheu, Campbell, 2014), the variability is likely to be more continuously distributed among the members of the population.

The **fourth** assessment method examines differences between the hands in actual skilled activities. The measures include speed and accuracy differences between the hands or perhaps differences in leaning trials. There are various elements that make up manual skill, such as grip strength, finger dexterity, sequencing ability, and coordination, all of which can be revealed in different functional tasks (Bishop, 1990). These measures can produce more precise descriptions of individual variability of hand-skill differences. Of course, this fourth method is affected by hand preference differences which can lead to practice differences between each hand. Thus, skill differences have to be assessed with tasks that bear little resemblance to more highly practiced common manual actions (originally derived from hand-use preferences) with the hope that there are no simple transfer effects from the highly practiced actions to the relatively novel actions. Novel tasks are believed to identify the underlying processing differences between the hemispheres that produce the functional differences of handedness. However, even moving pegs from one set of holes to another nearby set likely involves transferred skills from other manual actions of grasping, relocating, and releasing an object.

This fourth method ought to provide insight into the organization of the neural circuits that control different kinds of manual actions (e.g., finely-timed, serially-ordered motor control of finger movements versus finely-timed, serially-ordered motor control of shoulder, elbow and wrist movements, or visually-guided actions versus more ballistic or proprioceptive-guided actions). Also, the assessments from this fourth method ought to correlate with praxis in neuropsychological functioning. Although the preferred hand is generally more skilled at performance-based tasks than the non-preferred hand (Hausmann, Kirk, & Corballis, 2004), McManus, et al. (2016) argue that measurements of performance, rather than reported preference, ought to be relied upon when investigating hemispheric specialization of function. Performance tasks likely tap into the neural mechanisms underlying lateralization of functions.

Several studies have used performance-based measures of preference, such as midline crossing tasks (e.g., Bryden, Singh, Steenhuis, & Clarkson,1994) to assess handedness. These tasks measure the point at which reaching across the midline into contralateral (i.e., opposite) space with the preferred hand becomes too awkward and participants switch to the non-preferred hand to complete the task. Unfortunately, since there is no agreed upon set of novel tasks to measure the different aspects of hand differences in skill nor agreement on how to combine the speed and accuracy differences between the hands across tasks to create a general manual difference score. Also, since such performance tasks require the participant's comprehension of instructions and a motivation to perform the task as quickly and accurately as possible, this method is not appropriate for studying handedness development during infancy and early childhood. Finally, to date, this method has not incorporated any measure of RDBM (but see Wolff, Michel, & Ovrut, 1990), which may be the most important component of the expression of human handedness because so much of historical and even current tool-manufacture and tool-using skills involve RDBM actions (e.g., Gonzalez & Nelson, 2015; see also, Kuo & Fisher, 2020 about RDBM in professional musicians).

Comparison across each of these four methods of assessment results in too many individuals being classified differently (Flindall & Gonzalez, 2019; McManus, et al., 2016). A self-identified right-hander may become a weak left-hander by questionnaire, observed preference for use, or in measures of the differences in skill between the hands. Therefore, it is not surprising that across studies, there would be differences in the association of handedness with other forms of hemispheric specialization. Indeed, some conclude (e.g., Prieur, et al., 2018) that genetic and neuroimaging studies in human adults have failed to support any causal relation between the direction of handedness and the lateralization of language. However, most studies assessing hemispheric specialization of function still use self-identity (sometimes checked by writing hand) or a questionnaire (most often the EHI) to assess handedness (Edlin, et al., 2015).

A recent study (McManus, et al., 2016) compared performance differences between hands using the Tapley and Bryden task (TBT) of dotting inside sequences of "Os" and the Annett pegboard task (APT) and related these performance differences to the scores on a modified EHI and self-described handedness. When classified into groups, the distribution of LI scores on the mEDI was highly correlated with self-described handedness. I would interpret this result as the need of adult subjects to make their questionnaire answers consistent with the narrative identity of their handedness. McManus et al. (2016) also reported that despite the T&B performance task being a very good measure of direction (R or L) of handedness, it is not a good measure of degree of handedness. They conclude that differences between right- and left-handers and differences between strong and weak righthanders (or strong and weak left-handers) are due to different processes and different underlying mechanisms. As yet, there is no evidence for these different mechanisms.

However, it is likely that the neural mechanisms associated with controlling the sensorimotor skills involved with the actions that create handedness differences in performance or preference-for-use are different from those associated with self-identity or language-dependent questionnaire accounts of handedness, both of which depend upon declarative memory. I would argue that the neural mechanisms associated with identity and self-report assessments would bear little relation to those associated with the production of speech (a sensorimotor process that is more similar to the control of the hands). Therefore, I would not expect identity handedness to be related to measures of speech production and decoding.

Hickok and colleagues (2012; Hickok & Poeppel, 2007; Guenther & Hickok, 2016) also argue that the neural circuits involved in speech production and decoding are different from those involved with processing the conceptual-semantic aspects of speech. They propose that the processes used to produce speech (and decode it before subsequent semantic analysis) are associated with circuits that are involved with other sensorimotor processes. Indeed, there appear to be neural circuits that support the interface between auditory and motor processing of speech similar to those involved with sensory-motor integration. These supramotor functions (e.g., sequencing actions and the precise timing of muscle contractions and relaxations) are not specific to speech but underlie all action preparation (Pulvermüller and Fadiga, 2010).

Many models of speech motor planning posit that speech builds upon common action control and motor-sequencing mechanisms which support many different cognitive processes (Freund, Jeannerod, M., Hallett, & Leiguarda, 2005; Tremblay, Deschamps, & Gracco, 2016). Therefore, the neural organization of speech production is likely to overlap with those motor control regions likely involved with manual differences in those skills associated with handedness. For example, Broca’s area has been observed to be associated with various nonlanguage motor functions such as planning, recognition, and imitation of actions and tool use (Binkofski and Buccino, 2004; Higuchi, Chaminade, Imamizua, Kawatoa, 2009). Therefore, if handedness is to be related to hemispheric specialization for speech production, we need to focus on differences in hand preference or skill, not narrative identity or questionnaire scores (Michel, et al., 2013).

The sequencing of speech motor acts and the organizing of segmental information into words and sentences prior to vocalizing, relies more heavily on the motor areas. Interruption of these motor regions via transcranial magnetic stimulation (TMS) has been shown to disrupt sequencing actions on a finger-tapping task and to impair performance of oral motor gestures (Tremblay and Gracco, 2009). Such results suggest that the cortical organization of motor and speech networks may be complementary (Gentilucci, 2003). Studies also show a clear role for the cerebellum and basal ganglia in translating motor planning into action for speech and manual actions (Tremblay et al., 2016) and deficits in cerebellar–parietal networks occur in children with developmental coordination disorder (DCD - Zwicker, Missiuna, Harris, & Boyd, 2011). Therefore, to understand the manifestation of handedness, it is important to understand the neuroscience of forelimb movements.

The Neuroscience of Arm/Hand Control

Bizzi and colleagues (e.g., Bizzi & Ajemian, 2020), using research with mice and monkeys, have proposed a sensorimotor feedback loop perspective for understanding the control of the arms and hands in humans. There are multiple sensorimotor loops involving various areas of the cortex, other brain regions, the spinal cord, and the sensorimotor periphery, all of which influence the cortical motor output regions. They argue that the continuous convergence of these loop activities at the cortical output regions somehow results in the emergence of functionally appropriate movement commands. Thus, supraspinal control of spinal cord dependent motor action emerges as a result of multiple sensorimotor loops converging on motor cortex (of course, there are other supraspinal projections to the spinal cord that contribute to the production of movement and the maintenance of posture).

The spinal cord produces motor actions (muscle movements) via motoneurons in the ventral horn which project directly to muscle cells. Also, interneurons in the cord form connections with multiple motoneurons. The activity patterns of interneuronal connections among motoneurons operate as action circuits or “muscle synergies” (Bizzi & Ajemian, 2020) coordinating muscle contractions and relaxations. The “memory” (likely via synaptic processes) of forces stored in these action circuits in the spinal cord represent motor primitives from which many movements can be formed via the imposition of neural impulses from supraspinal tracts. By differentially combining this relatively small set of muscle synergies, via supraspinal variations in the timing and sequence of their activity, the CNS can create a wide diversity of actions that likely are only constrained by the biomechanics of the skeletal-muscle system and the conditions of the task and context (Kutch & Valero-Cuevas, 2012).

Thus, the same spinal muscle synergy may be used in a variety of actions and different actions may be constructed from the same set of synergies by altering their timing and scaling factors. The development of new skills can lead to the formation of new specialized task synergies (Gentner, et al., 2010), but these may involve cortical sensorimotor loops creating synergies in primary motor cortical cells (M1) and dorsal premotor cortical cells (PMd).

There is some evidence that the synergies in the spinal cord of 5-day-old rats do not change further during development (Yang, Logan & Giszter, 2019). However, the life of a lab rat is not particularly complex nor does it require adjustments to a changing environment. Therefore, developmental psychobiologists Robinson, Brumley, and colleagues have demonstrated that from embryonic day 19 through postnatal day 7, the fetal and young rat pup is capable of learning new and unusual coordinative patterns of limb activity that likely involve new spinal synergies created by sensory feedback (Brumley, Strain, Devine, & Bozeman, 2018; Brumley, Kauer, & Swann, 2015; Brumley & Robinson, 2012; Robinson, 2005, 2015, 2016; Robinson, Kleven, & Brumley, 2008). Therefore, it is quite likely that the synergies established in the prenatal spinal cord are influenced during their development by feedback from the spontaneous myogenic and neuromotor activity of the fetus and newborn. Any lateral asymmetries in such feedback would impose asymmetries in the spinal synergies (Previc, 1991).

During movements, the muscle synergies together with their muscle spindles, joint, and skin receptors generate a flow of diverse sensory signals that provide feedback to the establishment and maintenance of the synergies. These sensory signals, by way of multiple ascending pathways, provide the M1 and PMd cortical cells with the feedback that contributes to the regulation of these cells as they activate the movement that permits conformance to the external world. Thus, any lateral asymmetries in spinal synergies could influence the development of lateral asymmetries in cortical motor mechanisms.

Bizzi's sensorimotor loop perspective argues that all movement involves a continuous interplay between system inputs/outputs and behavioral "predictions"/realizations (Saurbrei, et al., 2020). Effective functioning of arm/hand actions needs simultaneous feedback of position, velocity, and force information for modulating effective performance in the event of possible perturbations. In adult humans, the M1 and PMd cells become active during preparation for movement. They also become active when thinking about performing an action or observing others perform the action.

Besides activating the muscles for the performance of an action, the motor system must anticipate and cope with movement-related challenges (postural adjustments to maintain stability during action, inhibition of antagonistic muscles for the action, setting of expected gains in afferent sensations, and the processing of corollary discharge signals). Thus, among the array of sensorimotor loops that involve the motor regions of the cortex are the frontal-parietal (F-P) loops, the thalamic (T) loops, the basal ganglia (BG) loops, and the cerebellar (C-C) loops. Neural activity in the putamen and cerebellum appears to follow the onset of neural activity in the cortical motor areas. This suggests that the basal ganglia and cerebellum receive something akin to an efference copy of the M1 and PMd state of activity. The BG loops seem to be involved in habit and skill formation by organizing motor actions into chunks (Amya & Smith, 2018) and several loops seem to possess sub-movements that could be combined to form more complex movements.

The cerebellum seems to provide continuous adjustments to motor output based on the inflow of the system's state. Signals from cerebellum, basal ganglia, thalamus, and sensory cortical areas converge upon the diverse types of neurons of M1 and PMd, as well as the secondary motor area (SMA - which is involved in motor sequence learning), the cingulate motor area, and a portion of area 5. These, in turn, also form loops with M1 and PMd. The convergence of these inputs mobilizes the pyramidal tract neurons of M1 and PMd, into forming time-varying control signals sent to spinal cord interneurons and motoneurons to activate spinal synergies. Although the patterns of activity for individual fingers seem to be organized in M1, the population level activity of PMd is involved in the production of sequentially organized finger movements (Ohbayashi, Picard, & Strick, 2016).

The spinal motor neurons innervating the distal muscles of the forelimb (wrist and hand) receive more monosynaptic cortico-motoneuronal projections from the M1 and PMd regions than those controlling the proximal muscles innervating the shoulder and elbow (Rathelot & Strick, 2006, 2009). This means that there is more cortical control of the action of the motor neurons that enable more precisely-timed, sequentially-organized movement of the wrist and fingers of the hand. Since such fine motor actions of the hand depends upon such direct projections from the contralateral M1 motor cortex (e.g., Muir & Lemon, 1983), these differences in cortical control become important when trying to determine the neural mechanisms of handedness (Andersen & Siebner, 2018). Moreover, such information shows why questionnaire assessments of handedness may not be very revealing of those neural mechanisms that also might be employed in other lateralized functions such as speech production and decoding (cf., Keane, 2016; Pulvermuller, et al., 2006).

A wide range of subtrajectories or movement fragments seem to be represented in M1. These fragments are thought to be controlled by the different classes of motor cortical cells which raises the question of how the supraspinal system manages to recruit the synergies in the correct spatiotemporal pattern to effectively control movement. Given the presence of so many sensorimotor loops, it seems clear that there is no single controlling mechanism but rather, control emerges from a highly distributed scheme. Also, it seems likely that differential experience in moving the forelimbs (i.e., feedback via spontaneous actions, practice, or learning) can contribute to differences in the mechanisms of control and these differences can have wide-ranging consequences on brain structures other than the motor cortex and its direct loops Doyon, et al. 2018). My perspective on handedness development incorporates the consequences of such feedback for the organization of the mechanisms of handedness (Michel, 1987, 2002, 2018).

A review of studies of individuals who had to change their handedness because of injuries (Marcori et al., 2019) revealed that neural asymmetries related to handedness are likely a consequence of lateralized practice since they correlate with modifications in the behavioral patterns. Also, musicianship is related to a higher prevalence of atypical language dominance in healthy left-handed individuals (Villar-Rodríguez, et al. 2020). Nicolini, Harasym, Turco, and

Nelson, 2019) provide some problematic evidence that human motor cortical organization is influenced by handedness (as measured by EHI but without noting handedness cut-point scores). Despite the extensive evidence for sensorimotor loops between motor cortex and cerebellum and the role of the right cerebellar hemisphere (contralaterally connected to the left cerebrum) in language expression (Schmahmann, Macmore, Vangel, 2009), studies fail to reveal any relation of handedness to cerebellar structure/functions (Kavaklioglu, et al., 2017; Polat, 2019). However, Kavaklioglu, et al. (2017) assessed handedness via a dichotomous selection item on a form and Polat (2019) used a French version of the EHI. Neither assessment is acceptable for evaluating hand differences in sensorimotor abilities.

The complexity of the loop system involved with manual actions makes it likely that some of the sensorimotor loops that are involved with handedness could be used in the control of other complex movements such as speech acts and their decoding. Hodgson and Hudson (Flowers and Hudson, 2013; Hodgson and Hudson, 2016, 2018; Hodgson et al., 2016) argue that a specialized speech-praxis computational network exists in the left hemisphere which specializes in processing motor action, visuomotor control, motor planning, phonological and auditory processing, and sequential control of complex “higher order” operations. They also propose that individuals who display atypical handedness or right hemisphere speech must use the callosal pathway to access this speech-praxis network. Thus, the connectivity between the hemispheres becomes more integral to successful functioning in atypically lateralized individuals because intra-hemispheric networking within the right hemisphere is presumed to be poorer and operationally less effective (Hodgson et al., 2016).

Left-handed individuals would have to use the corpus callosum (CC) to access the proposed left hemisphere speech-praxis network in order to control their left hand. Of course, this notion presumes that there is some sort of intrinsic left hemisphere speech-praxis network that is established early in development, independently of the feedback experiences provided by prenatal and postnatal differences in hand-use. The work of Robinson and Brumley make that unlikely. However, even for typically lateralized individuals, the CC may play a pivotal role in the development of left hemisphere specialization for language (Cowell, & Gurd, 2018).

Inter-Hemispheric Communication and Coordination

The corpus callosum (CC) is considered to be the primary mechanism for coordinating the two hemispheres especially for integrating the complementary processes of those functions that differ between the cortices. Investigations on callosotomized patients revealed many of the different functions of the two hemispheres and the role of CC in the coordination between them (cf., Gazzaniga, 1975). The CC is believed to inhibit the actions of one hemisphere as the other engages in processes which would be compromised if both hemispheres were simultaneously active. Also, the CC is believed to use sequential inhibition/activation to create collaborative functions involving contributions from both hemispheres.

Partial callosotomy has shown that CC is topographically organized, with transfer of visual, auditory and somatosensory information in its posterior parts (approximate area of the splenium) and of attentional resources and higher cognitive information in more anterior regions (Cowell & Gurd, 2018). The CC contains both small diameter fibers, typically providing inhibitory consequences (likely via activation of GABAergic interneurons within the receiving hemisphere) across secondary multimodal associative areas, and large fast-conducting fibers providing excitatory connections on primary and unimodal associative areas. Thus, it is difficult to infer the CC role simply from gross anatomical variables. Since the topographical organization of CC is complex and fine-grained, most investigations have mainly relied on the total surface area or on some parcellation scheme (e.g., Denenberg, Kertesz, & Cowell, 1991).

Bimanual coordination of sensorimotor skill and the intermanual transfer of tactile (haptic) experience are considered good behavioral indicators of interhemispheric communication. Anatomical evidence suggests that much of the sensory and motor innervation of the hands and fingers in humans is restricted to the contralateral cerebral hemisphere. However, some cortical neurons do have both ipsilateral and contralateral connections with the hands and fingers (Kuypers, 1982). This means that some ascending information from sensory receptors in the hands has both ipsilateral as well as crossed projections to the cortical hemispheres and some descending activity of each cortex has both ipsilateral and crossed influence on the hands and fingers. Nevertheless, for many aspects of fine motor control and more sophisticated haptic perception (especially in adults), the hemispheres possess primarily a contralateral relation with the hands. Unfortunately, there is too little research examining the development of the contralateral and ipsilateral factors coordinating the two hands (hemispheres) for action and perception.

Evidence from callosotomized adult monkeys and humans shows that the corpus callosum is involved in the intermanual (interhemispheric) transfer of certain sorts of haptic perception and for the control of certain kinds of bimanual skills (Preilowski, 1972, 1975; Selnes, 1974; Sperry, Gazzaniga, & Bogen, 1969). Although each hemisphere seems capable of monitoring proprioceptive information from both sides of the body (likely via extralemniscal and spinal-thalamic ipsilateral pathways), callosotomized patients seem to be unable to mimic with one hand the postures imposed on the fingers of the other hand, nor are they able to retrieve with one hand an object from an array that matches an object held in the other hand (Sperry et al., 1969). Also, familiar bimanual tasks involving interlimb coordination of simultaneous actions of the hands can be performed after callosotomy but novel tasks involving asymmetric but synchronous actions cannot be (Preilowski, 1972, 1975; Zaidel & Sperry, 1977). Thus, in the absence of callosally mediated interhemispheric communication, certain forms of haptic experience and manual skill may be restricted to one hemisphere. However, this restriction derives from a small sample of adults whose brains have had years to decades of intractable epileptic seizures before undergoing callosotomy.

Notably, in a small sample of 5 callosotomized children (to control seizures), the three that were callosotomized before 10-years-of-age exhibited little effect of callosotomy (Lassonde, Sauerwein, Geoffroy, & Decarie, 1986; Lassonde, Sauerwein, Chicoine, & Geoffroy, 1991). Such young children are capable of naming shapes in their non-dominant hand and they exhibit intermanual transfer nearly immediately post-operation. To account for these minimal postoperative deficits, some functions of the immature CC must be shared with alternative pathways; most likely the proprioceptive feedback provided by the ipsilateral extralemniscal and spinal-thalamic pathways. Moreover, some children callosotomized after age 10, but before mid-adolescence, recovered from their interhemispheric disfunctions, unlike adults. Thus, continued development must lead to the cortex rewiring through elimination of overproduced connections (Innocenti & Price, 2005); perhaps via experience and learning (Blumenfeld-Katzir, Pasternak, Dagan, & Assaf, 2011; Markham et al., 2009). Clearly, such results indicate that the functional development of the CC needs more extensive investigation (de Haan et al., 2020).

Although some evidence suggests that the corpus callosum does not exhibit anatomical or physiological maturity until the end of the first postnatal decade (Salamy, 1978; Yakovlev & Lecours, 1967) and perhaps as late as the third decade (Knyazeva, 2013), the contribution of the corpus callosum to behavioral development has not been examined systematically (de Haan et al., 2020). Anatomically, there are many late gestational and early postnatal changes in the CC involving axonal elimination and redirection (cf., Knyazeva, 2013). Myelination of the CC begins about 3-4 months postnatally and continues well into adulthood. EEG data suggest the synchronization of cortical pre- and post-synaptic activity begins in 7- to 12-month-old infants (Stroganova, Orekhova, & Posikera, 1999). Farber and Knyazeva (1991) reported that interhemispheric synchronization rapidly increased between 2- to 7-years of age but the rate of increase slowed progressively from middle childhood to adolescence (17 years). It is likely that the relatively low level of functional cooperation between hemispheres in the young brain means that local intrahemispheric mechanisms underlie most functioning in early childhood (Knyazeva, 2013).

The primary sensory and motor areas of the cortex subserving the hands mature rather early in infancy (Jones, 1981), but these areas are callosally connected only indirectly via “association” cortex with the opposite hemisphere (Kaas, 1993). Thus, the sensorimotor cortical areas must establish connections within a hemisphere with those association cortical areas in order for the callosum to subserve interhemispheric coordination for the hands. These other cortical areas are involved with the processing of multimodal sensorimotor information involving the hands (Georgopoulos, Kalaska, & Caminiti, 1985) and they reach anatomical and physiological maturity later in infancy (Jones, 1981). Therefore, certain forms of intermanual transfer of haptic information and bimanual coordination may be developmentally delayed by normal immaturity of parietal and frontal "association" areas as well as immaturity of the corpus callosum. The feedback provided by a hand-use preference during this phase of development would likely affect the development of the pattern of sensorimotor loop mechanisms within each hemisphere.

The degree of interhemispheric communication could be measured by assessing the inter-haptic perceptual abilities and intermanual skills of infants and children during the period of callosal immaturity. Thus, Streri and colleagues (cf., Streri & Gentaz, 2012), beginning in the mid-1980s, demonstrated intermanual transfer of haptic discrimination of object contours (prism vs. cylinder) not just in newborn infants and very young infants but also in premature infants as early as 28 weeks gestational age (Lejeune, et al., 2010). In all publications, the testing took place during the infant's calm alert state and with very minimal loss of infants as a consequence of state changes or other factors (< 5%).

Streri and colleagues used a haptic discrimination task that involved presentation of a cylinder-like object versus a prism-like object placed in the hands and recording time to drop the object. Repeated presentations of the same object (e.g., cylinder) resulted in more rapid dropping which did not happen if a novel object (prism) was presented (the novel object was held longer). Streri observed that habituation to the repeated presentation of one object (e.g., cylinder) for the treated hand was transferred to the non-treated hand. Since recovery from habituation (e.g., presenting the novel prism) was demonstrated for both the treated and non-treated hand, CC functioning was presumed to be present even in premature infants. Interestingly, Lassonde, et al. (1991) warned that proprioceptive feedback for haptic stimuli that relied upon angularity and curvature could be carried via ipsilateral mechanisms. Thus, assessing interhemispheric communication via intermanual transfer of haptic information depends upon the stimuli used. Since my perspective on handedness development involves a relative independence of the hemispheres early in development, I would welcome independent replication of the results of Streri and colleagues.

Before the publication of Streri's early work, we had used a head-turn conditioning procedure to assess the intermanual (interhemispheric) transfer of a learned haptic discrimination (unpublished but see Michel, Ovrut, & Harkins, 1984) by 35 7- to 14-month-old infants. Two stimuli differing only in texture (rough vs. smooth - in order to avoid ipsilateral proprioceptive feedback) were presented singly to the right hand of the infants in a semi-random pattern. During the presentation of each stimulus, an assistant appeared to the left- or right-side of the infant and played peek-a-boo. Each texture signaled the direction (right or left) from which the assistant would appear. An overhead video camera recorded the direction of the infant's head turns during the stimulus presentation periods, but before the appearance of the assistant. Directionally appropriate head turns for four consecutive stimulus presentations defined discrimination learning.

Only 7 infants (one each at 10- and 12-months of age; the remaining five were over 12 months) learned the discrimination. After learning, intermanual transfer was assessed by presenting the stimuli four times to the left (untrained) hand without reinforcement. None of the seven infants showed any evidence of transfer; however, each showed correct head-turning (without reinforcement) when the stimuli again were presented to the trained right hand. Although only preliminary and subject to concerns about the ease of learning the task, these data suggest that the callosum may not transfer certain learned sensorimotor experiences between the hemispheres during the infant's first year. Since infants establish hand-use preferences for reaching and object manipulation in their first year and if they cannot transfer certain learned

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tactile discriminations intermanually, then the preferred hand is likely to establish more haptic experience and to have engaged in more actions with objects than the nonpreferred hand.

The potential absence of interhemispheric transfer during a period of early hand preference for manipulation of objects would mean that the infant's haptic experiences with the preferred hand would be restricted to the contralateral hemisphere and not shared with the relatively naive hand/hemisphere. Theoretically, the supraspinal sensorimotor loops involved with control of the preferred hand, along with the corresponding spinal synergies, would have a different pattern of feedback than those involved with control of the non-preferred hand. Thus, early differences in hand use could play an important role in the organization of the nervous system (Michel, 1987, 1991).

Trevarthen (1974, 1978) showed that for adult monkeys, who previous to the surgery have learned a complex RDBM skill (in which each hand must perform separate actions), callosotomy did not affect the sequential unimanual performance of the skill when the RDBM action is prevented by restricting the use of one hand. That is, during the visuomotor learning of the RDBM skill, the information was shared between hemisphere so that each hemisphere retained the sequence needed for the manifestation of the skill. In contrast, callosotomized monkeys (lacking interhemispheric communication) who learned the RDBM skill, only the hemisphere that is actively controlling the actions of the hand involved in learning its part of a RDBM skill (i.e., the hemisphere contralateral to the performing hand) will incorporate the visual information produced by these actions into the visually coordinated sensorimotor schemes needed to do the task. When the RDBM action is prevented by restricting the use of one hand in these callosotomized monkeys, they could not perform the skill sequentially. Thus, the callosum is important for interhemispheric transfer of certain visually controlled manual skills during their acquisition. Trevarthen's studies (1974, 1978) show that callosotomy permits different sensorimotor skills to be established separately in each hemisphere, even when both hemispheres have visual information of the performance of each hand.

If callosal functioning is limited during the period of infancy (e.g., Cernacek & Podivinski, 1971), when hand-use preferences in object play are prominent, then the sensorimotor skills created in play could be restricted to the hemisphere contralateral to the playing hand, even though visual information about the skills are available to both hemispheres. When both hands engage in manipulatory play, the action differences induced by a hand-use preference will result in the establishment of different sensorimotor schemes or loops in each hemisphere.

Of course, there are many ways whereby the two hemispheres may share information (de Haan et al., 2020). There are subcortical systems (involving the cerebellum, basal ganglia, and superior colliculus) that project between the hemispheres and operate in interhemispheric coordination. Also, manual actions are not completely lateralized. There is bilateral control of the shoulder and upper arm and this can play an important role in RDBM. Moreover, functional systems that may be isolated within a hemisphere can have time during development to acquire subtle cues for communication and coordination that need not rely on neural connections between the hemispheres. Feedback of various sorts from facial muscles, eye-movements, postural shifts, etc. can provide rather reliable information transfer between hemispheres (Volz, Hillyard, Miller, & Gazzaniga, 2018). These may account for the lack of a disconnection syndrome in children with early callosotomy.

Thus, the issue of interhemispheric coordination is complex, involving many neural mechanisms beyond the CC. Current theories about such coordination are too simple and restrictive (most often to the CC) to likely be informative about the development of handedness or other forms of hemispheric specialization. Nevertheless, it is very likely that interhemispheric coordination (perhaps, via different mechanisms at different phases in development) plays an important role in hemispheric specialization. For example, young children exhibit a number of unintended synergies during fine motor movements of the hands and fingers which interfere with intermanual coordination in motor skill (Connolly & Stratton, 1968; Wolff, Gunnoe, & Cohen, 1983). These unintended cross-manual synergies (sometimes called mirror movements or associated movements) decline with age and the synergies have been proposed to represent immature callosal functioning (Dennis, 1976; Milner & Jeeves, 1979). Interestingly, only during the second half of their first year do infants exhibit bimanual coordination of the movements of their arms and hands (Kimmerle, Mick, & Michel, 1995). Since such coordination likely relies on the CC (Liuzzi, et al. 2011), we (Goldfield & Michel, 1986a) used a large object to reliably elicit bimanual reaching during this age period.

Although both 7- and 11-month-old infants showed the same frequency of bimanual reaching, the spatial coordination and temporal coordination of their arm movements were not the same. For 7-month-old infants, the timing of the movements of each arm was more tightly linked to that of the other arm than for 11-month-old infants. Moreover, at 7 months, the direction of each arm's movements matched the direction of the other arm's movements. That is, if one arm moved to the right, the other moved to the right at the same time. At 11 months, the hands converged on the target (i.e., when one arm moved to the right, the other moved to the left, etc.), with greater independence in the timing of each arm's movements.

It is not known whether one hemisphere is controlling the spatial and temporal coordination of the movements of both arms during bimanual reaching at 7 months. However, a hand-use preference does affect the pattern of coordination during bimanual reaching both when there is a minor impediment (low barrier) in the path of either hand and when there is no impediment (Goldfield & Michel, 1986b). For those infants with a hand-use preference, the impediment disrupted the pattern of bimanual reaching in 7- and 8-month-old infants but not in 11-month-old infants. The younger infants were more likely to hit the barrier when it was in the path of their non-preferred hands but not when it was in the path of their preferred hand.

If bimanual reaching was controlled by one hemisphere in the younger infants, with bimanual coordination achieved by simultaneous contralateral control of the preferred hand and ipsilateral control of the nonpreferred hand, then the tight spatial and temporal linkage in the movements of each hand during bimanual reaching and the pattern of disruption of bimanual reaching caused by the presence of an impediment in the path of the non-preferred hand might be expected. Subsequent development of more effective functioning of interhemispheric coordination would permit each hemisphere to control the spatial and temporal parameters of movement of the contralateral hand according to the requirements of the task, the actions of the other hand, and the conditions affecting its trajectory.

It is likely that the developmental changes in the coordination of bimanual reaching during the first year could reflect developmental changes in the functioning of the interhemispheric coordination (Liuzzi, et al. 2011). Recently, no transfer of a learned sequence of finger movements was observed between unimanual and bimanual movements in adults. The authors interpreted these results to mean that the integration of both hand sequential movements is coordinated at a different level of organization than one hand movements (Yokoi, Bai, & Diedrichsen, 2017). Thus, knowing how haptic experience is transferred intermanually and how bimanual action is coordinated is important for understanding the development of interhemispheric collaboration.

My Perspective on Development.

To many researchers, development is a process that operates during the early phases of a lifespan and it has an endpoint (e.g., the production of an adult). The changes that occur towards the end of a typical lifespan are labeled as aging and not development. Of course, defining an adult is difficult for humans. For many animal species, an adult is that phase of the individual's lifespan during which reproduction is possible and often occurs. However, for many human cultures the transition of puberty is not considered to be the onset of adulthood. Rather, a construct of adolescence has been created to characterize the period from the pubertal transition to some later phase of the lifespan when the individual is extended the rights, privileges, and responsibilities of adult members of that society. Of course, post-pubertal individuals are capable of reproducing but the cultural norms may inhibit such reproduction until the individual has effectively transitioned into adulthood via some rite of passage (even if it is simply some arbitrary number of years *postpartum* (e.g., 18 or 21 years), as in many Western societies).

In neuroscience, human adulthood is often defined by some gross anatomical measure of the brain (e.g., extent of myelination of cerebral axons, amount or pattern of white matter among cerebral areas, electrophysiological evidence of "adult-like" wave forms, etc.). However, even these definitions are assumed to be captured readily enough by adoption of some conventional age marker (e.g., 21-25 years *postpartum*). However, myelination can continue for many years after age 25 (although most of it is completed before then) and synaptic connections can continue to rearrange themselves throughout the life span (although major reorganizations are much less likely to occur after the age of 6-7 years). Oddly, few studies focus on what factors limit or reduce the likelihood of reorganization across the lifespan; hence, the young brain simply is considered to be more plastic than the older brain. Therefore, development sometimes may be considered a process of reduced brain plasticity for structural and functional reorganization.

Rather than approaching developmental phenomena as directed toward some end-state (a "development to" adult-like traits approach), many developmental psychobiologists consider developmental traits to emerge from the transactions/coactions among physiological processes internal to the individual operating in collaboration with those experiences provided by the individual's context resulting in a "development from" earlier traits approach (Michel, 2010). Such developmental coaction produces new traits or maintains traits at a particular level of function. Common endpoints are not ignored in a "development from" approach but rather these do not direct the pattern of investigation. This permits discovery of "multiple trajectories" in development that accounts for how initial differences early in the developmental pathways can lead to similarities in later phases and how initial similarities in early developmental pathways can lead to differences in later phases. The task for the researcher is to identify what factors during development contribute toward maintaining the consistency of the individual's trajectory and what factors contribute toward changing the trajectory.

Studies (operating within a "development to" framework) measuring hand preference from early childhood to adolescence (i.e., ages 3–12) provide no general consensus regarding the age at which adult-like handedness is attained (Scharoun & Bryden, 2014). Whereas, the "development from" approach examines the development of handedness throughout the lifespan as emerging from a cascade of developmental processes operating during the preceding earlier phases of the lifespan (Michel, et al., 2013). Thus, "adult-like" handedness can be examined, within this framework, as a foundation for the development of subsequent asymmetric hand actions that appear at later phases of the lifespan (e.g., Kalisch, et al., 2006).

Since lifespan differences in handedness are seldom sought in neuroscience, we have a discipline that clumps people in their mid-twenties with those in their mid-fifties who, perhaps, have developmental differences that may increase their variability during testing. Viewing development as an “emerging from” orientation is different from viewing development from a “development to” orientation. If the “development from” approach were applied to more aspects of hemispheric specialization of function, the early forms of lateralized cognitive, language and spatial abilities may be seen to cascade into different forms throughout the lifespan.

Application of the “development to” approach is common in lateralization research. Functional MRI (fMRI) studies show that those cortical regions in the left hemisphere, known to be part of the neural network for language in adults, are activated in newborns in response to hearing sentences as opposed to music (Dehaene-Lambertz et al., 2002, 2004, 2010). Even premature infants as young as 28 weeks show activation of their left hemisphere when presented with speech sounds whereas there is just general activation of both hemispheres when presented with other sounds. It is difficult to know what this information means for the development of hemispheric specialization. Dahaene-Lambertz and colleagues interpret these results as indicating that the nervous system is set to react to speech sounds even during late pregnancy. Hence, the development of hemispheric specialization must begin with a circuitry prepared for language; perhaps, derived from some sort of genetic programming. However, there may be something about the mammalian auditory system that makes speech sounds discrimination more likely than the discrimination of other sounds. Thus, Chinchillas can discriminate human speech sounds despite any evidence that their own vocal systems use such discrimination (Kuhl, 1981).

Moreover, the premature and newborn nervous system is quite different from that of even the nervous system of older infants. Until some months postnatally, those synapses using GABA as a neurotransmitter are likely to promote action potentials from post-synaptic neurons rather than inhibiting action potentials. The cortex of the neonate, albeit in general form similar to the older cortex, is still undergoing extensive sculpting of synapses and thousands of neurons are dying daily. Therefore, many of these studies need replication, particularly those involving fMRI. Only since 2014 have appropriate statistical and methodological changes been instituted for fMRI research which make earlier studies highly suspect (cf., Chen, Lu, Yan, 2017; Cremers, Wager, & Yakoni, 2017; Poldrack et al., 2017; Vul et al., 2009). Moreover, it is quite difficult to obtain reliable data from very young infants and premature infants because their posture powerfully affects their movements and manual actions (Michel, 1991; Schwartz & Michel, 1991, 1992).

Finally, evidence indicates that vestibular system develops quite early and can affect the development of the auditory cortex along with other cortical systems (Leong, et al., 2019). Since asymmetries are present quite early in vestibular development (Previc, 1991) and likely contributes to the development of the auditory system; perhaps, the premature and neonatal left hemisphere activation derives from some developmental influence of the vestibular system on cortical functioning (Ferrè & Haggard, 2020).

The recent application of functional connectivity magnetic resonance imaging (fcMRI) techniques to infant, neonatal and fetal brain development is another example of the application of the "development to” approach. This fcMRI technique uses spontaneous, low frequency (< 0.1 Hz), coherent fluctuations in a blood oxygen level dependent (BOLD) signal to identify connections among cerebral areas (neural networks) during a “resting state” (Smyser, Snyder, &

Neil, 2011). This technique has identified an organized, baseline mode of brain activation (the default mode network – DMN) in adults and perhaps in children. In adults, fcMRI also reveals resting state networks (RSNs) encompassing cortical and subcortical regions that seem to relate to motor function, sensation, visual and auditory stimulus processing, memory, language, and attention; all independently of variations in states of consciousness (Zhang and Raichle, 2010).

By adopting a "development to" approach, researchers have sought RSNs in full-term and preterm infants similar to those observed in adults. In neonates (and preterm infants tested at term-equivalent age), six RNSs were found in temporal, occipital, prefrontal, parietal, basal ganglia, and sensorimotor cortices as well as a 'proto' DMN (van den Heuvel & Thomason, 2016). Indeed, the proto DMN has been reported for the mid-gestation fetus via *in utero* fcMRI scanning (van den Heuvel & Thomason, 2016). Since the posterior cingulate cortex (PCC) is an important component of the adult DMN and seems to be a central 'hub' in brain connectivity in infants, intrauterine establishment of PCC connectivity has been claimed to be foundational to the emergent architecture of the developing human brain (van den Heuvel & Thomason, 2016). Also, the fetal brain seems to exhibit modular organization and these modules comprise areas that will later support vision, movement, language, and data integration. Thus, the "development to" approach apparently has discovered proto RSNs, characteristic of adults and children, in neonatal and preterm infants.

Although application of fcMRI enables assessment of the earliest forms of likely functional connectivity, fcMRI has several technical problems that apply not only to studies of adults (e.g., RNS nonstationarity) but especially to newborns or preterm infants (e.g., level of arousal and movement artifacts, Smyser et al., 2011). For example, the most common techniques for identifying spatial patterns in BOLD activity are seed correlation analysis (SCA) and independent component analysis (ICA). SCA involves correlating activity of a particular region with all other regions of the brain and involves *a priori* assumptions about the regions of interest (ROIs). ICA statistically reduces data sets to maximally independent components based upon the signal intensity time course of spatial maps (and these along with the definition of intensity must be specified, *a priori*). For each technique, these and other a priori assumptions are derived from studies of adults. Thus, subtle differences in methodology at many steps in the collection and analysis of data have been reported to profoundly affect results (Elliott et al., 2020; Smyser et al., 2011).

For example, the BOLD signal has not been adequately calculated to establish standardized values for identifying significant differences in the signal that would be relevant for neonate and infant brains, much less for preterm and intrauterine brains. Therefore, arbitrary thresholds are used. Also, magnitude measures of the correlation thresholds are selected arbitrarily. The impact of brain development on the BOLD signal is unknown and test–retest reliability of fcMRI results (pertinent to establishment of normal limits) has not yet been established for different ages. Consequently, adequate fetal and neonatal templates and atlases for analysis of fMRI data are missing. Thus, apparent similarities of phenomena across age inspire speculations about proto traits that will develop into the adult traits without indicating the role that those early proto traits play in the functioning of the young individual nor in whether the proto trait is empirically related to the adult trait by processes other than similarity.

The “development to” approach can lead to potentially misleading conclusions. Using a development to approach to the study of handedness development, Hepper and colleagues examined one-time, brief (<10 minute) ultrasound recordings collected from a large number of pregnant women (as part of the standard prenatal exam) to conclude that the formation of handedness takes place prenatally. By 9–10 weeks gestation, fetuses exhibit independent limb movement and the ultrasound recording seemed to show that 75% of 10-week fetuses moved their right arm more frequently than their left and 13% moved their left arm more frequently (Hepper, McCartney, & Shannon, 1998). At 15 weeks, the majority of fetuses had their right thumb in their mouth (Hepper, Shahidullah, & White, 1991). This right thumb bias was highly correlated with their handedness (as reported by parents) at 4 years (Hepper, Wells, & Lynch, 2005). Because this fetal manual asymmetry is related to childhood right-handedness, it was interpreted as reflecting early hemispheric specialization for handedness.

Unfortunately, these differences in fetal lateralized thumb sucking and arm movements were not independently confirmed by a systematic ultrasound study involving weekly longitudinal imaging of 10 fetuses scanned for over an hour each visit (de Vries et al., 2001). The longer scans from de Vries et al. permitted the collection of information on the direction of the ultrasound pulser and receiver and the position of the fetus. This information is necessary because at the time of these studies, the ultrasound image was like a slice through a 3D object and not like the flattened image of a 3D object to a 2D picture. To interpret the position of the limbs relative to body parts required the type of precise information provided by the de Vries et al study. Modern “3D” ultrasound should be used to replicate the Hepper studies.

For studies of handedness, the “development from” approach does not seek evidence of handedness in the fetus, but rather, examines the fetus and its processes to determine how those combine with the conditions prevalent *in utero* to produce the hand-use asymmetries of the neonate. Then, what factors during the neonatal phase contribute toward maintaining or changing the developmental trajectory of such asymmetries. Since neonatal hand-action preferences are not homologous with those of older infants and toddlers, these should not be considered evidence of adult-like handedness (even if there are similarities of proportion of right and left preference distributions or if there is a correlation with childhood handedness identity as reported by parents). Rather, lateral differences in fetal forelimb actions should be examined for how they might contribute to the development of later hand-use preferences, and so on. Do these early asymmetries contribute to the developmental scaffolding needed to achieve the pattern of "adult" lateralization?

My Perspective on the Development of Handedness.

After decades of research using the "development from" approach, I proposed that the trajectory of handedness development during infancy (Michel, 2002) reflects a complex cascade of contingencies involving prenatally influenced congenital postural asymmetries that feed into the establishment of early infant sensorimotor asymmetries of the use of the arms and hands. These lateral asymmetries, in turn, promote hand-use preferences initially for acquiring objects and eventually for RDBM, construction skills, and tool use by the individual's second year postpartum (Michel et al., 2013, 2018). Also, handedness for RDBM during the toddler period (18–30 months) likely cascades into the development of handedness in skill differences that begin to appear in the preschool period.

The asymmetries, throughout the trajectory, interact with the caregiver's handedness (also, a result of the caregiver's development within a specific cultural context) to further shape the individual's hand use such that by 18–24 months, most children have a hand-use preference across a range of unimanual and bimanual skills that will form the basis of all future hand actions. I, also, proposed that the origin of handedness need not reside in the prenatal differences in hand or limb use but rather may reside in some other asymmetrical biases, such as fetal posture and position, that would affect lateralized asymmetries in control of the arms and hands.

The neonate's postural preference approximates its prenatal posture (Dunn, 1975). Intrauterine position is considered to be a major contributor to the organization of postnatal posture and "reflexes" (Caesar, 1979; Schulte, 1974). After the 16th week of pregnancy, the size, shape, and specific gravity of the fetus combine with the shape of the uterus, sigmoid colon, and pelvic ring to restrict movement and position of the fetus in the uterus. The most prevalent uterine position is left vertex that places the fetus's head "down" and the left side "pressed" against the mother's backbone and pelvis (~85% of fetuses set in a left occiput anterior or transverse - LOA/LOT - uterine position and ~12% with a ROA/ROT position). The LOA/LOT position constrains left arm movement and head turns directed toward the left side of the fetus whereas the ROA/ROT position constrains right arm movements and rightward head turns.

The maintenance of fetal posture throughout much of the latter half of pregnancy likely affects the elasticity of the skin and muscles as well as calibrates some general "set points" in the muscle spindle cells in the muscles of the arm and neck and may produce lateral asymmetries in the organization of spinal synergies. According to Previc (1991), the uterine position could produce a lateralized asymmetry in the development of the vestibular system. After delivery, gravity induces muscle stretch that violates spindle set points that initiate contractions that produce the characteristic neonatal postures and their similarity to fetal postures (Caesar, 1979) and the asymmetry of the vestibular sensitivity would produce a directional head-turn in order to create a balance of vestibular excitation. These factors could account for the neonatal population level rightward head orientation preference (Michel, 1981; Turkewitz, 1977). Subsequent recalibrations of spindle set points and greater supraspinal influence eventuate in a postural change as a result of greater control relative to gravity and visual field, with head orientation preference moving toward midline (Rönnqvist, Hopkins, van Emmerik, & de Groot, 1998).

The neonate's supine head orientation preference (NSHOP) is predicted by the fetal position *in utero* as estimated during delivery (Michel & Goodwin, 1979). Unfortunately, estimates of uterine position from delivery data are relatively weak and, in this study (unlike in Michel, 1981), only 52% of the neonates showed significant NSHOPs. However, 80% of neonates with a leftward NSHOP were so predicted from the delivery estimate of their atypical (ROA/ROT) uterine birth position and 75% of neonates with a rightward NSHOP were predicted by the delivery estimate of their typical (LOA/LOT) uterine position. HOP is likely a consequence of asymmetrically lateralized activation of neuromotor mechanisms at the level of brain stem nuclei, cerebellum, thalamus and basal ganglia (Rönnqvist et al., 1998) that have been established *in utero* and partly influenced by the fetus' position rather than simply a reflection of hemispheric specialization (Michel, 1983, 1988).

As a consequence of the HOP, a neonate is more responsive to auditory and tactile stimulation of one ear and cheek, respectively, then to the other (Turkewitz, 1977). Turkewitz (1977) proposed that the neonatal lateralized asymmetry of sensory and motor characteristics is an early predictor of later forms of other lateralized functions, including handedness. In a study of more neonates, Michel (1981) reported that the HOP of 150 (81 males) neonates was normally distributed but with a sharp rightward shift similar to the handedness distribution in adults (Annett, 1972). About 10-12% of neonates showed a significant leftward HOP. From this group of neonates, 20 (11 males) were selected to have their hand-use preferences for prehension assessed at 12, 16, 22, 32, 40, 51, 60, and 78 weeks postpartum. Ten (5 males) had a significant rightward NSHOP and 10 had a significant leftward NSHOP.

The supine HOP of these 20 infants was assessed more extensively at 3, 6, and 8 weeks postpartum. The correlation between their brief neonatal and more elaborate post-neonatal HOP assessment values was significant, but 5 of the 20 infants seemed to have changed from their NSHOP assessment (3 with initial leftward NSHOP became rightward SHOP and 2 with initial rightward NSHOP became leftward SHOP). However, both the NSHOP and the post-neonatal SHOP were significantly predictive of infant hand-use preferences for prehension throughout the eight assessments. However, the post-neonatal SHOP had the largest predictive relation (Michel & Harkins, 1986). What is remarkable about this study is that it was able to predict left hand-use preference for reaching for objects from the infants leftward SHOP.

HOP results in differential proprioceptive and visual experience of the hands and limbs that is important for the development of their visually guided control. Even relatively minor asymmetries in neuromotor action and visual experience of the left and right hands can produce differences in the cortical and subcortical mechanisms controlling motivated hand use (McFarland, 2009; Spinelli & Jensen, 1982). The direction of HOP also affects limb differences with the face-side hand/arm exhibiting more movement and grasping actions and being more available for visual regard (Michel & Goodwin, 1979; Michel & Harkins, 1986).

Neonates are reported to move their right arms more frequently and to take “swipes” at objects in their field of view. Also, objects placed in the hands during the first 2 months postpartum elicit a stronger grasp (Tan, Ors, Kurkcuoglu, & Kutlu, 1992) with longer duration of holding (Caplan & Kinsbourne, 1976). Because the neonate’s HOP affects such limb differences, it is likely that these reported asymmetries are a consequence of the HOP (Michel, 1983). Positioning the infant’s head opposite to the preferred HOP results in the infant’s hand and arm movements shifting to the “new” face-side hand (Michel, 1981). Hence, the HOP seems to be affecting directly the bias in hand and arm movements (Rönnqvist et al., 1998).

Ocklenberg et al. (2010) examined 58 7- to 11-year-old children who suffered from congenital muscular torticollis (CMT) which tilts the infant's posture and head toward one side. Their handedness was assessed via acting out the EHI questions but left- and right-handedness was defined simply as less-than or greater-than 0, respectively. All of the 31 children who had CMT with a left head tilt were right-handed; whereas, only 78% of those with a right head tilt were right-handed (92% of the 54 control children were right-handed). The authors argue that the head tilt rotates the face and eyes to the opposite side resulting in greater visual experience of the hand opposite the head tilt (right hand for left head tilt babies). However, this observation needs replication because even the authors' picture shows that the hand may not be in the visual field for the head tilt. I have argued that it is the relative amount of time and movement of the hands in the visual field that likely affects the establishment of the visual-proprioceptive correspondence map that contributes to the success of one hand obtaining an object before the other (see below). Thus, investigating the handedness of children with CMT may not reveal the role of HOP in the development of infant handedness.

By 8–10 weeks, the HOP has disappeared and the infant maintains a midline position for the head (Rönnqvist & Hopkins, 1998). Michel and Harkins (1986) found that the hand that was used initially for swiping at visually presented objects in the infant's midline at 12–16 weeks is the same hand that was on the face side during the earlier observed HOP. By 4 months, infants exhibit "directed reaching" toward objects but acquisition was unlikely. Again, the predominant hand for this reaching (left or right) is the face-side hand from the previous HOP. By 5–6 months, infants are able to acquire objects and they use the same hand that they used for directed reaching. Infants maintained this preference for acquiring objects for their next 12 months. Thus, the development of handedness during infancy begins with an HOP that creates asymmetrical

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motor actions and hand regard. These asymmetrical “experiences” predict the hand that will be later used for reaching.

It is likely that the HOP results in an asymmetry of visual–proprioceptive map of space because the face-side hand is moved more, creating more proprioceptive and corollary neural activity associated with that hand’s position in visual space and its “felt” position relative to the body. Therefore, the face-side hand ought to have an advantage in reaching for objects located in space relative to the infant’s body. That advantage concatenates into a greater probability of contacting the object, acquiring it, and building more extensive cortical–basal ganglia reentrant circuits for the “motivational” control of that arm (McFarland, 2009).

We have found large individual differences in the trajectories of handedness for object acquisition (Ferre et al., 2010; Michel et al., 2014), and nine monthly assessments permit identification of the nonlinear individual and group developmental trajectories. Fewer assessments during this age period fail to identify any developmental trend (Ferre, et al., 2010). Using a reliable and valid assessment procedure (Michel et al., 1985) capable of identifying significant differences ($p < 0.05$) in the use of each hand at each monthly assessment visit during the 6- to 14-month period (Michel et al., 2002), we assessed the longitudinal character of hand-use preference for 383 infants.

Four types of developmental trajectories for acquiring objects were observed (Campbell, Marcinowski, & Michel, 2018; Marcinowski et al., 2016): those who manifest an early stable right hand-use preference (about 32%), those who manifest an early stable left hand-use preference (about 12%), those (25%) who manifest a later developing right-hand preference, and those (30%) who do not exhibit a stable hand preference during this age period. Thus, although there is variability across visits, these groups are distinguished by their hand preferences, which likely represent different patterns of neurobehavioral development. Even during infancy, right hand-use preference is predominant over left hand-use preference. Yet, 30% of infants do not manifest a consistent preference of hand use for acquiring objects. Therefore, additional longitudinal research is needed.

Unimanual (e.g., banging or shaking the object) and nondifferentiated bimanual actions become more frequent from 7 to 12 months postpartum (Kimmerle et al., 1995). A hand-use preference for unimanual actions appears by 11 months, and that preference is predicted by the previously established hand-use preference for acquiring objects (Hinojosa, Sheu, & Michel, 2003; Campbell, Marcinowski, Babik, & Michel, 2015). Furthermore, the hand-use preference for acquiring objects predicts the hand-use preference in RDBM (Babik & Michel, 2016). As a result of the hand-use preference for acquiring objects and manipulating them, the preferred hand will have established many more “programs” or “schemas” (Michel, 1991) that can be employed with any object that affords RDBM (Kimmerle, et al., 1995).

Although infants exhibit RDBM as early as 7 months (Kimmerle et al., 1995), it is only a minor part of their repertoire (until 13 months) and seems to emerge entirely from the properties of the object, rather than from the coordinated actions by the infant. By 13 months, infants begin to exhibit a hand-use preference for RDBM, and only at 13 months, do RDBM actions appear to be coordinated by the infant (Kimmerle, Ferre, Kotwica, & Michel, 2010). Thus, during the 6- to 14-month period, both unimanual actions and RDBM actions are only a small portion of the infant’s manual repertoire and hand-use preferences in those actions appear only in the later months.

By 11 months, infants manifest a hand preference for unimanual manipulation which is predicted by their preference for acquiring objects (Campbell et al., 2015). Consequently, the action of acquiring objects is the only manual skill that is relatively constant in the manual repertoire that exhibits hand-use preferences during the 6- to 14-month age-period. However, by 12–14 months, the strong hand-use preference for acquiring objects will appear to "weaken" as the infant more frequently uses the nonpreferred hand to acquire an object so as to engage more immediately in RDBM actions with the preferred hand (Michel et al., 1985).

By 18 months, infants are engaging primarily in RDBM with objects and can solve many tasks that require an RDBM action (Nelson, Campbell, & Michel, 2014). A toddler's hand-use preference for RDBM is predicted by his/her hand-use preference for acquisition as infants. Moreover, a group of toddlers, who had no hand-use preference for acquiring objects as infants, developed a hand-use preference for RDBM during the period from 18 to 24 months (65% right-handed and 30% left-handed). Using her peg-moving task, Annett (1985, p. 392) provided evidence that by 3–5 years of age, the distribution of skill differences between the hands was equivalent to that of adults. Hence, the same right shift in handedness skill shown by adults is apparent in preschool children. Although children may change their hand-use preference after 5 years of age, their subsequent pattern of handedness is likely to be different from that of children who do not change the pattern established during their first 5 years (Bryden & Steenhuis, 1991). So, the right bias in hand-use preference can be observed quite early in infancy and may relate to the proficiency bias observed in preschool children's peg-moving and other manual skills.

Recently, Latta (2020) was able to test the handedness (using a RDBM problem-solving task) of 58 five-year-old children of the 383 infants from whom we had collected data on infant hand-use preferences for acquiring objects at 6- to 14-months of age and toddler hand-use preferences for RDBM at 18- to 24-months of age. Preferences for both infant and toddler age groups were determined via latent class analysis.

Latta found that 35 (60%) had right-hand preferences and 11 (19%) had left-hand preferences as infants (21% had no preference). Of these infants, 74% (26) of those with a right-preference retained a right preference as toddlers (two showed no preference) and 45% (5) retained a left preference as toddlers (four showed no preference). Comparing the infant hand preference to the hand preferences at 5 years of age, 74% (26) of those infants with right preference retained a right preference at 5 years of age and 55% (6) of those with a left preference retained their left preference. However, toddler RDBM hand-use preferences were a better predictor of five-year hand preference with 92% (33) of those 36 with a toddler RDBM right preference retaining their right preference at five years and 78% (11) of those 14 with a left preference as toddlers retaining their left preference. If no preference consistencies are included in the analyses, the 79% of the hand preference of 5-year-old's is predicted from toddler RDBM preferences whereas only 58% of the hand preference of 5-year-old's is predicted from infant hand preferences for acquiring objects.

Infant hand-use preference likely derives from prenatally and neonatally established postural asymmetries that facilitate a bias in visually guided hand use. Those same postural asymmetries exhibit a continuous distribution with a profound shift toward a right bias, but with a left minority, which would account for the early development of a left hand-use preference. Differences in hand-use preference during infancy could be further separated into actions that resulted in the contact with, and acquisition of, objects (CA), unimanual manipulation (UM) of objects, and role-differentiated bimanual manipulation (RDBM) of objects beginning in the latter half of the infant's first year. Each of these hand use preferences emerged in sequence during the infant's first year of sensorimotor development and each only after the manual skill on which the hand preference was based had achieved a particular level of proficiency. Moreover, each

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preference served as a base upon which the subsequent preferences could build. Thus, unimanual manipulation preference reflected the earlier appearing acquisition preference and the later appearing preference for RDBM reflected the earlier preferences of CA and UM. Of course, RDBM preferences serve as the basis for the establishment of a wide range of tool-use, artifact construction, and manipulation skills manifested throughout childhood and adult handedness.

Since this sequence did not reflect the manifestation of a serial homology of infant handedness (derived from the same underlying mechanism that was maturing), the handedness in the sequence was neither absolute nor necessarily consistent. Rather the relation across manifestation was probabilistic: right or left handedness for contact/acquisition was stochastically associated with right or left handedness in unimanual manipulation or RDBM, and so on. The trajectory of development assured a right-hand predominance in the population with a left-hand minority but, essentially, handedness is a continuously distributed trait (not categorical) with a right shift for each manifestation. Nevertheless, there is a very good predictive relation across the manifestations for both a right and especially left preference. This cascading effect of the postural origin of handedness provides a developmental explanation for both the right bias in the population, for the maintenance of a minority of left-handedness, and the continuum of handedness across individuals.

Significance of Handedness for Hemispheric Specialization and Coordination

The reason researchers investigate the relation of handedness to people's cognitive, social, and emotional functioning is because handedness is thought to represent different *patterns of hemispheric specialization*. It is the pattern of hemispheric specialization (not handedness, per se) that is believed to affect psychological functions. Studies of children and adults (Casasanto, 2009; Casasanto & Henetz, 2011) suggest that left- and right-handed infants may be developing symbolic and abstract concepts differently. Also, it is important to remember that left-handedness is not the mirror image of right-handedness (Michel, 1998) but represents its own pattern of neurobehavioral organization (Jones & Martin, 2010; Knecht et al., 2000) and development (Campbell et al., 2018). What, then, does that mean for the large proportion of infants (~30%, Campbell et al., 2018) who exhibit no hand-use preference? Does developing handedness status early or late affect development of language abilities, object construction skills, tool-using skills, visual–spatial abilities, executive functioning, etc.? Are the four patterns of developing handedness that we discovered associated with differences in the development of these abilities?

Kotwica, Ferre, and Michel (2008) found that infants without a consistent hand-use preference were slower at developing the kind of object management skills that Bruner (1973) considered to be important in the development of symbolic abilities. Similarly, Marcinowski and colleagues observed that hand-use preferences during infancy predicted advances in the development of the skill for stacking blocks (Marcinowski et al., 2016). Infants with early left- or right-hand-use preferences exhibited stacking skill earlier than infants both without a preference and those who only later developed a right-hand-use preference. Moreover, advanced skill for stacking blocks during infancy predicted advances in the comprehension of spatial words at three years of age without any general advances in language skills or cognitive ability (Marcinowski & Campbell, 2016).

Nelson and colleagues discovered that toddler hand preferences for RDBM predicted language skills at 2, 3, and 5 years of age. Indeed, infants who showed consistent early right-hand-use from 6 to 14 months of age had advanced language skills (Bayley Scales III) at two years of age; whereas, those children who were inconsistent in their handedness as infants but later developed handedness as toddlers were not advanced for language development (Nelson et al., 2014). Also, toddlers who had the strongest and most consistent right-hand-use preference from 18 to 24 months had higher expressive and receptive language scores at three years of age (measured with Preschool Language Scales, 5th edition) than toddlers with a left-hand-use preference or with a weak right-hand-use preference (Nelson et al., 2017). By five years of age, children, who as toddlers had a strong right-hand-use preference, scored significantly higher on both expressive and receptive language skills (PLS-5) compared to those with a left-hand-use preference or a weak right-hand-use preference (Gonzalez, et al., 2020). Thus, individual differences in fine motor skills (RDBM) during toddlerhood can have cascading effects on language ability during the preschool years.

If handedness is relevant for advancing the development of tool-using skills (Babik, et al, 2021), symbolic abilities, and so on, then infant handedness must play a fundamental role in the theories about, and empirical investigations of, infant cognitive, social, and emotional development. Some developmental scientists have argued that during human development various cognitive, social and emotional abilities are built upon, scaffolded by, or bootstrapped from, early sensorimotor skills (e.g., D’Souza & Karmiloff-Smith, 2011). Indeed, **embodied cognition theory** proposes that every psychological construct (e.g., executive function, symbol use, thinking, emotional communication, etc.) derives from sensorimotor development and the experiences that development provides (e.g., Martzog, Stoeger, & Suggate, 2019; Pezzulo, 2011).

As the trajectories of handedness development are charted into the school-aged period, it may elucidate how preschool measures of design copying skills manage to become excellent predictors of middle school mathematics, science, and reading achievement test scores (Cameron et al., 2012; Grissmer, Grimm, Aiyer, Murrah, & Steele, 2010). Although skills for copying designs are conventionally interpreted as visual–spatial abilities, they may more appropriately represent visual–motor manual skills (cf., Suggate & Stoeger, 2017; Suggate, Pufle, & Stoeger, 2019). As such, individuals with early hand-use preferences ought to exhibit better skills when copying designs than those without early hand-use preferences. If early handedness development is related to better design-copying skills of children, then the four patterns of infant handedness development may represent the four patterns of neurobehavioral development highly relevant for the development of scientific, reading, and math skills.

Since neural organization and processing can be extended and/or modified during development (Finlay, 2007; Michel, 1991) to produce neural systems for subsequent psychological functioning that may not resemble their earlier developmental character, studies of adult HS/HC are unlikely to reveal much about the character of their developmental origin. For example, there appear to be fundamental differences between the way in which the developing brain and the adult brain process and produce speech and language (cf., Ballantyne, Spilkin, Hesselink, & Trauner, 2008). Consequently, investigation of the development of handedness, hemispheric specialization, and hemispheric communication and coordination should be a priority both in neuroscience and clinical neurology (Ferre, Babik, & Michel, 2020).

Elsewhere, I have sketched out a program for how to examine the relation of the development of handedness to the development of other cognitive abilities (Michel, 2018). Moreover, we (Michel et al., 2018) described how modern developmental biological processes of heterochrony, heterotopy, heterometry, and heterotypy can apply to the study of human psychological development. Application of these processes to the development of those psychological functions that are the current focus of investigations of HS/HC would avoid the use of misleading concepts that cause scientists to seek evidence of nature-nurture interactions in development, biological essentialism in the formation of functional categories, and the adoption of a “development to” approach in their investigations. It is time to challenge the conventional wisdom.

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