The Concept of Homology in the Development of Handedness

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Abstract:

The construct of homology in the development of behavior is examined using human handedness. Research on the development of hand-use preferences in infants provides some evidence that it may be homologous with adult handedness. Nevertheless, I propose that the construct of homology may not be relevant to the study of human behavioral development. However, other constructs from developmental biology may prove useful in improving developmental psychological research.

Article:

INTRODUCTION

Handedness is handedness is handedness! Or is it? That is the fundamental question in the study of homology in the development of handedness. When is a characteristic the same across species and across development (serial homology)? The problems of identity become much more problematic when the characteristic is not morphological but physiological or behavioral (Atz, 1970). What part of the organism's behavioral repertoire should be recorded and measured and how should this measurement be done? How can behavioral definitions distinguish specific acts within the continuum of action, given both within and between individual variability? In ontogeny, how is both stability and change in the behavioral trait defined and measured as these occur throughout the lifespan? Thus, underlying all attempts to homologize traits (even static morphological traits) are the questions about how the trait is described and defined.

Owen (1,843) defined homology as "the same organ in different animals under every variety of form and function" (quoted from Minelli,2009, p. 120). To identify this presumed underlying archetypical sameness, three criteria used (systematized by Remane in 1961 and translated by Atz, 1970, p. 57): (1) position—homology results from a structure occupying the same position

in comparable systems of structures (for handedness this involves its presence in various forms of forelimb use; for example, eating, initiation of crawling, manipulation, defensive action); (2) special quality—similar traits can be homologized without regard to position if they agree in several unusual characteristics (for handedness, the distinct bias toward the predominance of right handedness might be an unusual character); (3) constancy or continuity—even dissimilar and differently located traits can be homologous if intermediate, connecting traits (based on criterion 1 above) can be shown to exist. The connecting traits may be ontogenetic stages (for handedness these may include fetal hand-use, infant hand-use, and child hand-use preferences) or members of taxonomic groups (for handedness this can mean hand-use in other primates).

Early ethology employed the concept of homology in behavioral studies as a means of exploring the phylogenetic history of species-typical behaviors (Tinbergen, 1951). The character of species-typical behavioral patterns was compared across species to ascertain both their phylogenetic relationship and the ancestral behavioral characteristics. To the three original criteria for identifying homologies, ethologists added two that were more relevant for the study of behavior: (1) peripheral structures—movements employing homologous structures (defined by morphological criteria) in similar ways may be considered homologous; (2) nervous system— behaviors dependent on homologous regions of the brain may be considered homologous (Pribram, 1958).

Unfortunately, seemingly nonhomologous behaviors may be based on homologous structures (Atz, 1970). Moreover, 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 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 using homologous aspects of the nervous system.

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. Unfortunately, over 40 years of subsequent behavioral research has failed to employ these three requirements for determining behavioral homology. The intent of the current article is to help initiate movement toward meeting the requirements posed by Atz (1970) for the study of behavioral homology.

I study the development of human handedness—a species-typical behavior pattern that 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 differences in how

the preferred and nonpreferred hands are controlled in humans. 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). But is handedness a homologous trait, either phylogenetically across species or serially across development?

WHAT IS HANDEDNESS?

Humans, as do most vertebrate species studied, exhibit a limb preference for unilateral activities. However, two characteristics of the human limb preference are thought to distinguish it from that of other vertebrates: (i) the preference is the same across a variety of manual tasks with few or no task demands or motor skills in common (handedness consistency); and (ii) the handedness consistency is unevenly distributed in the population with a distinct right-handed skew. Depending on the criteria used to define handedness, 70–90% of humans exhibit a consistent right-hand preference for manual activities (Annett, 1985). These two characteristics fit the criterion of special or unusual quality.

The population bias in the distribution of hand preference has been prevalent for much of the natural history of humans (Corballis, 1991) and is present in all cultures (Annett, 2002). Anthropological evidence suggests a population bias toward right-handedness in our hominid ancestors as far back as 1.8 million years (McManus, 2002; Toth, 1985). The evidence shows both a right-hand dominance in tool construction and an asymmetry of tool form such that its use would be much more manageable with the right hand. Thus, the right bias in human handedness seems to be an evolutionary extension of a right bias in hominid handedness.

Several theorists have proposed that the human hand, brain, and the upright posture and bipedal pattern of locomotion coevolved (cf. McManus, 2002) and that the population bias in handedness likely derives from the evolutionary changes in the brain and posture. The cross-lateral pattern of innervation of the hands means that the right bias in human handedness is another aspect of the human pattern of cerebral lateralized asymmetry of function and is most closely associated with the hemisphere specialization for language functions (Serrien, Ivry, & Swinnen, 2006). These aspects of handedness fit the Ethological criteria for behavioral homology: employment of homologous peripheral structures (forelimbs) and neural structures.

Many different species of vertebrates show evidence of "handedness" (i.e., individuals use one limb more often than the other for tasks involving the use of one limb) because it may reduce cognitive load (Flowers, 1975). That is, each time a single limb action is to be initiated and there is no bias in the situation (an asymmetry of the individual's posture or in the spatial coordinates of the goal of the action), there is a time delay and information-processing cost associated with the decision of which limb to use. A "preference" (biased use of one limb) greatly reduces such

cost across a large number of mundane unilimb tasks (e.g., initiation of locomotion, "pawing" an object). Therefore it is not surprising that both cerebral and limb lateralization exist at the species level in many nonhuman vertebrates, including fish, frogs, birds, and mammals—especially primates. However, there is nothing in the benefits derived from reducing cognitive load for any individual that requires a distinct shift in the distribution across individuals to the use of one limb. Something else must be responsible for the shift.

Although it is often suggested that handedness and cerebral asymmetry resulted from some genetic mutation at some point after the split of the hominids from the other great apes (Annett, 2002; McManus, 2002), several researchers (Halpern, Güntürkün, Hopkins, & Rogers,2005) have proposed that cerebral asymmetries of structure and function (including "handedness") are homologous across vertebrates. Vallortigara and Rogers (2005) report on many population level biases in lateralized asymmetries of behavior (e.g., direction of turning in escape from predators) and they conclude that "the overall similarities across species strongly support the hypothesis of a common origin of lateralization in vertebrates" (p. 578). In contrast, they also suggest that the evolutionary pressures for lateralization are indifferent as to whether it is the product of homology or convergent evolution. Yet, the issue of whether vertebrate lateralization is a homology is critical for determining whether the cerebral and manual asymmetries in humans somehow set our species apart in a fundamental way from all other species.

MacNeilage, Studdert-Kennedy, and Lindblom (1987) proposed that because right-handedness and language are distinctly human and associated with cerebral asymmetry, investigation of the evolution of handedness by comparing handedness among different species of primate might reveal the evolution of language. Their review of 75 studies of primate handedness supported their postural origins theory (POT) of the evolution of handedness and cerebral asymmetry for language. POT proposes that early in primate evolution, their arboreal habitat (e.g., ancestors of prosimian and New World primates), required that they stablize their bodies on branches as they reached to acquire food. Apparently fortuitously, the left hand became preferred for reaching while the right hand was used for postural support. Because of the subsequent evolution (e.g., ancestors of Old World monkeys) some species did not feed in the trees and spent more time on the ground. Consequently, the right hand was freed from its postural support duties and was able to accomplish manipulation activities. MacNeilage et al. proposed that right-hand gripping skills preadapted it for manipulation and so it would dominate in bimanual manipulation. Because the reaching hand typically is the hand that first obtains the object, the reaching left hand is preadapted to provide support for the right-hand manipulations. Subsequently, this role-differentiated bimanual manipulation (RDBM) evolved (in humans and perhaps chimpanzees) into a generalized right bias for all hand use, including reaching.

Thus, according to the POT, the evolution of handedness (and hence cerebral asymmetry for language) may be identified by comparing various suborders of primates for their hand use when reaching for food. Unfortunately, reports of a population bias in primate handedness are mixed,

in part because studies do not precisely define how handedness is assessed or specify how a population-level bias is determined (in violation of Atz's requirement # 1).

McGrew and Marchant (1997) examined 241 published studies on nonhuman primate handedness and found that only 48 met their criteria for evaluation of the relation of primate handedness to human handedness (i.e., independence of data points, data from adults, and sufficient data points per subject for binomial analysis of lateralization, well-defined manual task, raw data, identification of species, and data from more than six subjects). They reported that the 12 acceptable studies of prosimian handedness provided evidence for individual handedness but no evidence of any biased asymmetry of handedness within any species or for the group as a whole. Also, the 19 acceptable studies of New World monkeys and the 11 studies of Old World monkeys failed to show anything more than individual handedness. For the 18 studies of apes that met the criteria, there was some evidence, especially from chimpanzees, of a population bias in handedness. McGrew and Marchant (1997) concluded that their review did not reveal evidence in support of the POT or any "human-like laterality of hand function" (p. 227) and that laterality of hand preferences in *Homo sapiens* may be uniquely associated with our specific evolution and self-domestication.

A detailed meta-analysis by Papademetriou, Sheu, and Michel (2005) of 62 studies published since 1987 and meeting requirements similar to those specified by McGrew and Marchant found some evidence for a left hand-use bias in some species of prosimian and Old-World monkeys and a right hand-use bias in chimpanzees. Nevertheless, they concluded that there is no evidence for the predicted evolutionary shift from a right-hand postural support role to a right-hand manipulative role. Also, the evidence did not support the proposition that nonhuman primate handedness is homologous with human handedness.

HOW DOES HANDEDNESS DEVELOP?

Typical investigations of the development of any trait begin with the earliest expression of the trait. In behavioral development, that requires especially good descriptions of the trait so that it can be identified at all stages of development. For handedness in children and adults, the descriptions have depended on measures of speed and accuracy of timed repetitive movements (e.g., peg-moving, dotting rows of circles), relative influence of each hand in controlling bimanual actions (e.g., "etch-a-sketch" drawing, alternating hand finger-tapping rhythms), pantomimed or verbalized expressions of the hand used for unimanual or bimanual tool-use (e.g., hammering), or the score on a questionnaire. Unfortunately, since all of these measures require that the individual follows instructions, they are not useful for infants. Nevertheless, all of these measurement techniques reveal the "special quality of handedness." That is, scores are continuously distributed across individuals with a predominance of people with scores on the right-handedness portion of the continuum and a minority with scores on the left-handedness portion. Also, there is some portion of people on the continuum of these various measures who

are neither clearly right-handed nor clearly left-handed. Although there are significant correlations among these measures, they are not equivalent.

Since description is the most important aspect of the study of the homology of behavior (Atz, 1970), I proposed that during the infant's first year, handedness be defined as hand-use preferences for three common activities—acquiring objects, unimanual manipulation of objects, and RDBM. Each of these manual skills emerges during the infant's first year, eventually becoming integral components of all manual skills in the adult. The infant's preference in each of these activities is presumed to reflect differences in the neural mechanisms involved in their sensorimotor control (Serrien et al., 2006; Volkmann et al., 1997). That is, the infant's "preference" depends upon differences in the control mechanisms for hand use (much like those involved in adult hand differences in speed and accuracy).

My collaborators and I (cf., Michel, 2002) have identified many early differences between the limbs in moving the arms (e.g., bringing the hand to the face and mouth), controlling the fingers of the hands (e.g., grasping and independent finger movement), swiping at visually presented objects, acquiring objects, unimanually manipulating objects, and RDBM (one hand supporting the haptic exploration of the object by the other hand). But are any or all of these hand differences in infancy equivalent to handedness in children and adults?

To avoid problems associated with the description of handedness in very immature individuals, some researchers have chosen to assume that all instances of asymmetric biases in lateralized functioning (including any difference in hand use) are the expression of the same underlying mechanism (Kinsbourne & Hiscock, 1977). And that mechanism is responsible for the manifestation of hemispheric differences in all functions (e.g., left-hemisphere predominance in the population for the control of speech and other language functions). Hence, it is that mechanism which is responsible for the eventual manifestation of handedness. This invariant lateralization theory has dominated in the field (Kinsbourne, 1981; Witelson, 1985). Hence, all lateralized asymmetries are equivalent because they are presumed to represent the same underlying, genetically controlled, cerebral neural asymmetry present very early in development. For example, some have proposed that there is a right hand bias in thumb-sucking by fetuses in utero, but there is no firm evidence for it (De Vries et al.,2001).

I propose that if we employ the five criteria proposed for identifying homology, we can determine whether early forms of handedness are "homologous" with later developing forms. Also, if we can chart the developmental process of handedness, we maybe able to extrapolate this knowledge to the development of other forms of hemispheric specialization of function or by analogy to the development of other psychological functions.

Early forms of handedness obviously use the same peripheral structure (the arm and the hand) for the manifestation of the behavior (Ethology criterion 1). Unfortunately, it is not certain whether the same neural circuits are involved in the different forms of handedness examined at

different developmental periods. It is likely that there will be some overlap in circuits (Ethology criterion 2). However, actions that depend on precise timing of the serial order of muscle contractions for the successful execution of the manual action (e.g., RDBM, peg-moving) likely have a more extensive overlap in circuits than those that do not (e.g., unimanual object-shaking/banging, finger tapping).

We have found that all of our measures of infant hand-use preference exhibit the same special quality as measures of adult handedness (Owen's criterion 2)—a continuous distribution across individuals but a predominance of those with a right bias and a distinct left minority. This special quality also extends to another laterally asymmetrical behavior of infants—the neonatal head orientation preference (HOP, cf., Michel, 1981; Turkewitz, 1977). When supine, neonates prefer to turn their head to one side. This pattern is continuously distributed with the majority exhibiting a rightward HOP, a minority a leftward HOP, and for others the preference is less distinct (Michel, 1981). The HOP elicits lateralized differences in the infant's arm and hand movements and creates differences in the visual, proprioceptive, and tactile experiences of the hands (Michel & Harkins, 1986). Moreover, infants with a leftward HOP prefer to use their left hand for acquiring things throughout their first 18 months, whereas those with a rightward preference prefer to use their right hand (Michel & Harkins, 1986).

Currently, we cannot distinguish whether the neonate's HOP is a precursor to, or a determinant of, infant hand-use preference or whether it may be an early manifestation of the lateralized asymmetry of the cerebral hemispheres (Hiscock, 1988; Witelson, 1985). The neonatal HOP is associated with the position of the fetus in utero during the last trimester of pregnancy (Fong, Savelsbergh, van Geijn, & de Vries,2005; Michel & Goodwin, 1979). This prenatal position can have consequences on the development of lateralized differences in the functioning of the fetal vestibular system, the auditory system, and postnatal posture (Kurjak et al., 2004; Previc, 1991). Neonatal hand-use differences (e.g., grasping durations, arm movements, face touching, thumb-sucking) do depend on postural asymmetries associated with supine HOP which, in turn, likely reflects prenatally influenced asymmetries in the activation of the vestibular system and brain-stem mechanisms (Michel, 2002).

Consequently, my collaborators and I have proposed that handedness development in infancy is a complex cascade of developmental contingencies with early appearing forms of infant handedness contributing to subsequent forms (criterion 3). The neonatal HOP is maintained for the first 8–10 weeks postnatally and affects several differences between the hands via brain-stem mechanisms (Michel,1981; Michel & Goodwin, 1979; Michel & Harkins, 1986). These differences promote differences between the face-side and skull-side hands that permit correspondent mapping in the nervous system of "felt" arm position, "seen" arm position, and "programmed" arm movements. The direction of the neonatal HOP predicts the hand preference for swiping at objects by four months of age (Michel, 1981). These laterally asymmetrical swiping actions lead into hand-use preferences for reaching for and acquiring objects, including food (Michel & Harkins, 1986).

Throughout the 6- to 14-month-old period, reliable hand-use preferences are observed in reaching for and acquiring objects (Ferre, Babik, & Michel, 2010) and a majority of infants (54%) exhibit a consistent right hand-use preference and 8% a consistent left hand-use preference (Babik, Campbell, & Michel, submitted). The remaining 38% of infants exhibit a significant linear developmental trend toward right handedness during this age period. Also, during this age period, the hand-use preferences for acquiring objects subsequently spreads into hand-use preferences for unimanual manipulation of objects (Hinojosa, Sheu, & Michel, 2003) and finally into hand-use preferences for RDBM and tool-use. In each instance of this spread of the preference, the infant exhibits the manual skill months before a hand-use preference appears. When that preference appears, it is predicted by the infant's preference for reaching. Because of this longitudinal cascade of the manifestation of handedness, infant HOP is predictive of infant hand-use preference in RDBM.

Examination of these same infants' handedness for RDBM during the period from 18 to 24 months of age reveals that those who had a consistent hand-use preference for acquiring objects at 6–14 months exhibited the same hand-use preference in their pattern of RDBM (Nelson & Michel, in preparation). Those toddlers, who as infants did not manifest a consistent right hand-use preference, began manifesting a preference for RDBM with most exhibiting a right preference. Thus, early handedness development appears to be a spreading cascade across different manual skills rather than simply an increase in hand preference within a skill. Michel (2002) proposed 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 for all future manual actions and hence their "handedness."

Currently, we are charting the relation of the hand-use preferences in these infants and toddlers to their handedness, as measured by the standard peg-moving and circle-dotting skills, during their third to fifth year of age. Such charting will provide evidence of the developmental relation of infant hand-use preferences to the handedness of children and adults. This detailed charting of the developmental trajectories for handedness can serve as a model for how behavioral developmental research should be conducted if it is to emulate the successes of developmental biology. Although the construct of homology has not been particularly useful for understanding the development of handedness, that does not mean that other constructs from biology (particularly developmental biology) may not useful for developmental psychology.

CONCLUDING REMARKS

(1) *How might developmental psychologists use the homology construct?* Developmental psychologists could employ phylogenetically relevant comparative developmental research to identify better animal models of human behavioral characteristics (based on their evolutionary lineage) that would permit more extensive experimental investigation of the potential factors affecting the development of these homologous behavioral characteristics in humans.

(2) *How might we determine if a characteristic present in adults is homologous to a characteristic present earlier in development?* The developmental biology concept of "deep homology" (Wake, Wake, & Specht, 2011) may prove useful. Common developmental genetic mechanisms underlie features that long were considered classic examples of convergent evolution. The paired appendages of tetrapods (e.g., frogs, lizards, mammals) and arthropods (e.g., flies, lobsters, spiders) evolved independently, but research shows that homologous gene clusters (sharing ancient common ancestry) are responsible for the initial outgrowths from the body in both vertebrates and arthropods. Thus, while the morphological structures expressed in adults (e.g., legs of flies and legs of humans) are not homologous (because they were not present in a shared ancestor), homology may lie within the organization of their genes and their regulatory networks. This deep homology reduces the differences between convergent and parallel evolutionary phenotypes and raises problems for developmental homologies. Consider human handedness.

Several theorists (Corballis, 1997; Crow, 2002) propose that a genetic mutation in hominid evolution promoted preferential use of the right hand. Family, twin, and adoption studies provide evidence for a genetic contribution to individual differences in adult handedness (McKeever, 2000; Risch & Pringle, 1985; Sicotte, Woods, & Mazziotta, 1999). Also, family history of sinistrality affects both individual handedness and assessments of hemispheric specialization of function (Annett, 2002; Corballis, 2009). Although the nature of the genetic influence on handedness remains unknown, a segregation analysis of family data (Risch & Pringle,1985) concluded that the patterns were consistent with either a single-locus or a polygenic model of inheritance.

Annett (1995, 2002) proposed a single locus genetic model that accounts for the distribution of handedness in the adult population and its relation to hemispheric specialization of function. In Annett's model, handedness is a continuously distributed trait with three underlying groups representing different genotypes (rs+/+, rs+/−, rs−/−) that are important for establishing distinct patterns of hemispheric control of speech. In a recent study (Michel, Sheu, Babik, & Campbell, in preparation) of 171 infants, we found that despite a continuous (but right shifted) distribution of the hand-use preference scores for acquiring objects during infancy, infants can be categorized into three latent groups underlying infant hand-use for acquisition. Moreover, the distributions of the latent group significantly matched the proportions predicted by Annett's single-gene model of hemispheric specialization. Also, we found that the infant's hand-use preference significantly predicted his/her membership in a latent group. This means that the infant's hand-use preference for acquiring objects (like adult handedness) could be predictive of potential differences in an underlying genetic character. This could support the notion that infant and adult hand-use preferences are homologous (perhaps, via a deep homology in the genome).

(3) *How can we use the concept of homology to help developmental psychologists formulate novel, empirical research questions?*Although infant hand-use preferences have characteristics in common with adult handedness, there is insufficient evidence to conclude that infant handedness

is homologous with adult handedness. Infant hand-use preferences may contribute to the development of adult handedness without being homologous. Only systematic comparative developmental research, using precise definitions of handedness (appropriate for different stages of development), can permit assessment of the homology of handedness.

If we can use the investigation of the study of handedness analogously, then I would argue that it is premature to use the construct of homology in developmental research on any psychological trait (numerical skills, attachment, imitation, emotional expression, etc.). Nevertheless, I do believe that attention to the theoretical constructs of developmental biology would be relevant for formulating novel research questions in developmental psychology.

Gilbert's and Epel's (2009) construct of "Heterocyberny" can be applied to development of psychological traits as a way of seeking sources of variations in developmental trajectories. They proposed four sources of developmental variation: heterotopy, heterochrony, heterometry, heterotypy. In heterotopy a behavioral trait appears as a component of a different pattern of the individual's repertoire—"shyness" may appear with behaviors addressed to familiar as well as unfamiliar companions. In heterochrony, a behavioral trait appears at a different time during development relative to other developmental events—handedness develops during the toddler phase rather than during infancy. In heterometry, a behavioral trait occurs with different intensity—over- or under-emotional reaction to common social interactions. Heterotypy is a change in a developmental trait's relation to other developing traits—hand-use preferences become involved with the development of arousal regulation (thumb-sucking) rather than with the development of "knowledge" about the properties of objects. Comparative developmental research on behavior should search for trajectory patterns that exhibit any of these heterocybernic patterns. This likely will improve our understanding of developmental variability and its underlying mechanisms.

NOTES

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