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ON THE DEVELOPMENTAL ORIGINS OF HUMAN HANDEDNESS¹

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One of the oldest controversies about human behaviour concerns the origins of handedness. Many speculations have been offered, but few have withstood scientific examination. Part of the lure of this seemingly straightforward expression of the motor system is the claim that it is a uniquely human trait that is closely associated with the acquisition of language. Such claims are currently the focus of intensive programmes of research concerned with the origins of human development and evolution. With regard to the developmental origins of handedness, there are presently a number of empirically accessible models which differ from each other in important ways. In the present paper we examine the strengths and weaknesses of these models in an attempt to distil what might be fruitful directions for future research. However, before attempting this task we ask two essential questions: Why should developmental psychologists study handedness, and what is meant by handedness? We conclude by, among other things, posing a number of questions about the development of handedness that still need to be addressed by subsequent theory-building and testing. Answers to such questions will only come from process-oriented models on the developmental (and evolutionary) origins of handedness which can illustrate how early motor asymmetries may be linked to later biases in manual functions.

Key words: hand preference ; manual specialization ; prenatal asymmetries ; headedness ; primates

1. Introduction

There has been a long history of debate and research into the origins of human handedness, much of which has been captured in an excellent review by Harris (1983). In contemporary man, handedness assumes a J-shaped distribution in which 85-90% of the adult population demonstrate a right-sided bias, depending on which measures of hand use are employed. Explanations for this bias, which has been held to be culturally invariant and species-specific, have been inextricably linked with questions about the developmental and evolutionary origins of language. Both in development and evolution, it was assumed that handedness was simply an epiphenomenon arising from the acquisition of language. This assumption led to two conclusions which have been only recently challenged, namely, that handedness is late-occurring phenomenon both in development and during human evolution. These conclusions had the effect of assign-

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ing handedness a marginal role in the evolution and development of human abilities. More importantly, they precluded attempts at seeking empirical evidence for the origins of a distinctively human trait prior to the ontogenetic and phylogenetic attainment of language. To have admitted prelinguistic origins would have further dismantled deep-seated beliefs about the unique position accorded to *Homo sapiens* in the animal kingdom. Thus, questions about the origins of human handedness are by no means trivial, but rather go to the very heart of what it is that distinguishes us from other animals. Recent answers to these questions form the focus of the present contribution. Given the enormity of the topic, its focus will be restricted to the developmental origins of handedness. However, some questions about evolutionary origins will be raised. The first question to be raised though is "Why study handedness?"

2. Why study handedness ?

For developmental psychologists unfamiliar with the vast literature on handedness, it may not be immediately obvious why this behavioural trait should be of interest to them. At a general level, handedness is a readily observable phenomenon that as such enables one to address a number of the grand issues that continue to confront developmental psychologists. Such issues include gene-behaviour relationships, brain-behaviour relationships, constancy versus change (e.g. between pre- and postnatal life), sensitive periods and the role of experience. Given the apparently unambiguous nature of handedness, it may be possible to generate findings relevant to these issues which are generalisable, in the sense of a developmental principle, to other domains of development.

This claim is by no means new and can be found, for example, in the writings of Baldwin (1890 ; 1894), one of the founding fathers of contemporary developmental psychology. In studying the development of his own daughter using experimental methods, Baldwin paid particular attention to reaching and grasping and their lateralization on the assumption that they provided a window to mental development. More recently, and continuous with Baldwin's thinking, Young (1990) has proposed an ambitious theory which links the development of lateralization (mainly handedness) to a number of cognitive achievements (most notably language). Termed an inhibition theory of complementary hemispheric specialization, it results in a 20 step model of development. The basic assumption is that the cerebral hemispheres contribute differentially to processes of behavioural inhibition with the left hemisphere being the site of a sophisticated mixture of activation and inhibition which serves to control the sequencing of acts in both language and fine motor abilities. In contrast, the right hemisphere is more specialized for spatial processes and less so for any manifestations of dynamical inhibition. The question then, which remains largely unanswered in Young's theory, is what are the exact relationships between changes in the lateralization of functions and the development of cognitive abilities (which in Young's case are defined in Piagetian terms)? Are they in some sense unidirectional or bidirectional in nature? The most that can be said at the present time is that changes in the development of lateralization (and in particular handedness) appear to 'flag' new achievements in the cognitive-linguistic domain. This assertion is amply illustrated in Ramsay's (1980 a ; b) pro-

gramme of research on the codevelopment of hand preference and speech. What Ramsay found were coincidences between *a*) the onsets of canonical babbling and a right-handed preference for manipulation, and *b*) the onsets of reduplicated babbling and bimanual coordination. He went on to speculate that speech production precedes the appearance of manual asymmetries at 6 months, whereas at 12 months the reverse is the case.

For the clinically-oriented developmental psychologist, the development of handedness merits more than a cursory glance. Many studies have demonstrated that left-handers are clearly overrepresented in groups with severe and generalized cognitive deficits (see Pipe, 1990 for an excellent review on this topic). What is less clear is whether non-right handedness is also associated with specific deficits such as reading disability, perceptual problems, stuttering and mild intellectual retardation. What is almost completely opaque concerns the mechanisms by which central nervous system dysfunctions are expressed as deviations in handedness—a situation arising from lack of carefully-designed prospective studies.

The utility of handedness for addressing fundamental and clinical issues of relevance to developmental psychologists should now be clear. The outstanding stumbling block to further progress on both fronts emanates from a lack of a clear understanding of the developmental origins of handedness. Thus, the main problem to be tackled in this paper is how the right bias in human handedness could originate. To this end a number of current theories which concern this topic will be considered in terms of their explanatory vigour. Some attempt will be made at forging links between them although this will be kept to a minimum as the theories involved are, in their present states, very disparate in nature and hardly conducive to a sensible integration. However, before embarking on this task, we should realise that any attempt at explanation assumes that we have an unequivocal understanding of the term handedness. Unfortunately we do not and this constitutes a problem, namely, what are we seeking the origins of? And consequently, what is it that develops? These questions will be addressed (section 3) before discussing the theories of interest (section 4). Subsequently, a six-point summarising commentary will be given that may serve to guide fundamental research in the future on the development of handedness (section 5). With a similar intention, the paper ends with a number of questions (and some tentative answers) that are ordered in terms of what I consider to be their relative importance (section 6).

3. What is handedness?

It is becoming clear that handedness is a multidimensional, rather than a unidimensional, trait. It can no longer be conceptualised as a rigid reliance on one side of the body regardless of the task conditions. At the very least we need to make a distinction between hand preference and manual specialization (Young et al., 1983). Accordingly, hand preference can be defined as the consistent use of one hand on simple and familiar tasks and manual specialization as lateralized usage on more complex, less familiar tasks which may involve either hand. In terms of development the relevant questions are then: how does a hand preference originate and how does it relate to later-occurring forms of manual specialization? To examine such questions requires

assessments of hand use across a range of tasks at different ages, something which is hardly done in studies on infants. One of the few studies to do so was carried out by Michel et al. (1985). Here 12 infants at each month from 6 to 13 months (thus 96 in total) were examined on three different tasks (reaching for objects, manipulating objects and carrying out complementary bimanual actions). At all ages, the right hand was preferred for manipulation, as it was for reaching, with the exception of 13 months. Bimanual manipulation (which is evidence of manual specialization in that one hand manipulates the object while the other supports it) was not clearly evident until 12 months. Once again it was mainly the right hand that did the manipulating. At 13 months, most of the infants' preferences during reaching and bimanual manipulation were no longer compatible. By this age it appeared that the nonpreferred hand reached to and secured the object so that the preferred hand could then manipulate it. Thus, by using a variety of tasks, it was possible to arrive at the conclusion that a right-sided preference for reaching at 6 months of age is incorporated into more complex abilities at later ages. If only reaching had been used as an index of handedness, then hand preference would have appeared to fluctuate during the second half of the first year.

What is known about the development of handedness during the first half of the first year? Here the picture is less clear with evidence for a consistent righthanded preference (Michel & Harkins, 1985) as well as for fluctuations between hands across age (Carlson & Harris, 1985). At the root of these differences in findings is whether a left hand preference appears before a rightsided one. Both Gesell and Ames (1947) and Seth (1973) reported that reaching initially showed a leftsided bias, but these studies were subsequently criticized on statistical and methodological grounds (Young, 1977; Annett, 1978). More recent and better controlled studies provide conflicting findings. Some have reported an initial rightsided preference (von Hofsten, 1982; Young et al., 1983) and others a leftsided bias appearing before or at about 3 months (Coryell & Michel, 1978; DiFranco et al., 1978; McDonnell, 1979). A similar lack of correspondence has been found between studies on grasping a rattle placed in the hand. Three found a righthand preference around the same age (Caplan & Kinsbourne, 1976; Hawn & Harris, 1983; Petrie & Petes, 1981) while a fourth could not find any bias (Yu-Yan et al., 1983). At the present time the most we can conclude is that the earliest signs of hand preference appear to be task-specific in that they are dependent on whether the task involves control of the proximal muscles (as for reaching) or the distal segments of the hand (as for grasping). Furthermore, it may be questioned whether reaching before 3 months, which does not involve prehension, should be used as an index of handedness. It seems more appropriate to treat it as an indication of arm preference and then to ask how it can be reconciled with a hand preference for grasping.

All of the above lead to the following conclusions. Firstly, better definitions and more precise measures of handedness are needed. Secondly, the use of a variety of measures of handedness that can account for developmental changes in manual abilities. Thirdly, the need to incorporate the emerging abilities of the nondominant hand into the definitions and measurements of handedness. Fourthly, to pay more attention to

individual differences, for example, through using the distinction between the direction and degree of handedness. Few studies on the development of handedness in human infants appear to have given consideration to all these points. In these respects, we have much to learn from recent investigations of hand use in nonhuman primates (e.g. Hopkins, W. D. et al., 1989).

4. On the developmental origins of handedness

There is a plethora of speculations on developmental events that may lead to a righthanded bias in humans, many of which have a long history (Harris, 1983). In the last decade a number of these speculations have been reworked into testable models. For the present purposes they will be termed the biased oocyte, the biased gene, the biased brain, the biased head and the biased uterus. Each of these models has its own idiosyncratic shortcomings which mitigate against a comprehensive model on the developmental origins of handedness. However, where possible, points of contact between these models will be indicated.

a. *The biased oocyte: the left-right maturational gradient model*

According to this model, lateral asymmetries such as handedness are governed by a left-to-right maturational gradient coded in the spatial structure of the unfertilized egg rather than in the genes (Corballis & Morgan, 1978). It is based on the fact that all living cells have intrinsically asymmetrical properties. What is unique to this model is that it incorporates maternal effects that do not rely on a strict genetic interaction between mother and father. Accordingly, the gradient is laid down during oogenesis by factors intrinsic to the cytoplasm and not to the nuclear genes. However, the actual expression of an asymmetry ultimately depends on genetic and environmental influences.

The shift from an initial left to a righthand preference may be related to this gradient, but as we have seen, there is contradictory evidence as to whether functional development begins with a sinistral bias. As we shall see, there are cerebral asymmetries which do not perfectly correlate with hand preference as would be predicted if both were based on the same maturational gradient. Furthermore, embryological evidence supports neither a left-right or right-left gradient, but rather suggests cyclical or fluctuating asymmetries during growth (Mittwoch, 1978). The main stumbling block for this model is, however, the lack of evidence that cytoplasmic inheritance plays a role in vertebrates. On the contrary the inheritance of lateralized traits is through the nuclear genes. Thus, if there are maturational gradients underlying the origins of handedness, then they should be under some form of direct genetic control. This is assumed in the most widely accepted genetic model of handedness which we turn to next.

b. *The biased gene: the right shift gene model*

Proposed by Annett (1985), this model stresses that handedness is not a discrete variable but one with a continuously varying gradient. Thus, there are degrees of preference which are systematically related to a continuous distribution of differences between the hands in the performance of particular tasks. The model has two compo-

nents: one genetic and the other environmental or more properly accidental in nature. The majority of individuals inherit a gene which predisposes them to left-hemisphere control of speech and as a by-product a righthanded preference. A minority of individuals lacking this right-shift factor will have their cerebral dominance for speech and hand preference determined at random. Accordingly, for these individuals there is an equal likelihood that they will have a left or righthand preference, and in these cases a dextral bias can arise from environmental pressures. Thus, unlike the two-gene model of Levy and Nagylaski (1972), which assumes two directional alleles, Annett's more probabilistic model can account for the high percentage (60%) of right-handedness with two left-handed parents. Despite such predictive power, it should be borne in mind that the right-shift gene model rests on an assumption that has neither theoretical nor empirical support, namely, that both dominant and recessive alleles are present in the population at a frequency of 50%.

The importance of Annett's model for the present purposes is that it directs attention to the neglected role of familial handedness in the development of hand use. The findings of one study that included this factor complied in part with the predictions of Annett's model while at the same time stressing the need to account for the ways it may interact with the sex of the infant (Carlson & Harris, 1985). Using a longitudinal design, it was found that familial righthanded (FRH) boys and girls showed an increase in rightsided reaching from 24 to 52 weeks. However, from 27 weeks onwards, the FRH boys had a left arm preference, but by 52 weeks no lateral bias. In contrast, neither FLH boys nor girls had a lateral preference at 24 weeks, which was then followed by a right to left trend up to 52 weeks—this shift occurring earlier in boys. These findings run counter to any notion of a simple maturational gradient and cannot be straightforwardly reconciled with Annett's model (in particular those concerning FRH boys). On the other hand, the fluctuating trend manifested by the FLH group is in accordance with the model as presumably these infants lacked the rightshift gene and were therefore more susceptible to variations in environmental influences. While this study was not concerned with the developmental origins of handedness, it clearly points to the need for including both the sex of the infant and familial handedness in addressing this issue.

The data Annett has gathered in support of her model are based on children older than two years and adults. To constitute a valid model for the developmental origins of handedness, then it should be able to account for the distribution of structural and functional asymmetries during early development that have been proposed as precursors for the establishment of handedness.

c. The biased brain model

Many gross neural asymmetries have been found to be evident as early as the second trimester of pregnancy. However, it is unknown whether they arise during embryogenesis or during later stages of brain development (viz. during neurogenesis, neuronal migration and maturation). The processes by which such asymmetries arise are also poorly understood: do they reflect suppression of development on one side, an enhanced development on the other or a combination of both processes? According to

the neuronal loss hypothesis (Galaburda et al., 1987), the cortical hemispheres initially have an equivalent rate of development followed by involution on one side. Thus, there is an initial period of symmetrical neuronal (over) production of neurons, axons and synapses which are then pruned down more on one side by trophic factors and activity leading to that side becoming smaller. This hypothesis is not easy to relate to what is known about cerebral asymmetries that appear during fetal life. Structures such as the Sylvian fissures and the planum temporale are larger on the leftside. Other evidence points to an initial rightsided bias: from 10 to 40 weeks, it was found that the development of presumptive language areas such as the supramarginal, angular and transverse temporal gyrii was more advanced on the right side (Chi et al., 1977). In addition, the Rolandic fissure on the right became convoluted some 3 weeks earlier than its homologue on the leftside. Thus, the most one can draw from these findings is that some parts of the right hemisphere initially develop faster, but that there is later a catch-up in growth for the left hemisphere which eventually becomes the larger of the two. While this could be taken as support for an initial leftsided bias in reaching, it is highly questionable whether there are any contralateral cortical fibres that are functional when this action appears for the first time. In fact, assessments of local metabolic processes in the neonatal brain by means of Positron Emission Tomography have demonstrated little or no functional activity in any neocortical structure (Chugani & Phelps, 1986).

It is doubtful whether all the evidence for the existence of such prenatal cerebral asymmetries will help us to understand the origins of handedness. What we need is more information about the development of asymmetries in structures known to be involved in motor control, particularly at the subcortical level. A recent study of 18 normal brains, some of them as young as 28 weeks gestation, revealed the globus pallidus in the basal ganglia had a larger volume on the left side. This asymmetry was found in all brains younger than 4 years (Kooistra & Heiman, 1988). While it would be tempting to associate this asymmetry with an initial rightsided bias in reaching, it should be remembered that the basal ganglia do not have direct connections with nuclei or cortical regions which give rise to motor pathways projecting directly to the spinal cord. Furthermore, the precise role of each nucleus of the basal ganglia is currently a controversial topic.

In terms of the descending motor systems, it is known that the ventromedial system, which includes the vestibulospinal tract, develops earlier than the direct corticospinal system (Kuypers, 1985). As for the rubrospinal tract of the lateral brain stem system, it is unknown if it has any function in humans. The vestibulospinal tract projects bilaterally to the spinal cord and controls the proximal muscles of the arm. Thus, when reaching first appears it would involve ipsilateral control. Depending on which hemisphere is functionally more mature at this time, there could be either left- or rightsided biases in reaching. Individual differences in this regard could explain why there is a lack of between-study agreement on whether the first reaching movements are left- or rightsided. In the direct corticospinal system which provides contralateral control of the fingers, it is known that in the fetus most fibres of the pyramidal tract decussate more completely from left to right than the other way round (Yakovlev &

Rakic, 1966). Thus, it is possible that corticospinal fibres destined to innervate the small muscles of the right hand may be more numerous than for the left. This finding may provide one explanation why most infants display a more consistent rightsided preference after about 6 months as assessments then are derived from the ability to combine reaching with grasping. However, this suggestion only accounts for dominant hand use and not for the superiority of the left hand in visuospatial abilities. The main point is that assessments of handedness involving goal-directed arm movements will be based on different motor systems at different ages. The question then is how a bias in the ventromedial system may induce one in the corticospinal system.

The models considered so far are essentially predictive in nature—biases in maturational gradients, genes or fetal brain structures should portend an ultimate right-handed preference in most individuals. They have little to say about the processes that lead to the establishment of a dextral preference in contrast with the last two (interrelated) models.

d. *The biased head and uterus models*

A number of studies have demonstrated that the orientation of the newborn's head in supine has a similar dextral bias to that found for adult handedness. The same neonatal bias has also been found for head turning when it is released from a midline position. Previously the lateralized head position adopted by the young infant was purported to be a by-product of the Asymmetric Tonic Neck (ATN) reflex (Gesell & Ames, 1947). This is clearly not the case as a spontaneous ATN position only becomes dominant at about 3 months (Touwen, 1976). Thus, the question of interest is whether the neonatal head position preference, and not the direction of the ATN position, is predictive of handedness at later ages in infancy. This question has been addressed in a series of studies by Michel and colleagues. In general, both the assumption (Michel & Goodwin, 1979) and the maintenance (Goodwin & Michel, 1981) of lateralized head position predict the arm that will be used for reaching. Subsequently, it was shown that these early functional asymmetries provided predictions of hand preference at 60 (Michel, 1981) and 74 weeks (Michel & Harkins, 1986). Michel offers a plausible and testable explanation for how 'headedness' may be related to later manual specialization. The basic idea is that the neonatal head orientation induces a lateral asymmetry in hand regard and activity in the first couple of months. Greater experience of one hand leads to it being preferred for visually-guided reaching which in turn ensures that it will become specialized for fine motor abilities. Thus, as each functional asymmetry appears it is transferred to a subsequent ability, not because each asymmetry stems from a common neural mechanism, but because there is a continuity in experience of using one hand rather than the other. The developmental origin of righthandedness is to be found in the head position preference of the newborn. What then is the origin of this neonatal asymmetry in function? One suggestion has been the position of the fetus in the last few weeks of pregnancy.

Two-thirds of the fetuses born in a left vertex presentation have their backs towards the mother's left side some 3 to 4 weeks prior to fullterm delivery. In this position, with the rightside of the head facing outwards, movements of the left arm (as

well as its arterial blood) are restricted by the pelvis and backbone of the mother. Given the close relationship between head position at birth presentation and its position in the weeks before in most fetuses, it was asked if the former predicted 'headedness' after birth (Michel & Goodwin, 1979; Goodwin & Michel, 1981). It was found that a left vertex presentation was significantly associated with a rightsided head preference. This was not the case for those newborns with a right vertex presentation: their preferences were randomly distributed rather than leftsided as predicted—an indication that these infants may have had a history of FLH.

Why do most fetuses assume a lateralized position with the rightside of the head facing outwards? The plausible answer is that this position is an adjustment of the growing fetus to asymmetries in the uterus. In most cases, the uterus has a torsion to the right resulting in the maternal bladder and rectum as well as the placenta being positioned to the right. Under these conditions, there is more room for the head and body on the left side of the uterus when the fetus assumes a left vertex position. Why this position should be associated with a head position preference to the right postnatally has recently been addressed by Previc (1991) in his vestibular dominance or left otolithic dominance hypothesis.

According to this hypothesis, vestibular lateralization may arise from the asymmetrical position of the fetus during the latter part of the final trimester of pregnancy. In the left vertex position, the forward acceleration and the backward inertial force generated by maternal walking would be preferentially registered by right and left sides of the vestibulum respectively. In short, when the mother walks there is an unequal shearing of the hair cells in the two otoliths of the fetus resulting in a left-otolith dominance. Impulses from the maculae of the utricles travel centrally to the brain stem and cerebellum. In the brain stem they terminate on the vestibular nuclei, one of which (Deiter's nucleus) is the origin of the vestibulospinal tract. Almost all the fibres of this tract are uncrossed and most end on interneurons in the spinal cord. The main function of this tract is the ipsilateral control of extensor muscles. For head turning, the most important muscle is the bilateral sternocleidomastoid—the left of which is activated when the head is turned to the right. Thus, a left-otolith dominance should be related to a left-sided bias in the activation of this muscle and thereby a rightsided head preference.

Previc's general theory successfully disassociates questions about the developmental origins of handedness from those about language. He does so by proposing independent mechanisms for the origins of a rightsided motor dominance and a right-ear sensitivity. In this respect alone, Previc's intriguing theory represents a considerable advance on previous attempts to link prenatal neural asymmetries with the developmental origins of handedness. We are now in a position to make cross-species comparisons as a means of addressing how a dextral bias in handedness could have arisen in hominid evolution without getting this issue confused with that pertaining to the evolutionary origins of language.

Summarizing comments

1. The measurement of handedness during infancy should take account of rapid

changes in motor abilities. There is no single task (e.g. reaching) that will provide a valid index of handedness even during the first year.

2. During the first half of the first year, it may not be hand preference that is being measured, but rather arm preference.
3. The question of whether the initial arm preference for reaching is right or left-sided is still unresolved. As such, it stresses the need for including measures of familial handedness. Should these measures be derived from questionnaires or direct tests of handedness and should they then be treated as a binary or continuous variable?
4. Of all the models discussed, only Annett's single gene model provides a reasonable prediction of those individuals who will be right *or* left-handed. However:
5. We still lack a satisfactory process-oriented model for the developmental origins of handedness and for how early motor asymmetries are linked to a later bias in handedness. What should be clear is that there is no common neural mechanism which is shared by earlier and later motor asymmetries.
6. We badly need comparative primate studies on the development of motor asymmetries. These should include ultrasound recordings of fetal movements and posture in the great apes.

6. Questions (and some answers)

In answering some of the questions I will draw on published and yet-to-be published findings from the Amsterdam Laterality Study (ALS) currently being carried out at the Free University.

The Big Ones

1. What are the problems confronting current models on the developmental origins of handedness?

I will only deal with two here: those subscribed to by Michel and Previc.

- a. *Michel*: differential visual regard of the hands arising from a lateralized head position is proposed to lead a biased use of one hand in such actions as reaching. There are two problems with this proposition. Firstly, congenitally blind individuals have a righthanded bias in reading braille (Bradshaw et al., 1992). But this is only one task which may be subject to teaching strategies biasing the right hand. Difficult though it would be, what is needed is a longitudinal study of infants blind at birth. Do they show a rightward head position preference? Do they initiate reaching with the right or left arm to an auditory stimulus? Secondly, a lateralized head position lasts only for 2-3 months and then is replaced by a preference to hold the head in the midline (Hopkins et al. 1990). Unless we propose a sensitive period hypothesis (which is not supported by the findings on blind patients), then this seems to be an inordinately short space of time in which to establish a rightsided dominance in subsequent motor abilities. Perhaps there are other asymmetries in the spontaneous movement repertoire that persist beyond the age when a head midline position becomes dominant. We found that in newborns one hour after birth, hand-mouth (but not hand-face) contacting was highly lateralized (Hopkins et al. 1987): all newborns contacted the mouth with the hand ipsilateral to the

head position and most did it with the right hand. After 6 weeks this synergy breaks up and the infant is just as likely to contact the mouth with the right or left hand. However, by 18 weeks we noted the reestablishment of a right hand preference. but now with the head in the midline (Hopkins, Savelsbergh & Butterworth, submitted).

- b. *Previc (1991)*: he concludes that "...the origins of vestibular asymmetry in man lie in a *neural* rather than structural imbalance favoring the left utricle" (p.318). What is known about the development of the vestibular system suggests otherwise. The system is structurally mature very early in prenatal life (Humphrey, 1964). Despite this fact, there is no evidence that it is functional before birth. Experimental work with guinea pigs has revealed that the system is functionally inhibited by low levels of oxygen tension as experienced in utero (Schwartz & Schwartz, 1977). In the human, shaking the maternal abdomen from side-to-side failed to change the heart rate pattern or induce movements in the near-term fetus which would be expected if the vestibulum was functional prior to birth (Visser et al., 1983). It is unlikely, therefore, that movements of the endolymphs and hair cells in the vestibulum of the fetus will be registered centrally in terms of action potentials. All of this suggests that a structural imbalance may be induced by the differential stimulation of the two otoliths which then exerts its neural effects after birth. Findings on preterm infants are relevant to Previc's hypothesis. In the ALS project we have recently found preterm infants born before 32 weeks gestation demonstrated a rightsided bias for the maintenance, but not for the assumption, of a head position at 35 weeks (Geerdink, Hopkins & Hoeksma, 1993), a finding in agreement with other studies (e.g. Gardner et al., 1977). It is difficult to know how to reconcile these differences in performance with Previc's hypothesis.
- c. *Michel & Previc*: both models can account for the origins of right—but not leftsided motor asymmetries. Previc (1991) does try to redress this problem in suggesting... "a greater percentage of lateral positioning reversals prior to birth among sinistrals" (p. 301, footnote 3). I know of no evidence to support this suggestion. A recent study observed thumb sucking in the fetus using realtime ultrasound recordings on the assumption it may be a precursor of handedness (Hepper et al., 1990). In 274 fetuses there was a clear bias for sucking on the right thumb as early as 15 weeks of gestation which was hypothesised to be related to head turning after birth. There was no relationship found between intrauterine position and thumb-sucking preference. Of 28 right thumb suckers, 23 turned to right and for the four left thumb suckers, 3 had a left and 1 a right turning bias. Thus, it was concluded that thumb sucking initiates development of brain lateralization. The challenge of the study is that if the fetus sucks the right thumb, then the theoretical link between 'headedness' and handedness may reside in a more fundamental asymmetry which appears many weeks before a lateralized fetal position. The limitation of the study is that it included only 4 left thumb suckers. In addition, we have found in the ALS that it is very difficult to observe thumb sucking in the fetus on a regular basis, and due to the 2-dimensional image of the fetus there are problems in arriving at reliable estimates of whether the right or left hand is

involved. However, we have been able to observe a lateralized head position appearing at 36 weeks gestation (van Gelder, Dijkman, Hopkins, van Geijn & Ho-Meau-Long, 1990; Ververs, de Vries, van Geijn & Hopkins, 1992). Before that age the head was predominantly in the midline position. Given that preterm infants also show an asymmetrical head position preference for the first time at around this age, it clearly indicates that this postural bias is due to neural maturation and not to mechanical influences emanating from uterine asymmetries. It is interesting to note that the appearance of a lateralized head position coincides with the appearance of stable behavioural states (Nijhuis et al., 1982).

2. What is the clinical relevance of research on early motor asymmetries?

There is a predilection among developmentalists to seek for stability in behavioural development. It is becoming clear, however, that intraindividual variability may be a cardinal feature of normal motor development (Touwen, 1978). Handedness appears to fluctuate, particularly during the first 6 months. For 'headedness' there are too few longitudinal studies to know with any degree of certainty whether it is also a fluctuating asymmetry within individuals. In the ALS, we have observed some degree of stability in a lateralised head position preference up to 3 months (Hopkins et al., 1990), but a high degree of variability in hand-mouth contacting across the same age range. The point to be made is that a strongly lateralised asymmetry to the left *or* to the right for either 'headedness' or handedness may be indicative of underlying neuropathology. This view is in contrast to those models proposing that leftsided asymmetries, or a lack of asymmetrical behaviour, may constitute a pathological state (Bakan, 1971; Satz, 1972).

3. What do we need to know from the fossil record to help us better understand the evolutionary origins of handedness?

Endocranial casts of KNM-ER 1476 (a *Homo Habilis* specimen) dated at 2 million years BP have revealed left hemisphere asymmetries (Tobias, 1981). Analyses of artifacts (*viz.* flakes produced from knapping stone tools indicate hominids had become righthanded at about the same time (Toth, 1985). However, if the attainment of an upright posture was the prime mover for the appearance of manual specialization in hominid evolution, then handedness may have an even greater evolutionary age. The oldest fossil hominid is *Australopithecus afarensis* which has been dated at about 3.5 million years BP. The morphology of the pelvic girdle clearly indicates an upright posture and the ability for bipedal locomotion. What is not known is whether this hominid possessed manual specialization. The hands are intermediate between contemporary humans and chimpanzees and would have permitted a range of precision and power grips, but probably not a fully abducted pincer grip—however the latter does not necessarily exclude the potential for manual specialization. Thus, the evolutionary depth of handedness is still a matter of debate, although it now seems evident that its evolutionary appearance preceded that for language.

It would be interesting to know from the fossil record when the first evidence

for a lateralized fetal position appeared. Would it have been a left vertex position? Did it precede handedness or did they evolve together? The pelvic girdle of *Australopithecus afarensis* has a humanlike shape, including an oval inlet. While this does not necessarily imply a lateralized fetal position towards the end of pregnancy, some physical anthropologists contend that rotation of the fetus and flexion of its head would have been required to pass through the birth canal (Berge et al., 1984). Among primates, this mode of delivery is found only in humans. Until someone investigates whether there are asymmetrical markers in the pelvic girdles of australopithecines, we will not know whether these hominids also had another obstetrical feature in common with man, namely, a fetus who adopted a lateralized vertex presentation.

4. Can we categorically deny that nonhuman primates do not have a righthanded bias for handedness?

The short answer is "no". The long answer is less categorical. It is generally held that primates and mammals have a preference for one hand or paw over the other, but that only humans manifest a population bias in favour of one hand. Evidence for and against this view is, to say the least, contradictory. After reviewing many studies involving prosimians, New and Old World monkeys as well as the great apes, MacNeilage et al. (1987) concluded: a leftsided bias for reaching (particularly in prosimians and New and Old World monkeys) and righthandedness for manipulation (in some monkeys and apes, but not prosimians, i.e. in those with opposable thumbs). One of the problems with the literature on handedness in nonhuman primates is the lack of studies involving the great apes. It may be the case that the most consistently righthanded great ape is the gorilla who is also the most terrestrial of them (Bresard & Bresson, 1987; Fischer et al., 1982). The best controlled study I have come across involved 2 rhesus monkeys and 3 chimpanzees (Hopkins W.D. et al., 1989). Both species showed significant righthanded preferences in manipulating a joystick, but neither did in reaching for an edible reward. The biggest stumbling block in arriving at any firm conclusions about handedness in nonhuman primates is the small number of subjects involved in the majority of studies. This calls for a multicentred programme of research involving the same methods and the same definitions of handedness designed to test the MacNeilage et al. hypothesis across a range of primate species.

Because of a leftsided preference for cradling infants in humans (on the understanding that it enables the right hand to be used for manipulative activities associated with child care), the presence of this phenomenon has been sought in other primate species. Two studies found a leftsided bias in the gorilla (Fischer et al., 1982; Manning & Chamberlain, 1990), one of which also reported the same for the chimpanzee and orang-utan (Manning & Chamberlain, 1990). Once again the number of subjects involved was small. In collaboration with Herman Dieneske of the TNO Primate Centre, Rijswijk, we repeatedly observed nine pairs of chimpanzee mothers and their infants (Dieneske & Hopkins, submitted). No significant lateral cradling preference was found although there was a tendency for a rightsided

in the sample as a whole. Moreover, none of the mothers demonstrated a hand preference in reaching for food or other object. It was difficult to make a reliable observation of the hand use in the infants of these mothers. In another study, we attempted to observe if there was lateralized preference in head turning during the first month for 5 chimpanzee infants who had been separated from their mothers. It proved impossible to carry out—after releasing the head from the middle position it remained there for minutes on end in all 5 infants. In addition, no differences could be felt between hands in terms of the pressure exerted during the grasp response. The number of studies on the development of handedness in nonhuman primates is vanishingly small. The few that there are consist of case studies (e.g. Chorazyna, 1976; Cunningham et al., 1989).

In conclusion, it may be the case that most primate species show a population-bias for visually-guided reaching with the left arm and those with opposable thumbs a rightsided one for complex manipulations. If this possibility can be more firmly established, then the origins of human handedness may have an evolutionary depth of greater than 4 million years (based on the human—great ape divergence time derived from techniques used in molecular anthropology such as DNA hybridization). Such a depth would suggest handedness preceded the achievement of a persistent upright gait.

SOME (rather) Big Ones

1. Is the neonatal head position a robust phenomenon?

Most probably not. Fullterm newborns subjected to a head midline position for 15 minutes reduced or even lost temporarily a rightward bias in head turning (Turkewitz & Creighton, 1974; see also: Leiderman & Kinsbourne, 1980; Roberts & Smart, 1981). In the ALS, we found that infants of Caribbean origin who were massaged symmetrically on a daily basis by their mothers retained a rightsided bias in head turning, but not for the placing and stepping responses (Hopkins, submitted). Those who were not massaged retained a rightsided preference in all 3 movements—as did a group of Caucasian infants who were also not massaged. We have difficulties in accounting for these findings. The logical follow-up would be an experimental-control group study.

2. When does a lateralized bias for reaching into the contralateral space appear?

The notion that the ability to cross the midline is associated with the maturation of the corpus callosum has been overly stressed. On this view, spontaneous crossing occurs after 1 year. In collaboration with George Butterworth (Univ. Sussex) we found reaching across the midline at 11.3 months for the righthand, then 3 months later in the left. The majority of contralateral reaches terminated in precise finger grips.

3. What other contexts need to be taken into account in studying the development of handedness?

Most research to date has involved studying the lone hander. During

mother-infant interaction the following have been reported: more right hand movements at 2 months associated with positive expressions, more right hand opening at 9 weeks (Fogel & Hannan, 1985) and more right hand 'pointing' when a toy is present (more lefthanded when alone with mother) (Hannan, 1987). Conclusion: different contexts at different ages may evoke different lateralized functions.

4. When does adult-like handedness become established?

A long held view is that it is present at about 2 years (Gesell & Ames, 1947; Giesecke, 1936; Hildreth, 1949). More recent studies are less clear: it may be about 3 years (Annett, 1970) or not until after 8 years (Beaumont, 1974; Connolly & Elliott, 1972). Thus, there is little consensus about what constitutes the mature state.

5. Would the study of the development of handedness benefit from a dynamic systems approach?

At the very least, it would force us to identify the appropriate order parameters and to search for age-specific control parameters that might be the agents of change in the order parameters (Hopkins, Beek & Kalverboer, 1993). If there are such things as fluctuating asymmetries in early development, then they may be indicative of transitional periods. Synergetics (Haken, 1977) and catastrophe theory (Gilmore, 1981) provide formal criteria for detecting such phase shifts in order parameters (e.g. critical fluctuations, critical slowing down, sudden jump, bimodality and hysteresis).

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