

## The EPIC model of functional asymmetries: implications for research on laterality in the auditory and other systems

Judith L. Lauter<sup>1</sup>

<sup>1</sup>Human Neuroscience Laboratory, Department of Human Services, Stephen F. Austin State University, Nacogdoches, TX 75962

### TABLE OF CONTENTS

1. Abstract
2. Introduction
  - 2.1. Two levels of functional asymmetries (FAs)
  - 2.2. Methodological and theoretical problems in laterality research
3. The EPIC Model of Functional Asymmetries
  - 3.1. Four domains and two hemispheres
  - 3.2. Complementary sensory and motor asymmetries
  - 3.3. Testing the model: neurobiological and ecological validity
    - 3.3.1. Ecological validity test #1: Within-modality clusters of features
    - 3.3.2. Ecological validity test #2: Within-hemisphere clusters of skills
    - 3.3.3. Ecological validity test #3: Across-hemisphere coordination of complementary skills for “bilateral tasking”
4. Explaining individual differences: The Trimodal Model of Brain Organization
  - 4.1. Introduction: Mechanisms, including relation to functional asymmetries
  - 4.2. Three brain types: Differences in degrees of access
5. Implications for research on functional asymmetries
  - 5.1. Ontogenetic, clinical, and phylogenetic expectations
  - 5.2. Observations on experimental design
    - 5.2.1. Stimuli, tasks, interpretation: Guidelines and caveats
    - 5.2.2. Controlling for individual differences: Introduction
    - 5.2.3. Issues in individual differences: Gender
    - 5.2.4. Issues in individual differences: Handedness and the brain types
    - 5.2.5. Issues in individual differences: Shifting asymmetries
6. Conclusions and perspectives
7. References

### 1. ABSTRACT

More than a century after it was first suggested that behaviors such as speech production and perception might be lateralized in the human brain, many basic questions still remain regarding the nature and basis of right-left functional asymmetries (FAs). The lack of answers to what seem to be a straightforward set of questions may be due to two methodological aspects of laterality research which have hampered work in brain and behavior in general and lateralities in particular. The first is the absence of a biologically based, psychophysically-defined taxonomy of stimulus/gesture features for use in tests of laterality. As a result, many researchers resort to cognitive constructs for describing the bases of asymmetries, a decision which has created a gulf separating experimental as well as theoretical work on asymmetries from the biological realities of sensory and motor processing, within the brain as well as at the body periphery. The second obstacle is the lack of a valid taxonomy for individuals. Individual differences are ubiquitous in human subjects as well as non-human animals, yet are typically averaged away as noise rather than respected as possible sources of information. Studies of asymmetry often reveal dramatic individual differences in both the direction and magnitude of asymmetries, yet,

when subjected to averaging and group statistics, these often result in insignificant results. This paper reviews two taxonomies which may address some of these problems: the EPIC Model of Functional Asymmetries, and the related Trimodal Model of Brain Organization. The EPIC model classifies functional asymmetries according to four domains (Extrapersonal space, Peripersonal space, Intrapersonal space, and Coordination) and assigns responsibility for these four domains differentially to the two cerebral hemispheres -- the right side is seen as “polypotent,” responsible for processing in three of the domains, while the left side focuses on processing in peripersonal space. The EPIC model also proposes a “periodic chart” of complementary stimulus/gesture features which distinguish extrapersonal vs. peripersonal space, with analogues in all four somatic systems -- visual, auditory, somatosensory, and motor. The Trimodal model is based on research in psychoimmunoneuroendocrinology, and posits a continuum of individual differences created as a result of prenatal exposure to testosterone, and articulated in terms of access to the skills of the four EPIC domains. These two models together may yield guidelines not only for designing stimulus/task combinations but also for addressing individual differences.

## 2. INTRODUCTION

### 2.1. Two levels of functional asymmetries (FAs)

Organizational features of body design in chordates are articulated along all three body/brain axes -- rostro-caudal, dorso-ventral, right-left -- and for all three axes, functional asymmetry (FA) is a given. Thus the head does not do what the tail does, dorsal portions of the nervous system process sensations while motor work is done in ventral areas, and even though chordates are described for taxonomic purposes as "bilaterally symmetrical," the right and left halves of chordate nervous systems exhibit a basic asymmetry related to processing in only one half of space. These general principles apply to all parts of the body, including the four principal somatic functional systems -- visual, auditory, somatosensory, and motor.

Neural maps of this side-of-space basis of FAs, which we might call the first level of right-left FAs, are based on features of the periphery. Thus in the visual system of animals such as horses, stimuli from the right side of space fall on the retina of the right eye and are processed primarily in left-side cortex (and vice versa). Animals with front-facing eyes, including humans, require a translation into visual half fields, but the end result is the same -- stimuli from the right side of space fall on the left half of each retina (due to corneal physics) but end up, just as in horses, being processed primarily in left-side cortex. In the auditory system, even though it is described as "partially crossed," acoustic signals entering the right ear are eventually processed primarily in left-side cortex, and *vice versa*. In the somatosensory and motor systems, side-of-space refers to side-of-body, such that stimuli activating somatosensory receptors on the right side of the body are processed in left-side somatosensory cortex, and muscles on the right side of the body receive their commands from neurons located in basal ganglia and motor cortex on the left side of the brain.

In some animals, including humans, a second level of right-left functional asymmetry has been recognized which also affects the four somatic systems, and seems to be based on principles other than side-of-space. It is this second level of right-left FAs which is typically addressed in studies of "laterality," and has led to much confusion in the literature. For example, as of this writing, there is no general consensus among laterality researchers regarding: 1) the best way to describe these second-level FAs; 2) the possibility of analogous versions in different functional systems; 3) the nature of their ontogenetic and phylogenetic expressions; or 4) the principles on which they are based.

### 2.2. Methodological and theoretical problems in laterality research

There are, however, several features of research practice, methodological as well as theoretical, which do seem to enjoy a consensus in the laterality literature, but which may, unfortunately, have contributed to the confusion. We will see below how each can be addressed in ways which may clarify brain asymmetry research.

First, it is generally assumed that this second level of FAs is, like the first level, dichotomous, that is, a "separate-but-equal" or "equal-and-opposite" arrangement according to which the two cerebral hemispheres have complementary functions controlling similar proportions of body/brain function. Second, the terms of the dichotomy are typically drawn from cognitive research rather than sensory psychology or psychophysics, and thus tend to be abstract ("spectral vs. temporal," "analytic vs. holistic"), rather than specified either in terms of physical aspects of stimulus and gesture ("narrow-band vs. broad-band listening," "movement through 2 degrees of arc vs. 90+ degrees of arc," etc.) or in terms of receptors and effectors at the body periphery ("activation of Pacinian corpuscles vs. tactile disks," "foveal vs. extrafoveal stimulation," etc.).

Third, perhaps as an integral component of their cognitive science methodology, laterality reports are often surprisingly casual regarding aspects of *stimulus design* and *task specification* which researchers in psychophysics would consider to be crucial for drawing meaningful conclusions. In some cases, only a cursory description is provided for stimuli; in others, stimuli from different modalities are represented in inconsistent ways. For instance, a report on asymmetries for crossmodal processing may describe the visual component of the stimulus array in great detail, with concrete specifications cited in terms of luminance and degrees of visual angle subtended, but refer to the auditory component simply as "musical selections." Thus it can be difficult to judge the influence of the stimulus on the outcome.

Another version of this oversight is to make assumptions about "what the test tests" -- which can, of course, be crucial. For example, a researcher describing motor asymmetries for a task in which birds are asked to distinguish and pick up seeds mixed with small seed-like pebbles, may not only omit any physical specifications for the stimulus objects, but also reach the conclusion that the principle behind the observed asymmetry was "selection of objects." This is a *cognitive conclusion*, contrasting with the more parsimonious possibility that the asymmetry may have depended on physical features of visual and motor function -- the high spatial frequencies required for visually distinguishing seeds from pebbles, plus the fine motor control needed to pick up the seeds. Choosing a cognitive explanation could not only obscure the real basis of the asymmetry in this case, but also burden subsequent experiments designed to test "selection of objects" in which discrimination depended on whole-limb movements and lower spatial frequencies, thereby evoking an opposite asymmetry, and thus apparently contradicting the earlier findings.

Even in experiments which focus on physical aspects of stimuli, the same "what-the-test-tests" problem can arise if a researcher makes an *a priori* assumption about which physical features will be significant to the outcome and which will not. For example, a common distinction in the literature on auditory asymmetries is between "spectral" vs. "temporal" processing. In the reports of many experiments on this distinction, an author

**Table 1.** The EPIC model: Four domains of hemispheric specialization

Left brain
<ul style="list-style-type: none"> <li>• <i>Peripersonal space</i> (perception &amp; motor control very near the body surface)</li> </ul>
Right brain
<ul style="list-style-type: none"> <li>• <i>Extrapersonal space</i> (perception and motor control further from the body surface)</li> <li>• <i>Intrapersonal space</i> (general physical &amp; mental health)</li> <li>• <i>Coordination</i> (“handshaking” relations along all three body/brain axes; attention to both sides of space, including cross-midline scan and motor control)</li> </ul>

will describe two sound sets (one assumed to evoke temporal, and the other spectral, processing); and may also carefully describe both the spectral and temporal properties of each set. But when conclusions are drawn, one set of properties may be treated as though it did not exist, and it is assumed that the listeners (and the brain) concurred in the researcher’s original assumption as to which features would be relevant. For example, an asymmetry for chords which are frequency-modulated over a relatively small range at a relatively slow rate might be interpreted as depending on the spectral features alone, even though the temporal feature of the slow rate of change might have been more salient in producing the results.

Finally, in spite of the fact that reports on laterality experiments commonly refer to the “wide range of individual differences,” few attempts have been made to address this potentially crucial issue. Of course the problem is not unique to laterality research, but as we show later, it may be particularly important when studying aspects of right-left neural organization. This may also have greatly reduced the universality (including the clinical utility) of much work on brain and behavior, including studies on FAs. We will also discuss below why confidence in certain features (such as handedness and self-reported gender) for controlling subject heterogeneity may be seriously misplaced, and how proper definition of these two variables in combination with others could lead to better criteria for grouping subjects, and thereby greatly improve the clarity of laterality-test results.

## 3. THE EPIC MODEL OF FUNCTIONAL ASYMMETRIES

### 3.1. Four domains and two hemispheres

The EPIC model is a taxonomy of functional asymmetries designed to comprehend a broad spectrum of laterality phenomena under a single classification in a way which is biologically based (and realistic), as well as ecologically valid. It has grown out of conclusions regarding auditory asymmetries made more than two decades ago (1-3), later extended to include other functional systems (4), and more recently described in greater detail (5-9).

The acronym EPIC refers to the four domains which the model uses to classify functional asymmetries: Extrapersonal space, Peripersonal space, Intrapersonal space, and Coordination. The model posits that the right cerebral hemisphere has responsibility for functions in three of these domains (extrapersonal space, intrapersonal

space, and coordination), while the left hemisphere specializes in skills for working in peripersonal space (Table 1).

Under the model, extrapersonal-space processing involves stimuli and gestures employed in communicating with the “outside world,” with analogues in visual, auditory, somatosensory, and motor systems. These include: aspects of auditory and visual stimuli which can be perceived at a distance (emotional tone of a voice heard across a street, the shape of an animal running along a horizon), somatosensory stimulation involving deep pressure or movement across the skin (as in being hugged or licked), and the relatively large, “gross-motor-control” gestures employed in actions such as walking, throwing a ball, or climbing.

Note that this categorization is related to some of the more abstract cognitive terms used in laterality research (such as “holistic” or “global”), but as part of the EPIC model, it is firmly based on (and driven by) physical aspects of stimulus and gesture which can be objectively measured and described. (The specifics of these dependencies will be discussed in more detail in section 3.2.)

In a complementary way, peripersonal-space functions are defined by the model as involving events happening much closer to the body surface -- such as aspects of auditory and visual stimuli which can be perceived only when the sources are relatively close to receptor surfaces (the quick, quiet events of phonemic cues; text printed in a small font size); somatosensory stimuli which are static and highly local on the skin (the prick of a needle); or fine-motor-control gestures involving tiny movements of a few muscle fibers (writing, articulating an alveolar stop consonant). [Note that this definition of peripersonal space is somewhat different than the one used in neurological studies of spatial neglect.]

The term intrapersonal space refers to a wide range of features related to general body metabolism and function (10-13). Under the EPIC model, many of these are posited to depend on the right brain’s oversight of “handshaking” relations, based on the quality of connectivity along all three body/brain axes (6, 9, 14-15). These functions include such things as: maintenance of normal sleep/wake cycles; accurate perception of internal cues regarding how much and what to eat and drink; healthy balance between parasympathetic and sympathetic control of cardiovascular function; homeostatic management of immune response; and effective efferent modulation of afferent activity of all types, including visual and auditory input, and somatosensory sensations such as pain.

Finally, coordination refers to the oversight and governance of interactions among the three spatial domains, many of which also involve the dynamic “handshaking” connections referred to above. One example is general attention (i.e., to both sides of space, demonstrable in all four somatic systems); another is

**Table 2.** The EPIC model: complementary functional asymmetries in four somatic functional systems for processing in peripersonal space vs. extrapersonal space

Functional system	Peripersonal space	Extrapersonal space
Visual	Higher spatial frequencies	Lower spatial frequencies
	Static	Moving
	Color	Light/dark contrast
	Parvocellular/foveal system	Magnocellular/extrafoveal system
Auditory	Higher acoustic frequencies	Lower acoustic frequencies
	Rate of change > 10/sec (FM, AM, source)	Rate of change < 10/sec (FM, AM)
	aperiodic + periodic	long-term periodic
	broad-band “window”	narrow-band “window”
	basal-cochlear system	apical-cochlear system
Somatosensory	Small area of skin	Larger area of skin
	Static	Moving
	Surface light touch	Deep pressure
	Tactile disks, Meissner’s	Pacinian corpuscles
Motor	Tiny-angle movements	Larger-angle movements
	(fine motor control)	(truncal, whole-limb, postural control)
	small motor units	large motor units

crossmodal integration; and a third is the coordination of extrapersonal- with peripersonal-space skills required for bilateral tasking, a commonplace in many everyday tasks, such as speech perception, speech production, and reading.

Thus the EPIC model is not a “separate-but-equal” approach to hemisphere specializations, as most previous models have been, but rather considers the right hemisphere as “polypotent,” having a wider range of capabilities and contributions than the left side. The model assumes that access to the abilities of both sides, involving all four domains, is necessary for a complete functional repertoire. Thus, if this access is impaired -- whether through adjustments in neural connectivity which may occur during prenatal life under the influence of sex hormones (see section 4, below), or as the result of traumatic or disease-related neurological injury -- access to processing in one or more of the domains can be decreased. As described below, differences in the degree of access to the skills of one or both sides, *even in individuals considered neurologically normal*, may have been a confounding variable and a source of confusion in previous studies on laterality.

## 3.2. Complementary sensory and motor asymmetries

The distinction made in the EPIC model between extrapersonal and peripersonal space (cf. Table 2) is its principal link to previous research on second-level sensory and motor lateralities. Function in these two domains is seen as complementary, “equal-and-opposite,” and as will be noted, some of the details are taken from suggestions and findings reported in the laterality literature. Given these resemblances, it is not surprising that the groupings of physical properties in the EPIC model in some cases seem related to the terms of previous dichotomous taxonomies (such as temporal vs. spatial, analytic vs. holistic, or global vs. local). However, the ambiguity of such categories is avoided in the EPIC classification by its insistence on defining stimulus and gesture in terms of physical characteristics. For example, a basic confusion in the literature on auditory asymmetries relates to temporal processing, which is generally assigned exclusively to the left hemisphere. In fact, processing specializations of the two hemispheres may divide the temporal world on the basis of *rate of change* -- for the left side, a rate measured

in tens of milliseconds (e.g., events happening faster than 10/sec), versus a preferred rate for the right side which is more in the range of motor performance, e.g., 4-7 Hz and slower).

Beyond this, the EPIC classification in (Table 2) posits a framework within which previous findings can be incorporated (3), and on the basis of which further hypotheses can be generated (many of which are as yet untested). It can also provide a direct link to features of the body periphery which the model takes as the original template on which these asymmetries are based. As suggested in (Table 2) (and discussed in detail below), the EPIC model assumes that the cortical versions of these processing distinctions are simply the rostral elaboration of physiological categories inherent in the properties of populations of receptors and effectors at the body periphery. Note that the model does *not* require a hard-wired anatomical basis for the cortical lateralities (e.g., parvocellular vs. magnocellular visual pathways actually routed to opposite sides of cortex), but rather assumes the nervous system possesses physiological mechanisms for selective modulation sufficient to “bias” afferent as well as efferent information streams, and thus accomplish the functional distributions posited here (16, 17).

Also note that in designing laterality tests using these features, it is not necessary to create or physically alter stimuli in order to eliminate all but the features listed in either column of (Table 2). For example, in order to design an extrapersonal-space acoustic stimulus, one does not need to erase all the aperiodic elements of a test sound or filter out all but a narrow band of frequencies -- it is assumed that the perceiver can do this internally, and that successful performance of this type of physiologically-based selective attention will be characterized by the predicted laterality. In fact, in some applications, the most useful stimulus sets will combine both classes of features, where subjects are asked to accomplish different tasks using the same stimuli, in one case selecting out and focusing on the supposedly right-brain features, in the other, utilizing cues hypothetically evoking left-side specializations.

### 3.2.1. Visual system

According to the EPIC model, those visual features which are most accurately perceived when a

stimulus source is within the bounds of peripersonal space, and thus hypothetically evoking left-brain processing, include: higher spatial frequencies (there may be physically specifiable ranges of frequencies relevant here similar to those proposed for the auditory system -- see section 3.2.2); static properties; and color. Note that these are all attributes of the parvocellular component of the visual system, represented by response characteristics of certain cells in the retina and central visual pathways. Related task requirements might be to discriminate or identify high-resolution details; thus a quintessential left-brain visual task would be reading 9-point-type letters printed in color.

Features of visual stimuli which can be resolved even when originating at some distance from the body surface (perhaps viewed under less than optimal lighting conditions), and thus hypothetically evoking extrapersonal-space right-brain processing, include: lower spatial frequencies; properties of motion; and distinctions based on light vs. dark. These are attributes of the magnocellular component of the visual system, represented by response properties of certain cells at the retinal level and in central visual pathways. Related task requirements might be to capture the "gestalt" shape of a visual object; thus a quintessential right-brain visual task would be identifying animals based only on their dark silhouettes galloping or trotting or flying against a somewhat lighter background.

This distinction in peripersonal vs. extrapersonal space may also be expressed in functional asymmetries related to the upper vs. the lower visual half field (17-19). That is, distance vision for objects in the upper visual half field (i.e., lower half of retina) would be best processed in the right hemisphere, while items in near vision (lower visual half field, i.e., upper half of retina) would be best managed by the left hemisphere.

### 3.2.2. Auditory system

The model predicts that those acoustic features which are most accurately perceived only when a stimulus source is within the bounds of peripersonal space, and thus hypothetically evoking left-brain processing, include: higher acoustic frequencies (there may be a relevant range here, based on the cochlear biophysics of the species in question); rapid temporal changes in both frequency and amplitude (again, a range may be specifiable -- as discussed below); aperiodicity as a carrier of information; and broad bandwidth with inherent information. Although there are populations of auditory neurons which respond to each of these features, to date no one has proposed a grouping of cells based on this combination of response properties, on the model of the parvocellular component of the visual system. Related task requirements might be to resolve, discriminate, and identify sequences of sounds which change rapidly (with a time base of msec, involving both amplitude- and frequency-modulation [AM and FM] features) over a broad frequency range, including aperiodic elements as crucial details. Thus a quintessential left-brain auditory task would be to distinguish and identify a series of stop consonants (1-3, 20).

Features of acoustic stimuli which can be resolved even when originating at some distance from the

body surface (perhaps under less than optimal listening conditions, e.g., acoustically disrupted by objects such as leaves or by ambient sounds from sources such as wind or water), and thus hypothetically evoking extrapersonal-space right-brain processing, include: lower acoustic frequencies; slower temporal changes in both frequency and amplitude; periodicity as a carrier of information (assisted via the redundancies implicit in harmonic structure); and narrow bandwidth. Again, although each of these features is represented in the response properties of auditory neurons, no such grouping as suggested here has yet been identified, analogous to the magnocellular component of the visual system. Related task requirements might be to monitor a relatively narrow band of frequencies changing relatively slowly (with a time base of seconds, affecting both AM and FM features), in order to identify an acoustic "gesture." Thus a quintessential right-brain auditory task would be following a melody, whether produced by a musical instrument or a human vocal tract.

### 3.2.3. Somatosensory system

Tactile features which hypothetically evoke left-brain processing include: mechanical perturbation restricted to the epidermis; a lack of movement over the skin; only a very limited area of skin affected. These features match the response properties of "light touch" receptors in the skin such as tactile disks and Meissner's corpuscles. Related task requirements would be to identify the exact position of a light impression being made briefly on the skin. Thus a quintessential left-brain tactile task would be to detect and locate the point of a pin placed lightly on the surface of an index finger, or a touch at a particular point inside the mouth, such as might be used to monitor speech articulation.

Tactile features which hypothetically evoke right-brain processing include: mechanical perturbation of the skin to sub-epidermal levels; movement over the skin; and a relatively large area of skin affected. These features match the response properties of the encapsulated endings known as Pacinian corpuscles, located in the dermis and within muscles. Related task requirements would be to locate and track movements of a stimulus creating deep-pressure perturbations over the skin and/or underlying muscles. Thus a quintessential right-brain tactile task would be to identify the location, duration, and pressure of a squeeze applied to some part of the body (such as when one is hugged), or locate which part of the body surface is being stroked in a deep-pressure way (such as when animals are petted or licked).

### 3.2.4. Motor system

The features of muscular actions which are hypothetically governed by left-brain control centers are those generally referred to as "fine motor control," involving movement through a tiny angle about a joint, and/or over a very small amount of space. Such gestures are accomplished via "small motor units," that is, those in which a single lower motor neuron (LMN) manages a very small population of muscle fibers (e.g., 100). Related task requirements would be to create a gesture using only one or a very few small motor units, moving only slightly and

with great spatial and temporal accuracy. Thus a quintessential left-brain motor task would be to write 9-point letters inside small boxes using a sharp pencil, or to thread a needle.

Features of muscular actions which are hypothetically governed by right-brain control centers are those generally referred to as “gross motor control” (though they may be coordinated in very sophisticated ways which are anything but gross), involving whole-limb or truncal movements through relatively large angles, or the coordination of many different muscles in order to achieve stabilization of multiple areas of the body against perturbations by external forces (such as general postural control against the pull of gravity, or maintaining a stable position while being accelerated in a vehicle). Such gestures are accomplished via larger motor units, that is, those in which a single LMN manages a relatively large population of muscle fibers (e.g., 1000 or more), and typically require the temporal and spatial coordination of many such units. Related task requirements would be to create a fluent gesture or accomplish postural stability based on many larger motor units. Thus a quintessential right-brain motor task would be to throw a ball (however, not with demands for extreme accuracy -- which would evoke the addition of left-brain modulation via fine-motor control), or to cradle a baby securely in one arm while walking.

### 3.3. Testing the model: neurobiological and ecological validity

The classification system of the EPIC model remains to be tested, and its predictions are sufficiently specific to serve as design guidelines for a host of possible experiments. But there are other ways to test such a model. For example, one can examine the literature to see how well the model's predictions are supported by published results. Discussions of earlier versions of the EPIC model (7, 19) have found published findings (on several types of lateralities, including aspects of general body metabolism, physical health, mental health, and the distinction between extrapersonal and peripersonal space processing) to be consistent with the predictions of the model. One of these papers (19) also includes a detailed discussion relating the EPIC classification to published results on visual asymmetries (such as imagery and eye movements), particularly as employed in reading.

The same could be done for auditory asymmetries. Such an exercise can reveal commonalities across experiments which were not recognized in the original reports because of the authors' focus on cognitive constructs rather than stimulus features. For instance, in an earlier review (3), we re-analyzed the results of 13 previous experiments on dichotic listening in which a variety of stimuli, ranging from isolated vowels to melodies, were tested. In the reports of these experiments, the authors had attributed the observed asymmetries sometimes to the nature of the stimulus (described in terms such as: “vowels,” “patterned stimuli,” “linguistically structured stimuli”) or to the nature of the task (described variously as: “speech perception,” “verbal vs. nonverbal processing,”

“spectral vs. temporal processing,” or “voicing vs. place distinction”). Our re-analysis demonstrated how the results of all these experiments could be accounted for using only three acoustic features: event timing, bandwidth required for performing the task (narrow vs. broad), and number of dimensions changing over time.

In fact, this conclusion highlighting the importance of stimulus characteristics for auditory asymmetries, participated in a tradition extending back into the early 1970s (1, 21-26). However, students of laterality who focus on physical parameters of stimulus and response rather than cognitive categories have remained in the minority. This is true even for the auditory system, in which the only feature which continues to receive serious attention is rate-of-change (27-29). Findings in these studies generally agree with predictions of the EPIC model, i.e., faster rates-of-change evoke left-brain processing (Right Ear Advantages [REAs] for behavioral results, and/or Left Hemisphere Advantages [LHAs] if a physiological test such as qEEG, fMRI, or PET is involved); while slower changes are associated with Left Ear Advantages (LEAs) and/or Right Hemisphere Advantages (RHAs). However, most reports of asymmetry studies still tend to downplay the influence (and specifications) of details of stimulus and task, instead invoking cognitive explanations under rubrics such as “categorical vs. coordinative,” “species-specific communication,” and “what vs. where.”

There are other factors which complicate the process of testing EPIC formulations against published results. For instance, some aspects of experimental design can make it difficult to compare the reported outcomes with EPIC predictions. One crucial feature is the way subject groups are defined, and the degree to which information implicit in individual differences has been erased by the practice of averaging over subjects. This unfortunate practice is commonplace in behavioral as well as brain-imaging studies -- even though one of the great advantages of brain-imaging technologies is the exquisite detail they provide on individual differences (cf. comments and supporting data critiquing practices such as creating “group brains”)(1-3, 8, 15, 30-37). As discussed below, individual differences may be of vital importance to studies of lateralities, and must be addressed before meaningful interpretation of experimental results can be done.

Fortunately there is another and potentially much more useful means of testing a classification such as the EPIC model, namely to ask whether it is *ecologically valid*. The ecological validity of a model of brain asymmetries can be considered in terms of three categories: 1) within-modality clusters of features (e.g., the list in each cell of (Table 2)); 2) within-hemisphere clusters of skills (the crossmodal correlations implied by each column of (Table 2)); and 3) across-hemisphere clusters of complementary skills employed in the many instances of bilateral tasking which are the rule rather than the exception in everyday behavior. Bilateral tasking, after all, is the “reason” for biology to create asymmetrical brain organization in the first place -- to gain the obvious advantages of having two

specialists working in parallel on the same larger task at the same time, getting the output of “two brains” for the price of one -- “listening with two brains,” “looking with two brains,” “feeling and moving with two brains.”

### 3.3.1. Ecological validity test #1: Within-modality clusters of features

As indicated in the discussion in sections 3.2.1 - 3.2.4, the consideration of within-modality feature clusters represents a test of neurobiological as well as ecological validity. As noted in those discussions, the features listed in each cell of (Table 2) were derived by analyzing the stimuli used in previous work on asymmetries in all four of these functional systems, but they are also exactly congruent with the physiological properties of receptors or effectors which have previously been established in the same terms for three of these functional systems. (We will have more to say about the auditory system later in this section.)

With regard to ecological validity, the clusters of features in (Table 2) are accurate descriptions of categories of stimuli and gestures commonly encountered in everyday life. For instance, in order to visually distinguish whether an object on the branch of a distant tree is a bird or a piece of fruit, it is sufficient to capture a few characteristic “gestalt” features conveyed via light vs. dark contrasts and lower spatial frequency details, including overall shape and characteristic patterns of movement. (If it’s long and thin and hopping along the top of the branch, it’s probably a bird; if it’s round and swinging slightly back and forth below the branch, it may be a fruit.) Then, if additional levels of discrimination and identification are required, demanding information about high-resolution details and color, the perceiver will bring the object closer to peripersonal space and attempt to stabilize the image on the retina. (If a bird, is it a sparrow or a finch? If a fruit, is it an apple or a peach, and is it green, or ripe enough to eat?)

Auditory examples of feature clusters resembling those in (Table 2) are to be found in many types of naturally occurring sounds (1-3, 20). For instance, in conversational human speech, the features of phonetic cues match those in the auditory peripersonal-space cell of (Table 2). They are acoustically articulated as changes in several dimensions: frequency, amplitude (up to 100% modulation depth), event duration, and sound source characteristics (clicks, noises, periodic sounds, even silences). There are also co-variances among these characteristics -- for example, periodic components (such as the syllabic nuclei of vowels) tend to be longer and louder, while aperiodic components (such as stop bursts and frication) tend to be shorter and softer. All these changes occur quite rapidly, on a time base measured in msec -- stop bursts may be only a few msec long, fricative bursts not much longer, and even syllabic nuclei are not only relatively brief, but are hardly ever steady-state, consisting primarily of frequency- and amplitude-modulated complex tones (formant transitions) which only “point to” target vowels, as the vocal tract moves quickly toward the location for the next consonant. Over time, all these changes involve a broad band of frequencies, ranging

from the “nasal murmur” of nasal consonants (center frequency less than 500 Hz) to the high-frequency noises of fricative consonants (as high as 6 kHz and above). Thus a listener has to maintain a listening “window” characterized spectrally by a fairly broad bandwidth (6 kHz or more), and temporally by a quite fast “refresh rate” (updating perhaps every 5-10 msec, if not faster), in order not to miss any of these rapidly changing, multidimensional cues.

In contrast, the acoustic-feature clusters comprising cues to speech components such as linguistic stress and emotional tone are a good match to the set listed in the auditory extrapersonal-space cell of (Table 2). Acoustically, these cues are very different from phonetic cues, more like those of a melody played on a musical instrument. For speech as well as music, melodic “gestures” consist primarily of modulations in a complex tone (in speech, produced by the larynx) which is more or less continuously present throughout the gesture (the overall melodic pattern created by the laryngeal tone is not perturbed by the tiny interruptions required for stops and voiceless fricatives). Of course, instrumental melodies can be articulated either as in speech, as continuous sounds (e.g., using bowed-string instruments), or as sequences of separate notes (as on percussive instruments such as a piano or marimba). However, the melodic track in both cases is based on a sequence of periodic events -- neither vocal nor instrumental melodies are made of sequences of sounds which involve event-to-event source changes, in contrast to phonetic cues, where this is a common occurrence.

Finally, melodic changes occur on a time base which is more in the standard “motor” range than are phonetic cues, i.e., not much faster than 4/sec. They are, in fact, associated with the air puffs produced by the intercostal muscles to create the syllabic structure of speech. Changes in vocal melody involve both frequency and amplitude modulation (across a fairly small range for each), affecting primarily the fundamental frequency of the tone (upper harmonics also change in tandem of course, but in naturally-occurring complex tones such as animal voices, the fundamental tends to predominate). As a result, a listener can accurately follow melodic gestures using a listening window which is characterized spectrally by a fairly narrow bandwidth (1 kHz would be more than sufficient for music as well as speech), and temporally by a fairly relaxed “refresh rate” updating at what we’ve called “motor speed,” only every 250 msec or so.

Note that when applied to music, this type of listening window will be appropriate only if the listener is simply tracking melody and is not interested in other aspects of the sound. Professional musicians, including orchestra conductors, may need to listen to music in much more “speech-like” (i.e., left-brain) ways. That is, they may have to focus on speech-like features of musical production that go completely unnoticed by the untrained ear. Thus they will spontaneously maintain: 1) a broadband, rapidly-updated listening window in order to keep track of high-frequency, aperiodic drum noises played at the same time as the lower frequencies of melodies

bowed on a bass viol; 2) attend to multiple sources which are temporally mixed in intricate, overlapping relations (frications of brushed drums, clicks of drumsticks, bandpass noises from breathy flutes, complex tones of violins); and 3) focus on the accuracy of attack times (i.e., rapid transitions similar to those in speech) produced by many instruments representing a complex array of formant structures.

This is why simply describing a stimulus as “speech” is not enough -- one must specify exactly *which aspects of speech* are being targeted by a task -- the multidimensional, rapid acoustical actions used for phonetic cues, or the narrowband, slower gestures of vocal melody. Similarly, identifying a stimulus as “music” is not enough -- it is necessary to define (and control) exactly *which aspects of the sound* are relevant for a particular task.

Given these ecological realities, we can return to the question of how the features listed in (Table 2) might be related to the biological distinction between basal and apical cochlea. The first feature listed there, higher acoustic frequencies vs. lower frequencies, is the easiest to explain, because it refers to the tonotopic format of basilar-membrane (BM) physics, i.e., basal portions respond best to higher-frequency components of sounds (with a response which is spatially discrete, that is, very little of the membrane moves), while more apical portions respond best (and in a way that is spatially much more diffuse) to lower-frequency components.

Of course, the amount of membrane moving is correlated with the number of hair cells activated (outer as well as inner), which means that lower-frequency sounds activate more hair cells overall than do high-frequency sounds. This is suggestively analogous to the organization of known subdivisions of the other functional systems -- the motor-system distinction between large vs. small motor units; differences between magnocellular vs. parvocellular visual-system components; and processing characteristics of Pacinian vs. light-touch receptors in the somatosensory system. It is logical that a similar organizational principle might be at work in the auditory system, perhaps along the lines of the distinctions in peripheral function and central connections described for Type I vs. Type II spiral ganglion cells (38-42).

The EPIC model posits that the next three features (broadband vs. narrowband, periodic vs. aperiodic, and rate-of-change) are also related to the basal/apical cochlear distinction, but in a way which depends only indirectly on cochlear biophysics *per se* and more on the adaptive organization of the central nervous system (CNS) regarding the way in which signals from these two general subdivisions of the basilar membrane are processed. In order to make this case, we need to appeal to the ecological characteristics cited above, that is, the feature clusters which are typical of naturally-occurring (especially communication) sounds. As noted there, naturally-occurring sounds or sound components which are high frequency, basal-cochlear activators (such as the bursts of stop consonants) also tend to be: 1) aperiodic, 2) relatively

low in amplitude, and 3) very short. (The opposite holds for low-frequency, apical-cochlear activators.)

Thus it would seem to follow that the auditory CNS would be adaptively organized such that when basal cochlea activation occurs (or is anticipated -- someone opens their mouth to speak, and you prepare to listen), this would evoke a top-down modulation which we might call a “listening set” (a la Walter Cannon’s “set of the center”) (43) expressing a “physiological expectation” that subsequent acoustic events would be characterized by not one but the entire cluster of features -- that is, high frequencies occurring from time to time; broad frequency excursions ranging from very low to very high; dramatic FM, AM, and source changes; aperiodic as well as periodic events; and fast rates of change.

Activating this “peripersonal-space listening set” might involve at least three operations in order to accommodate the cluster of features. (The operations for the “extrapersonal-space listening set” will be outlined later.) First, to enable broadband-including-high-frequency listening, the CNS might send commands to outer hair cells (OHCs) along the entire extent of the cochlea, preparing them to respond in an appropriate way given the expected features. At the basal end, OHCs would be upregulated, in the expectation that high-frequency events would be relatively lower in amplitude, and therefore require substantial physiological amplification to ensure that the inner hair cells (IHCs) are activated, in order to capture and transmit high-frequency events to the CNS. In contrast, toward the apical end, OHCs might be downregulated, in order to somewhat dampen response to the lower-frequency sounds of the laryngeal tone, expected to be relatively high-amplitude. Also, there might be a means of selectively activating cells which oversee sets of OHC rows organized in octave steps along the BM, to support tracking of formant transitions, based on the parallel movement of upper harmonics along with fundamental frequency.

Second, to assist in broadband listening and also to be able to handle source changes, including alternating and sometimes simultaneous periodic and aperiodic components, the CNS might “tune up” populations of central neurons with response and processing properties such as the following: cells representing a range of characteristic frequencies (CFs); cells specialized at detecting and analyzing aperiodic sounds; cells with a variety of means of computing fundamental frequency (whether steady-state or FM) and formant structure (whether periodic or aperiodic, steady-state or FM); and cells sensitive to formant transitions of different parameters (rising, falling, specific frequency ranges).

Finally, the peripersonal-space listening set might be characterized by a management of OHCs designed to enable the “fast refresh rate” feature of this type of listening window (cf. Type II spiral ganglion cell innervation of OHCs) (38-42). The physiological goal would be to achieve a rapid damping of BM response immediately following every event detected -- for instance, as soon as a stop burst is finished, the response to that sound would be

damped, to prepare for whatever comes next. This type of top-down management could thus ensure accurate capture of short, relatively soft sounds such as stop bursts, and avoid their being masked by immediately following periodic sounds (though note that voiced formant transitions immediately following a stop burst always involve a relatively slow rise in amplitude, due to articulatory constraints, which aid in avoiding this type of backward masking).

The extrapersonal-space listening set would be much easier to configure. The CNS might not even send special commands to apical-end OHCs, since the low-frequency sound components carrying melodic information would be expected to be relatively high-amplitude. (Although, in speech perception, where vocal melody must be tracked in parallel with phonetic cues, CNS centers for tracking fundamental frequency might need to account for any turn-down in lower frequencies introduced by the operations of the peripersonal listening set.) Signals from IHCs toward the apical end of the cochlea would be processed in a very straightforward way by CNS cells, based on characteristic frequencies (CFs) and other response properties designed for spectral analysis and tracking slow changes in periodic spectra over time. There would be no demands for broadband listening, or for achieving a rapid refresh rate, since the normal damping physics of the BM might be sufficient to handle the slow rate of change characteristic of vocal and instrumental melodies.

### 3.3.2. Ecological validity test #2: Within-hemisphere clusters of skills

Another ecological test of the characteristics listed in (Table 2) concerns relations that pertain “vertically,” across the four cells of each column. That is, one can ask whether there are everyday tasks which depend on the suggested combinations of skills -- visual, auditory, somatosensory and motor -- for accurate performance. The technical term for this type of relation is *crossmodal integration* or *multimodal processing*, and is extremely common in everyday behaviors. As examples we will again make use of tasks related to speech and music. Both provide good examples of the efficiency gained by organizing crossmodal interactions on a within-hemisphere basis.

All four of these functional systems -- visual, auditory, somatosensory, and motor -- contribute skills for managing the phonetic component of speech, and all are drawn from the peripersonal-space skills column of (Table 2). To tell this story, it will help to read up the column from bottom to top. The motor system contributes to accurate production of phonetic cues via its skills for fine motor control (FMC), crucial for accurate management of the tiny, fast gestures of articulation -- the brief touch of the tongue tip to the alveolar ridge for a /t/, the carefully timed and coordinated touch-hold-release of both lips to create a /p/, etc. There are even fine motor control contributions by the larynx in phonetic cues -- not so much those related to the production of speech-voice, which does not require FMC (as will be described in a moment) -- but the high

degree of accuracy in timing required for producing the Voice Onset Time (VOT) cue important for distinguishing among stop consonants. At the same time, the somatosensory system supports these motor gestures via highly accurate feedback about local light touch (did that tongue tip touch the alveolar ridge? are the lips evenly held together to stop up the airstream for /p/?).

For the auditory system, we’ve already described how peripersonal-space skills are crucial for phonetic perception. When these cues are translated into the symbols of an alphabetic writing system, the visual system contributes its analogous peripersonal-space skills to transfer the symbols into visual memory, so the original acoustic referents can be reconstituted by the brain. As we have recently reviewed, (19), there is a general consensus in the reading literature that the parvocellular visual system is crucial for capturing and analyzing the high spatial frequencies of these visual symbols of phonetic entities as they appear in the typical font sizes used in printed text.

Managing the melodic components of speech offers a particularly good example of crossmodal organization based on complementary extrapersonal-space skills. In order to produce vocal melody, the motor system contributes skills for controlling a number of muscle systems coordinated over space and time. As noted above, the patterns of vocal melody depend on management of certain aspects of respiratory physiology, including shaping imposed on the airstream during exhalation by pulsed contractions of the intercostal muscles, responsible for the “syllabic structure” of speech. As these pulses of air approach the vocal folds, a number of laryngeal muscles must be coordinated in order to accomplish the gestures necessary for the production of voice -- adductors to bring and hold the vocal folds together across the midline, tensors to manage the rigidity of the folds, and abductor muscles relaxed.

For the production of voice used in conversational speech, laryngeal muscles do not require fine motor control. To meet much more stringent demands for extremely accurate and efficient pitch modulation, professional singers make use of a variety of fine motor control refinements, but for conversational speech, such special skills are not required. To produce voice, all that laryngeal muscles need to do is to bring the vocal folds together across the midline and stabilize them there, while air is forced up against them from below -- this air pressure (managed in part through widescale coordination of many muscle groups in abdomen and thorax), combined with the degree of rigidity and elasticity within the stabilized laryngeal muscles, and the Bernoulli effect, are sufficient to achieve and manage changes in voice pitch and loudness. The somatosensory system provides feedback on the accurate management of all these muscle groups, from abdomen to larynx, by way of deep-pressure sensors which are present in all muscles.

For auditory perception of vocal melody, we’ve already reviewed how extrapersonal-space skills listed in (Table 2) are exactly matched to the relevant acoustic

features. There is of course no visual equivalent of “reading” related to conversational melody (though some researchers have devised notation systems to use in describing changes in voice pitch associated with emotional tone). However, for musical melodies to be sung or played on instruments, systems have been devised which need to be “read” as visual patterns. Musical notation is notably much less demanding with regard to font sizes and reading speed than is the speech-cue notation of alphabets -- since notes cannot be played faster than 4/sec, they do not have to be read any faster, either; thus it is possible to use extrapersonal-space visual skills to accomplish this aspect of melody management.

### 3.3.3. Ecological validity test #3: Across-hemispheres coordination of complementary skills for “bilateral tasking”

It should be obvious from the preceding that everyday behaviors regularly depend not only on crossmodal interactions organized within hemispheres, but also on bilateral tasking, that is, teamwork coordination of peripersonal-space skills employed as “content” within the “frame” provided by extrapersonal-space skills.

Two prime examples relate to speech production and perception. A speaker with good access to both categories of this rich library of neurophysiological specializations can draw on a diversity of abilities for conveying meaning, in terms of connotation as well as denotation. Peripersonal-space motor skills backed up by analogous somatosensory abilities can be used to create the delicate, rapid articulatory gestures of phonemes, and these are monitored for accuracy in real time by auditory abilities for rapid, high-resolution acoustical analysis. At the same time, extrapersonal-space skills provided by motor, somatosensory, and auditory systems can be used in parallel to manage vocal melody for accurate expression of linguistic stress patterns, sentence-long semantic markers distinguishing questions vs. declarative statements (etc.), signs of intention such as joking or sarcasm, and an acoustical rainbow of emotional tones.

At the receiving end of the “speech chain” (44), in order to make the most use of this diverse package of information, a listener needs good access to left-brain auditory abilities in order to resolve the phonetic cues, while at the same time using right-brain skills to track fundamental frequency to retrieve the crucial information conveyed by “suprasegmentals,” so that comprehension will be enriched beyond what was said, to include how it was said.

Another task related to speech and language which depends on two-hemisphere coordination is reading. As summarized in a recent review (19), fluent reading requires a combination of peripersonal- and extrapersonal-space skills. First, visual peripersonal-space skills supported by the parvocellular system are needed to resolve and analyze the high-spatial-frequency details of small print, captured during the static portions of visual scan, and then visual extrapersonal abilities related to movement are used to “refresh” the visual image on the internal visual

“screen,” as the eyes move on to the next group of letters, in the gesture known as a “saccade.” The alphabetic symbols captured during the static intervals are transmitted to the left brain for translation by the auditory system’s interpretive skill known as “phonemic awareness,” closely associated with phonetic perception (19, 45). Finally, the coordination of the two eyes which is necessary if they are to move smoothly together along each line of text, and from line to line, is supported by a right-brain ability representing another EPIC category, coordination. Disruptions in one or more of these skills -- peripersonal, extrapersonal, or coordinative, can give rise to different types of reading problems, which predictably will require very different types of intervention if fluent reading is to be restored (19, 46).

Other motor behaviors offer additional examples of bilateral tasking based on coordinating skills for peripersonal- vs. extrapersonal-space processing. For instance, it is well-known that women prefer to hold and carry an infant cradled in the left arm (47-48) -- also true for macaque (49) and baboon (50) mothers -- a preference which is definitely consistent with the EPIC classification of motor capabilities regarding postural control. This observation is also pertinent to the left-brain bias endemic to industrial societies. The question used to elicit a report of “handedness” actually translates as “which hand do you use for fine motor control?” If the question were taken to mean, “which hand and arm would you use to confidently hold and carry a child?” most people would be considered left-handed.

When looking down at a baby held in this fashion, a woman is attending to the left side of visual space, also associated with right-brain activity, and when she speaks to the half-asleep child, she will also use her right-brain skills for vocal melody (for either talking or singing a lullaby) in a fashion designed to soothe and comfort the baby (and herself) by tuning up its parasympathetic nervous system, as opposed to arousing the sympathetic system. The tone of voice, speed of production, and words used in such “motherese” are reminiscent of the verbal patterns used in hypnotic induction -- also designed to activate the right side of the brain (51-53).

At the same time, holding and comforting a baby involves both sides of the brain, one of the things that make it so rewarding to the caretaker. As the left arm supports the child, the right is free for fine-motor-control gestures -- handling the tiny fingers, stroking the shell-like ears, tracing the lines of the eyebrows. The visual system is engaged by the bilateral physiological “harmony” represented by viewing the combination of the higher-spatial-frequency details against the background of lower-spatial-frequency shapes such as the round ball of the baby’s head and the curve of the arms. The somatosensory system participates in the combination of the deep pressure activation of the weight of the baby’s body against the mother’s side at the same time as light-touch receptors on the mother’s fingertips are stimulated as she caresses the baby’s skin.

The physical characteristics of “motherese,” particularly the type of soothing vocal melody directed to a baby, may actually contribute to the health of both baby and mother, through their effects on the right brain’s governance of immune response. Most mammal mothers spend a great deal of time licking their babies (a good right-brain motor gesture, slow and rhythmic), and this type of grooming is important for upregulating the immune system (which the EPIC model designates as one of the right brain’s intrapersonal-space responsibilities). Baby mice taken from their mothers, even if kept warm and well-fed, will sicken and die -- apparently because they lack their mothers’ licking; but if the same babies are brushed with a small wet paintbrush several times a day, they will thrive (11, 54-58).

Human mothers do not lick their babies, but they spend a lot of time caressing the tiny basilar membranes with motherese, using rhythmic acoustic movements of voice pitch to sweep the prominent second and third harmonics back and forth through the most sensitive regions of human hearing. Thus motherese may represent a kind of “acoustical licking,” which human mothers use instinctively as an acoustical complement to their breastmilk to enhance immune function in the child. (The “sweet-talk” exchanged by adult intimates may have much the same salutary, nurturing effect.)

#### 4. EXPLAINING INDIVIDUAL DIFFERENCES: THE TRIMODAL MODEL OF BRAIN ORGANIZATION

##### 4.1. Introduction: Mechanisms, including relation to functional asymmetries

Even given the specifics of the EPIC model -- the four domains overseen by the two hemispheres, the physical details of stimulus and gesture available for defining objective, biological bases for processing in peripersonal vs. extrapersonal space -- it can still be extremely difficult to demonstrate asymmetries which are statistically significant and consistent across subjects, whether measured behaviorally or physiologically.

However, such difficulty can be reduced (and perhaps even eliminated) if we do not limit ourselves to standard methods for selecting and grouping subjects, and for interpreting test results. Conventional approaches -- like sorting subjects by age, gender and handedness, and then averaging over individuals in each group -- may not be sufficient. The usual gender and handedness categories may be particularly problematical for interpreting results on brain asymmetries. As noted earlier, there is a great need for a biologically-based taxonomy to deal with the tremendous range of individual differences, whether we are testing humans or other animals.

The Trimodal Model of Brain Organization may provide just such a taxonomy. It is a neurotypology derived from psychoimmunoneuroendocrinology (5-9, 19, 59-62) and is assumed to apply to all mammals, including humans. The model posits a continuum of individual differences based on a spectrum of prenatal exposure to

androgens (primarily testosterone), in which androgens may work as pruning agents, simplifying neural connectivity along all three body/brain axes -- right-left, rostral-caudal, and dorso-ventral. The mechanism is believed to work in essentially the same ways in XX and XY embryos and fetuses.

The Trimodal Model incorporates the four-domain EPIC classification of functional asymmetries to frame predictions about individual differences: 1) changes in neural connectivity affecting the right-left axis have basic implications for a wide range of aspects of health, skills, and general behavior; and 2) due to an offlap in development of the two sides -- the right hemisphere develops earlier than the left, and continues to be more salient until into the second year of postnatal life -- disconnection events caused by prenatal testosterone will act first (at moderate levels of exposure) to cut off access to the left brain, and only later (at cumulatively higher levels) will access to right-side capabilities be affected. The Trimodal model posits that the earlier development of the right side is a sign that it has some degree of guidance over both sides during prenatal development (an instance of its coordinative function), and whatever interferes with this may not only cut off access to the skills represented by its three domains, but eventually result in an abnormal developmental “release” of the left side, causing it to “overgrow” in the absence of any regulation or nurturance from the right hemisphere.

##### 4.2. Three brain types: Differences in degrees of access

As a neurotypology, the Trimodal Model describes not only individual differences but also the biological origins of categories, or individual “types.” “Trimodal” refers to the premise that the continuum of individuals created by various levels of exposure to testosterone results in three principal modes or “brain types.” Furthermore, each type is represented in approximately one-third of the general population.

The ecological “reason” for the three modes is more a function of evolutionary psychology than brain laterality *per se*, and is thus beyond the scope of this review. However, the three brain types are presumably adaptive with regard to the three primary social roles found in the vast majority of mammalian species: 1) the females who form a stable, transgenerational social “center,” in which children are born and reared and from which all males depart at puberty; 2) those few males who are periodically invited by the females to join the group temporarily, to breed and also assist with protection against predators; and 3) the males who spend their lives as “juveniles,” either as solitaires or in small, unstable, all-male groups, who engage in conspecific violence (including attacks on females and young), and make no genetic contribution to the next generation.

The first of the three modes, the “polytropic” (‘many-skilled’) brain type, develops in an essentially “hormone-free” environment throughout prenatal life and early childhood, and is characterized by the most sophisticated and resilient neural connectivity of all three

brain types. In this brain, the nurturing, “polypotent” right hemisphere retains its salience throughout development, and the high level of connectivity along with the right brain’s oversight of brain coordination means that left-brain skills for working in peripersonal space will also be readily available. As a result, these individuals have excellent function in all four domains of the EPIC model, and are thus designated as “right-brain/whole-brain” to indicate this fact. (Also note that individuals with this brain type will be strongly right-handed, that is, with good access to the fine-motor-control skills of the left hemisphere.) Because testosterone is the operative agent, polytropic brain types are found primarily in XX individuals, though the occasional XY may be born with this type of highly connected brain.

The second mode, the “middle” brain type, develops under conditions of moderate exposure to testosterone, and as a result undergoes moderate reductions in connectivity, potentially limiting access to the EPIC skills of one or both hemispheres to different degrees. At low-moderate levels of exposure, this may result in a loss of access only to later-developing left-side skills such as phonemic awareness and fine motor control. This may cause problems in academic performance, such as certain kinds of reading difficulty (though this type’s intact mental imagery, a right-brain skill, may aid in reading comprehension). At mid-moderate levels, access to both sides may be compromised, resulting in some loss of right-brain as well as left-brain skills, creating a very different profile of academic problems. High-moderate levels may further degrade access to the right side in a way that somewhat “releases” left-side development, though incompletely. In general, individuals with the middle brain type will be somewhat lacking in fine motor control, due to their reduced access to this left-brain skill, and thus will exhibit a variety of versions of ambidexterity, including left-handedness as one variation.

The third mode, the “focal” brain type, is created under conditions of high prenatal testosterone, and as a result, suffers radical reductions in connectivity, essentially erasing access to the nurturing support and guidance of the right brain, and releasing growth (often over-growth) of the left side. Thus this brain has only left-side skills, and the three domains overseen by the right side, including the important capabilities associated with intrapersonal space, are highly compromised. As a result, focal brain types not only exhibit their own types of developmental and learning disorders (“hyperlexia” -- advanced phonemic awareness but with no comprehension, autistic spectrum disorders, hyperactivity, etc.) (6-8, 19, 63), but may also have problems with general mental and physical health -- poor immune function (and thus predisposition for allergies, chronic otitis media, cancer, and AIDS); poor general metabolism (thus prone to diabetes, sleeping disorders, eating disorders, and cardiac problems); and psychiatric difficulties (autism, asocial behavior, schizophrenia, psychosis, etc.).

However, their possession of highly-developed left-brain skills may make these individuals so adaptive in

left-favoring societies such as ours that their shortcomings (in health as well as “people skills”) may be overlooked, overshadowed by their achievements in the focal abilities of the left side. (Note that the left-brain access of these individuals will also make them strongly right-handed.)

## 5. IMPLICATIONS FOR RESEARCH ON FUNCTIONAL ASYMMETRIES

### 5.1. Ontogenetic, clinical, and phylogenetic expectations

Both the EPIC and Trimodal models posit a neurobiological basis for “second-level” functional asymmetries which are: 1) essentially the same in all mammals (and there may be analogues in other vertebrates) (64); 2) distributed in essentially the same ways in all brains (“situs inversus” regarding functional asymmetries is assumed to be as rare as it is for other body parts); and 3) established during prenatal stages of brain organization (or at least in the earliest days of life, perhaps the case in rodents). These predictions generate a number of expectations regarding issues such as: the time course over which functional asymmetries can be observed in individual development; the causation and nature of a wide range of disorders; and the incidence and similarities in functional asymmetries across a number of animal species.

For instance, if individual patterns of access to the four domains are established in humans before birth, as posited by the Trimodal model, it would not be surprising to find that children -- even newborns and infants -- exhibit evidence of functional asymmetries which resemble patterns described in adults. Thus patterns of motor postural control may be expressed fairly early (65), in parallel with preferential use of the hands for certain tasks (66), and handedness may even be correlated with testosterone measured in umbilical cord blood (67). Early attempts at speech production may be associated with signs of left-brain motor control (68). Ear differences should also be evident very early, and in line with the patterns of asymmetries supposedly established during prenatal development, whether measured using behavioral techniques such as head-turn (for melody perception) (69) or physiological methods such as otoacoustic emissions (responses to rapid clicks vs. sustained tones (70) or evoked potentials (responses to speech and nonspeech) (71). Other behaviors, such as style of play (72, 73) and performance on a mental rotation task (74), may also be correlated with measures of prenatal testosterone made via amniocentesis.

Individual differences in these expressions might also be useful to locate an individual’s placement along the Trimodal continuum, long before the child could participate in more complex behavioral testing. The implications for educational applications are obvious, since children representing different brain types will present with very different skill profiles regarding academic performance. A more sophisticated understanding of the neurobiological rainbow of children in our public schools may encourage us to introduce appropriate training programs (which are already available, but are not part of the conventional educational curriculum (19, 45, 46) in order to guarantee that all children, no matter their neurotype, are provided

with all the right-brain and left-brain skills needed to ensure their future mental, physical, and economic health.

Clinical applications of the two models would give us not only new hypotheses for the origins of developmental and learning disorders, psychiatric dysfunction, and physical problems ranging from cancer to heart disease, but also new insights to the nature of functional asymmetries in these populations. For instance, studies on topics such as immune dysfunction in autism (75), visual asymmetries in hyperactivity (76) and schizophrenia (77), and handedness in Alzheimer's Disease (78) can be interpreted in the context of the Trimodal prediction that all these conditions are related to relatively high levels of prenatal testosterone exposure (5, 7, 62).

There are also possible insights into the individual differences associated with brain injury. One of the sources of evidence that males tend to be "more lateralized" than females comes from experience in clinical neurology, where it has long been known that males suffering from unilateral brain injury present with different symptoms (more devastating losses) and different prognoses for functional recovery (more long-term persistence) than do females. This is consistent with the Trimodal model, which attributes it to the fact that for brains with reduced connectivity (due to higher levels of pre- and postnatal testosterone exposure), losses should be more severe and longer-lived than for brains with more extensive neurological backup. Reference to the Trimodal continuum would then make it possible to understand individual differences in neurological prognosis within males and females -- some males (right- or middle-brain types) might show milder losses and more rapid recovery than expected, while some females (with a premonitory left-brain configuration) might suffer more severe, long-term losses than their chromosomal identity would predict.

Finally, functional asymmetries should also be found in other animals (64). The classifications outlined in (Tables 1 and 2) should hold for all vertebrates, given their posited biological basis (presence of light-touch somatosensory receptors, distinctions between small vs. large motor units, etc.). For example, rhesus monkeys show a consistent preference (turning the right ear toward the sound) in response to their temporally-complex calls, but turn to the left when such calls are played backwards, in which case the familiar temporal structure is disrupted (79). Although there has been considerable controversy regarding handedness in chimpanzees, a recent meta-analysis and critique has concluded that they in fact share many features of handedness with humans (who are, after all, the "third chimpanzee") (80).

Ecological considerations are definitely important when looking for asymmetries in other animals -- one cannot impose criteria borrowed from the behavior of other species, but must design experimental tasks or behavioral observations which take into account the everyday needs of that species. For instance, some raptor birds need to balance on one foot while using the other to hold and eat their prey, and they seem to prefer to use the left foot for

balancing, and the right for the fine motor task of manipulating ("pedipulating"?) their food (81). Similarly, crows may depend on an equally strong fine-motor-control-type laterality for cutting and using their leaf-based tools (82).

## 5.2. Observations on experimental design

### 5.2.1. Stimuli, tasks, interpretations: guidelines and caveats

The classifications outlined in the EPIC model, particularly the features distinguishing between extrapersonal and peripersonal-space processing, suggest some straightforward guidelines for stimulus and task designs in laterality experiments, and also some caveats regarding interpretation. For example, the grouping of features as shown in (Table 2) could be used to describe a stimulus set as either "consistent" or "inconsistent;" i.e., including features representing only one side (all right-brain features, vs. all left-brain ones), or a mix of features associated with the two sides. It seems logical that the clearest asymmetries would be evoked by using consistent groups of features, because if each feature on its own can evoke asymmetrical processing, when several are combined in the same stimulus, their effects might be additive, resulting in even more dramatic laterality differences.

For example, to evoke left-brain auditory abilities, one might design stimuli characterized by rapid (faster-than-motor) changes *and* different sources *and* broad-band excursions, etc., even if only one of these is singled out for discrimination or identification by listeners. In fact, it should be possible to determine whether the clarity of sidedness results is improved as more and more "consistent" features are added to the combination. This resembles one of the subtests included in a previous experiment (1, 2), in which three-event sequences were manipulated to create stimuli changing along one, two, or more dimensions. Results indicated that as more "left-brain features" were incorporated in these three-event sequences, the more the ear advantage favored the right ear (presumably the left hemisphere), and vice versa.

A consideration of the types of stimuli used in past experiments on asymmetries suggests that many test outcomes may unwittingly have depended on such a "consistency" principle -- for example, the real speech and musical stimuli used in many tests of auditory asymmetries actually represent combinations of several "consistent" features. Outcomes in these experiments might have depended more on the additive effect of these features, than on the influence of cognitive categories such as "speech vs. music" typically invoked by the authors (1-3). Frequent use of such "natural" stimuli for tests on laterality may have been one of the reasons that many students of laterality have been content to employ cognitive terms to describe the clusters, and not felt challenged to explore the possibility of sensorimotor bases underlying the observed asymmetries.

This is not to say that "inconsistent" feature combinations might not also be useful, applied in a somewhat different way. For example, one could start with

stimuli based on sets of consistent features, and test whether results become less clear if inconsistent features are added or substituted -- e.g., the effects of a good left-brain specialization such as multiple sound sources might be muddled by timing the changes to occur at a right-brain, "motor" rate. Similar designs could be used to explore whether some features are more salient than others for evoking asymmetries. It might even be possible to create stimulus designs which implicitly "cancel" effects. For example, if a right-brain feature were combined with a left-brain feature having "equal salience," zero lateralities might be the result, and additional testing on both features in other contexts would be required to explore the rules and limits of this type of cancellation.

One elegant way of disambiguating the contributions of different hypothetically right/left features is to design a complex stimulus array based on inconsistent feature combinations, and then manipulate the task so as to focus on one feature or another, with the goal of evoking different functional asymmetries. An example of such a design for testing visual asymmetries (83) employed the same series of faces of famous people presented to subjects in two separate runs -- first displayed at high focus, where the task was to identify the actual person, and a second time at low focus, where the task was to identify the gender of the somewhat blurred faces. The results indicated a right-Visual-Half-Field (VHF) advantage for the identity task (presumably based on analysis of a complex of high-resolution details), while gender discrimination (supposedly depending on lower-spatial-frequency features such as the relative proportions of parts of the face) evoked a left-VHF advantage.

A classical auditory example of this approach is the elegant experiment in which the same stimuli -- short series of four letter names sung as different melodies by different singers -- were presented to the same subjects on three separate occasions. (84) In one session, subjects were asked to identify the letters being sung in each series; in another, the melodies; and in another, the singer. As outlined in the meta-analysis mentioned above (1, 2), it was not necessary to invoke abstract cognitive concepts to explain the different ear advantages resulting from the three tasks; rather, the physical features targeted by each task -- similar to those listed in (Table 2) -- were sufficient to explain the outcome.

Thus the observed right-ear advantage for letter identification could be attributed not to the demands of "linguistic" processing, but to the left-brain peripersonal-space ability of resolving phonemic cues. The left-ear advantage for melody identification could likewise be explained not as a case of a laterality for concepts as vague as "music perception," but as a combination of narrow-band listening (a right-brain skill, tracking melody as articulated by the changing fundamental frequency) combined with the fact that the changes in frequency were quite slow, in the right-brain, "motor" range. The intermediate ear advantage for singer identification, in the context of the greater range of individual differences also observed for this task, might be attributed to the fact that

different listeners used different cues to accomplish this very complex task, and had depended on different combinations of left-brain stimulus features (speaker-specific characteristics of phoneme articulation, etc.) vs right-brain stimulus features (e.g., gestalt perception of resonance properties characterizing different vocal tracts).

Design concerns highlighting "consistent" vs. "inconsistent" combinations of features could extend beyond sensory modalities, to include the motor elements of task demands as well. In many early reports of experiments on auditory asymmetries, it is impossible to separate the potential influence of sensory aspects of stimuli such as syllables vs. melodies, from the influence of motor aspects of tasks employed, which often were allowed to co-vary with stimuli. For instance, it was common when testing syllables to ask subjects to immediately repeat back what was heard on each trial (presumably evoking left-brain motor-control abilities such as the fine-motor management involved in phoneme articulation), but when testing melodies, to allow subjects to hum their responses (evoking right-brain abilities for controlling "motor-rate" changes in voice pitch) or match them to a later-presented set of multiple choices. In order to separate the effects of task and stimulus, it is clearly important to include conditions in which one is held constant while the other is manipulated (cf. the wide variety of three-event sequences, ranging from "more speech-like" to "more music-like" tested in one experiment (1, 2), in which the same response symbols and identification choices were used throughout).

Concerns with the motor components of laterality tasks may be particularly important with regard to handedness. The brain does not use the two hands in the same way, or even in complementary ways, even in subjects who are truly ambidextrous. Even so, one can find reports of laterality tests in which subjects are allowed to use the right hand to respond to one type of stimulus and the left hand to another, yet test results are interpreted as though stimulus were the only important independent variable, ignoring the possibility of interactions between sensory-perceiving-side-of-brain and motor-responding-side-of-brain.

The concept of stimulus sets interacting with tasks (including motor responses), which may differ in the degree of consistency of right/left features, points up the necessity of being precise about the determinants of any observed asymmetries -- whether one or another feature is more salient, whether combinations are important either in additive or cancelling ways. This recalls the previous comments about "what-the-test-tests." If a stimulus set contains two or more features compatible with one side of the brain, and subjects are asked to respond to only one of them, it simply cannot be assumed that the targeted feature is the only aspect of the stimulus which contributed to the outcome. The other features may have assisted in creating the outcome, for example, as a kind of "priming" of one side of the brain or the other. For example, stimuli for a melody-identification task in which complex tones changing in fundamental frequency across a limited frequency range (say, less than 1 kHz) once every 500

msec, combines two right-brain features -- one of which is more “spectral” (pitch range) and one which is “temporal.” It would not be accurate to attribute the resulting ear advantage to either feature alone, but should fairly be concluded to be the outcome of the combination of both features involved.

Certainly it is inappropriate to ignore such sensorimotor aspects of stimulus and task combinations, and make the mistake of over-interpreting results in terms of cognitive constructs. In our continuing attempts to understand the biological bases of behavior, it would be more parsimonious to assume that test results are determined by known neurobiological entities related to perception and motor response, and only invoke cognitive causes when sensorimotor principles cannot account for the findings. Of course, it is possible that behavioral as well as brain-imaging dependent variables can reflect the presence of more cognitive operations, but until we know much more than we do now about the relations between sensorimotor features of laterality tests and brain asymmetries, we might be advised to reserve more abstract explanations for cases in which sensorimotor features alone cannot account for the outcome. In short, we should probably assume that virtually any “mental” behavior can be accounted for by principles of sensorimotor processing until proven guilty of being cognitive.

### 5.2.2. Controlling for individual differences: Introduction

In spite of careful design of stimuli and tasks, and attention to the consistency of sensory as well as motor features, attempts to demonstrate functional asymmetries can be foiled by individual differences in subject performance. As indicated above, the Trimodal model posits dramatic differences in mammalian subjects regarding their access to right- and left-brain skills. Thus for a laterality researcher to average results over individuals characterized by such differences is like a botanist averaging measures such as color, nutrients, shape, and size over many types of fruits -- apples, oranges, kumquats, bananas, currants, watermelons, mangoes, etc. The result would be so general as to be virtually useless from a biological standpoint (except perhaps to distinguish fruits categorically from, say, nuts). On the other hand, one does not need to define a separate rule for every subject -- the Trimodal typology provides a means of disambiguating confusions arising from individual differences, by suggesting ways of grouping subjects which may be extremely helpful in laterality research.

Of particular importance to subject selection and grouping in studies of functional asymmetries are Trimodal predictions regarding gender and handedness. Many laterality researchers, hoping to meet the stringent demands regarding “significance” imposed by group statistics, try to avoid diversity in their subject groups. They do this primarily in two ways: 1) grouping individuals by self-reported gender; and 2) disqualifying those who are not right-handed (by self-report or testing). Although well-intentioned, these practices may have contributed to many

of the problems in our understanding of functional asymmetries.

### 5.2.3. Issues in individual differences: Gender

First, the Trimodal model (consistent with research in many disciplines) (72-73, 85-90) predicts that individual differences in exposure to pre- and postnatal testosterone may be more important in determining neurobiological features (such as laterality) than differences in sex chromosomes. Thus, for example, laterality findings in left-brain females should be more like those from left-brain males than those from females of other brain types. As a result, it might be better to *first group subjects by brain type*, rather than self-reported gender. Then, because absolute levels of testosterone may also be important (higher levels of testosterone creating more severe disconnection effects and therefore the male-typical “more lateralized” performance), the next step might be to subdivide the brain-type categories into XX and XY subgroups.

Brain-typing can be done using physiological methods such as qEEG and ABR (15, 34, 62, 63, 91-98), but more modest behavioral test batteries may also prove useful. We are currently developing a behavioral test battery based on relatively inexpensive tests which can distinguish among the three brain types. It may be possible to calibrate individual differences in prenatal testosterone exposure according to anatomical features dating from the earliest stages of development, such as relative length of index and ring fingers (99-105).

### 5.2.4 Issues in individual differences: Handedness and the brain types

Second, with reference to handedness, recall that under the EPIC and Trimodal models, “handedness” is understood as a left-brain-biased term, meaning the hand preferred for fine-motor-control tasks. Thus individuals from different points along the continuum of brain types, because of their differences in degrees (and quality) of access to this left-brain function, will exhibit marked distinctions in fine-motor-control ability, expressed loosely as “handedness.” Given such a continuum of characteristics, it is clear that classifying handedness according to only two categories, “right vs. left,” is procrustean and neurobiologically inaccurate.

For example, the Trimodal model predicts there are several types of right-handed individuals, and they represent quite different points along the continuum. Even distinguishing these as strongly vs mildly right-handed does not resolve the issue. In fact, the model identifies two types of “strongly right-handed” individuals -- the “right-brain/whole brain” and “left-brain” modes. Individuals from both these categories will exhibit high levels of fine-motor-control (FMC), but should perform in quite different ways on laterality tests (outlined below). On the other hand, “mildly right-handed” individuals should represent the very different middle-brain mode, primarily coming from the right-middle region.

Persons who are not even mildly right-handed predictably come from other points within the middle-brain mode, ranging from middle-of-middle into left-middle. Among these may be persons who can be described as left-handed, though the model would predict that: 1) it would be extremely rare to find a left-handed person who was strongly left-handed in an analogous way to strongly right-handed people (that is, there will be some use of both hands for different FMC tasks); and 2) no middle-brain individual of any sort will be as good at FMC with either hand as a strongly right-handed type is with the right hand. (Based on our laboratory experience, we believe that this symmetric, lower-FMC ability is what is commonly referred to as “ambidexterity.”) All middle-brain types will perform very differently on laterality tests, when compared not only with the strongly-right-handed types, but also with each other. (A complete discussion of middle-brain performance on laterality tasks is beyond the scope of this article, but the relevant principles can be deduced from a consideration of performance by right-handers -- see below.)

These predictions regarding handedness suggest that the handedness-grouping principles used in most laterality research are inadequate, serving not only to diminish the universality of outcomes, but also to cloud results in yet another instance of mixing apples and oranges. First, when researchers screen their subjects for strong right-handedness, they disqualify what may amount to a third of the population. A science which eliminates one-third of the population at the outset from the pool of “normal” subjects may miss critical information.

Second, if only strongly right-handed individuals are accepted, this might provide representation for a majority of the population, but still mixes categories. As noted earlier, strongly right-handed individuals can represent either the right-brain/whole brain or the left-brain modes, and each of these should perform differently in laterality tests. A brief discussion will illustrate the ways in which these distinctions can impact on the outcome of tests on functional asymmetries; our example will consider an auditory experiment, but the same principles apply to any type of sensory or motor asymmetry.

Our sample case, modelled on actual results (63), is a dichotic-listening experiment in which subjects are tested on two sets of stimuli: 1) one designed to evoke preferential processing by the left hemisphere (e.g., a set of synthetic syllables, each consisting of one of the six English stop consonants followed by the vowel /a/); and 2) one designed to evoke right-brain processing (e.g., a set of three-pure-tone melodies (106) involving frequency changes within a whole-tone pitch range [less than 200 Hz], with tone onsets separated by 200 msec).

The performance of right-brain/whole-brain individuals in such an experiment will be characterized by: 1) relatively high performance (not at ceiling -- i.e., indicating at least some competition from non-preferred ear inputs carried via an active corpus callosum) in the preferred ear for both sound sets; 2) mid-range performance

(neither ceiling nor floor; below-ceiling again reflects the presence of successful competition mediated via the corpus callosum, while above-floor indicates some help from the preferred side, again via the corpus callosum) in the non-preferred ear for each sound set; resulting in 3) a moderate ear advantage (EA) for each stimulus set, such that the pattern of “relative ear advantages” shows the EA for the syllables to-the-right-of the EA for the melodies (1-3, 30, 34).

In contrast, performance by left-brain individuals in this experiment will be characterized by: 1) very high performance (at ceiling -- in fact, approaching monaural levels) in the right ear for the syllables, combined with much lower performance in the left ear for the melodies (relatively low during monaural as well as dichotic presentation, indicating poor access to the right hemisphere); 2) extremely low performance (approaching floor, thus indicating no help via the corpus callosum from either preferred side) in the non-preferred ear for each sound set; resulting in 3) a large (and opposite, thus “strongly lateralized”) EA for each stimulus set, such that the pattern of relative ear advantages shows the EA for the syllables to-the-right of the EA for the melodies. Note that the pattern of relative ear advantages is the same in both cases (1-3, 30, 34), but is achieved in very different ways neurologically in the two classes of subjects. These reflect basic distinctions in the two brain types regarding access to right- vs. left-brain processing, including possible indicators of corpus-callosum viability.

The standard practice in laterality experiments for analyzing test results may introduce ambiguities in the apparent dynamic range of the dependent variable (the EA values). This methodology begins by averaging the right- and left-ear scores for each sound set over subjects and only then combines these average ear scores to calculate the group EA for each sound set. Put briefly, if both brain types were represented, this action would shrink the apparent dynamic range of EAs, thus calling into question the utility of EAs as a tool for studying functional asymmetries. This is true for two reasons: 1) with a restricted dynamic range, there is little room for manipulation (e.g., testing combinations of sound features); and 2) any variations which occur (such as in test-retest comparisons) might overwhelm this tiny range and lead to dismissals of EAs as “unstable” or “unreliable,” a conclusion which has unfortunately been drawn by a number of researchers.

### 5.2.5. Issues in individual differences: Shifting asymmetries

The “inconsistency” of asymmetries has posed a philosophical problem for students of laterality. For instance, in the sample experiment discussed above, a subject who exhibited a clear REA for the syllables in one block of a test session might show no EA at all, or even a LEA, in a later block of the same session, or on a subsequent day (1-3, 30, 34). The dismay of some investigators over such fluctuation has led some to abandon hope of ever identifying systematic principles behind these phenomena -- and even to question the existence of functional asymmetries (107-109).

## EPIC model of functional asymmetries

We have demonstrated (1-3, 30) that in spite of changes in the absolute EA for any one sound set, patterns of *relative asymmetries* (designated as “relative ear advantages” in those studies) comparing two or more stimulus sets are consistent over time. However, other researchers have not noted this finding, and therefore continue to doubt the validity of laterality results.

For instance, in early papers, Sergent (110, 111) confidently predicted that stimulus characteristics could be shown to be important determinants of functional asymmetries in vision. Two decades later, after repeated attempts to derive the relevant rules, this gifted researcher gave up, defeated by what she apparently believed to be insoluble methodological difficulties, particularly problems with “reliability” and “contradiction” --

None of the techniques appear to be self-sufficient, their reliability cannot be perfect, and they produce results that may sometimes contradict one another. . . It is now clear that the search for a single, bipolar principle that would encompass the functional properties of the two hemispheres would be futile. (109, p. 178).

Ironically, it is more likely that “shifts” in asymmetries sometimes observed on re-test in fact are the strongest evidence of their biological reality. Biology, after all, is not static but dynamic, involving systematic variation and changes-within-limits. Explorations into the nature of such changes, their limits, and the principles of variation, may reveal the secrets of asymmetries to a degree not possible if we continued to insist on stasis as the only criterion for reality.

Studying systematic variation in functional asymmetries is no more difficult than studying any other type of biological variation -- one simply needs to attend to individual differences and be aware of the nature and sources of physiological variation (15). First, it is crucial to recognize that every subject is characterized by a “resting asymmetry” (34, 112), which must be taken as the baseline against which asymmetries evoked by testing are measured and interpreted. The relation between a truly “naïve” resting asymmetry -- that is, unaffected by special conditions such as pharmaceuticals or preceding activity -- and the underlying related anatomical asymmetry, which presumably reflects the influence of prenatal exposure to testosterone, may be relatively direct. For example, Lauter & Plante showed that the resting physiological asymmetry comparing right and left-side auditory cortex measured in an individual using qEEG provides a good estimate of both the direction and magnitude of the anatomical asymmetry in the subject’s perisylvian cortex as measured with MRI (62, 113).

An individual’s resting asymmetry can be classified categorically based on brain type -- Left Hemisphere Advantage or LHA; Zero Hemisphere Advantage or OHA; Right-Hemisphere Advantage or RHA. These categories should roughly estimate anatomical as well as resting-physiological asymmetries. More usefully, the resting asymmetry can be measured exactly using

physiological techniques targeting the cortex such as PET, fMRI, or qEEG (31, 32, 34, 63, 113, 114, 115). In addition, it may eventually be possible to estimate cortical asymmetries using much less expensive methods such as the Repeated Evoked Potentials version of the Auditory Brainstem Responses (REPs/ABRs) (8, 15, 91-98), otoacoustic emissions (OAEs) (106), or even finger-length ratios, as mentioned earlier. Ongoing work in our laboratory using our Auditory Cross-Section (AXS) Test Battery (9, 15, 112-118) is directed to exploring the degree to which cortical resting asymmetries can be predicted based on these more peripheral and readily available measures.

Seen in the context of an individual’s resting asymmetry, shifts in functional asymmetries, whether measured behaviorally or physiologically, can be characterized as “riding” on the “carrier frequency” of more basic aspects of physiological asymmetries. Thus asymmetries measured during either activation or later control (resting) conditions may be affected by changes in the underlying biology attributable to factors such as: 1) systemic fluctuations, such as circadian or other generic biorhythms (116-121); 2) endocrine secretions, such as adrenaline, cortisol, and sex hormones, whether cyclic or acute, which can affect test-retest comparisons in males as well as females; 3) external biological factors, including pharmaceuticals such as antihistamines, methyphenidate, nicotine, or artificial hormones (14, 15, 114, 122, 123), and neuroactive contents of food or drinks, such as sugar or caffeine; and 4) external behavioral factors, such as the influence of preceding test conditions.

Regarding this fourth factor, Lauter (9, 34, 124) has shown, using both qEEG and PET, that asymmetries for auditory as well as motor tasks can be shifted toward the right or the left by preceding testing conditions, one example of the “neural persistence” effect first described by Lauter (34). Preliminary work in our laboratory on persistence indicates that the effects of a single test block (even for as simple an action as alternately flexing and extending the fingers of one hand) can be observed more than 45 minutes following cessation of the action. The possibility of such long-lasting effects is clearly crucial for the design of physiological experiments based on condition subtraction, in which measures taken during one activation condition are subtracted from those collected in subsequent conditions. As the schedule of test blocks proceeds, the cumulating “persisting” effects of responses evoked by successive test conditions may be virtually impossible to untangle.

## 6. CONCLUSIONS AND PERSPECTIVES

The many types of variation in functional-asymmetry studies have been of basic importance in this literature, contributing not only to confusions regarding the influence of stimulus and task and the significance of within- and between-subject differences, but even leading many to doubt the reality of asymmetries themselves. Scientists expect to see predictable variation. When surprised by test results, particularly in cases of

unanticipated variation, some will not only discard the data but dismiss the entire testing approach, instead of pursuing the nature and source of the variation. Thus they in essence throw the baby out with the bathwater.

One way to summarize the history of science is as a continued search for the “signal in the noise.” Of course it can be extraordinarily difficult to know when to keep searching, and when to conclude there simply is no signal to be discerned. However, it is also possible to err on either side -- either categorically condemning all variation as noise, or seizing on every variation as a new ‘signal’ (108), in which virtually every experiment is hailed as identifying another new functional asymmetry -- speech, formant transitions, music, speaker identification, selection of objects, face recognition, name-finding, names of tools, house recognition, etc. -- a modern manifestation, perhaps, of the medieval belief in “essences.”

Certainly the reality of what we have called the first level of functional asymmetries is indisputable -- e.g., the right side of the nervous system does control muscles on the left side of the body, at least in vertebrates. There is no reason to think that a second level is any less real, any less adaptive. The formulations of tables 1 and 2 certainly appear coherent, given the naturally-occurring clustering of features described above. A second level of functional asymmetries will surely follow the biological principles governing every other aspect of body organization, and we would be well advised to be parsimonious in our approach to studying them. The long-term benefits, including a more sophisticated understanding of the biological bases of behavior, may be rich indeed.

## 7. REFERENCES

1. Lauter J.L.: Dichotic identification of complex sounds. Unpublished PhD dissertation, University Microfilms, Ann Arbor MI (1979)
2. Lauter J.L.: Dichotic identification of complex sounds: absolute and relative ear advantages. *J Acoust Soc Am* 71, 701-707 (1982)
3. Lauter J.L.: Stimulus characteristics and relative ear advantages: a new look at old data. *J Acoust Soc Am* 74, 1-17 (1983)
4. Lauter J. L.: Brain asymmetries based on physical aspects of stimulus and gesture: Analogues in four somatic systems. Invited presentation to Conference on Nonspeech Complex Sounds, Chicago IL (1987)
5. Lauter J.L.: Dimensions of behavior: A view from above the central sulcus. Invited presentation to Conference on Approaches to Developmental and Learning Disorders in Children: Theory and Practice, Rockville MD (1997)
6. Lauter J.L.: The Handshaking Model of Brain Function: Notes toward a theory. *Med Hypoth* 52, 435-445 (1999)
7. Lauter J.L.: Functional asymmetries and the Trimodal Brain: Applications to developmental disorders. *J Develop Learn Disord* 3, 181-260 (1999)
8. Lauter J.L.: Neuroimaging: How Understanding Individual Differences can Improve Your Clinical Practice. [3-hr video presentation with manual.] American Speech-Language-Hearing Association, Rockville MD (2002)
9. Lauter J.L.: New approaches to understanding the human brain: Three theoretical models and a test battery. In: All in Good Time: A Tribute to Ira Hirsh. Ed: Lauter J.L., *Sem Hear* 25, 269-280 (2004)
10. Lane R.D., & J. R. Jennings: Hemispheric asymmetry, autonomic asymmetry, and the problem of sudden cardiac death. In: Brain Asymmetry. Eds: Davidson R.J. & Hugdahl K., MIT Press, Cambridge MA 271-304 (1995)
11. Wittling W.: Brain asymmetry in the control of autonomic-physiologic activity. In: Brain asymmetry. Eds: Davidson R.J. & Hugdahl K., MIT Press, Cambridge MA 305-357 (1995)
12. Porges S.W.: Orienting in a defensive world: Mammalian modifications of our evolutionary heritage. A polyvagal theory. *Psychophys* 32, 301-318 (1995)
13. Porges S.W.: Social engagement and attachment: a phylogenetic perspective. *Ann NY Acad Sci* 1008, 31-47 (2003)
14. Lauter J.L.: Neurophysiological self-control: Modulation in all things. *J Comm Disord* 31, 543-549 (1998)
15. Lauter J.L.: The AXS battery and neurological fingerprints: Meeting the challenge of individual differences in human brain/behavior relations. *Behav Res Meth Instru Comput* 32, 180-190 (2000)
16. Kitterle, F., & S. Christman: Hemispheric symmetries and asymmetries in the processing of sine-wave gratings. In: Advances in Cerebral Laterality Research: Data and Theory. Ed: F. Kitterle, Lawrence Erlbaum Associates, Hillsdale, N.J. (1991)
17. Christman S. D., & C. L. Niebauer: The relation between left-right and upper-lower visual field asymmetries. In: Cerebral Asymmetries in Sensory and Perceptual Processing. Ed: Christman S., Elsevier, Amsterdam 263-296 (1997)
18. Previc F.: Functional specialization in the lower and upper visual field in humans: Its ecological origins and neurophysiological implications. *Behav Brain Sci* 13, 519-575 (1990)
19. Lauter J.L.: The Trimodal Brain and reading I: A new synthesis and some predictions. *J Develop Learn Disord* 7, 65-84 (2003)

20. Lauter J.L., & I.J. Hirsh: Speech as temporal pattern: A psychoacoustical profile. *Speech Comm* 4, 41-54 (1985)
21. Haggard M.P., & A.M. Parkinson: Stimulus and task factors as determinants of ear advantages. *Q J Exp Psychol* 23, 168-177 (1971)
22. Berlin C.I., S.S. Lowe-Bell, J.K. Cullen, Jr., C.L. Thompson, C.F. Loovis: Dichotic speech perception: An interpretation of right-ear advantage and temporal offset effects. *J Acoust Soc Am* 53, 699-709 (1973)
23. Cullen, J.K., Jr., C.L. Thompson, .F. Hughes, C.I. Berlin, D.S. Samson: The effects of varied acoustic parameters on performance in dichotic speech perception tasks. *Brain Lang* 1, 307-322 (1974)
24. Divenyi P.L., R. Efron, W.E. Yund: Ear dominance in dichotic chords and ear superiority in frequency discrimination. *J Acoust Soc Amer* 62, 624-632 (1977)
25. Lauter J.L.: Dichotic identification of complex sounds. *J Acoust Soc Am* 67, S100 (1980)
26. Schwartz M., & P. Tallal: Rate of acoustic change may underlie hemispheric specialization for speech perception. *Science* 207, 1380-1381 (1980)
27. Belin P., M. Zilbovicius, S. Crozier, L. Thivard, A. Fontaine, M.-C. Masure, Y. Samson: Lateralization of speech and auditory temporal processing. *J Cogn Neurosci* 10, 536-540 (1998)
28. Brown C.P., R.H. Fitch, P. Tallal: Sex and hemispheric differences for rapid auditory processing in normal adults. *Laterality* 4, 39-50 (1999)
29. Poeppel D.: The analysis of speech in different temporal integration windows: Cerebral lateralization as asymmetric sampling in time. *Speech Comm* 41, 245-255 (2003)
30. Lauter J.L.: Contralateral interference and ear advantages for identification of three-element patterns. *Brain Cognit* 3, 259-280 (1984)
31. Lauter J.L., P. Herscovitch, C. Formby, M.E. Raichle: Tonotopic organization in human auditory cortex revealed by positron emission tomography. *Hear Res* 20, 199-205 (1985)
32. Lauter J.L., P. Herscovitch, & M.E. Raichle: Human auditory physiology studied with positron emission tomography. In: Auditory Pathway. Eds: Syka J. & Masterton R.B., Plenum, New York 313-317 (1988)
33. Lauter J.L.: Imaging techniques and auditory processing. In: Central Auditory Processing: A Transdisciplinary View. Eds: Katz J., Stecker N. & Henderson D., Mosby, New York 93-115 (1992)
34. Lauter J.L.: Processing asymmetries for complex sounds: Comparisons between behavioral ear advantages and electrophysiological asymmetries based on quantitative electroencephalography (qEEG) *Brain Cognit* 19, 1-20 (1992)
35. Lauter J.L.: Visions of speech and language: Noninvasive imaging techniques and their applications to the study of human communication. In: Human Communication and its Disorders, Vol. IV. Ed: Winitz H., York Press, Timonium MD 277-389 (1995)
36. Lauter J.L.: Noninvasive brain imaging in speech motor control and stuttering: Choices and challenges. In: Speech Production: Motor Control, Brain Research, and Fluency Disorders. Eds: Hulstijn W., Peters H.F.M., & Van Lieshout P., Elsevier, Amsterdam 233-258 (1997)
37. Lauter J.L.: Neuroimaging in developmental speech and language pathology. In: Communication and its Disorders: A Science in Progress. Eds: Dejonckere P. & Peters H.F.M., Nijmegen University Press, Nijmegen 499-502 (1999)
38. Berglund A.M., & M.C. Brown: Central trajectories of type II spiral ganglion cells from various cochlear regions in mice. *Hear Res* 75, 21-130 (1994)
39. Rosbe K.W., B.J. Burgess, R.J. Glynn, J.B. Nadol, Jr.: Morphologic evidence for three cell types in the human spiral ganglion. *Hear Res* 93, 120-127 (1996)
40. Jagger D.J., & G.D. Housley: Membrane properties of type II spiral ganglion neurones identified in a neonatal rat cochlear slice. *J Physiol* 552 (Pt 2), 525-533 (2003)
41. Reid M.A., J. Flores-Otero, R.L. Davis: Firing patterns of type II spiral ganglion neurons in vitro. *J Neurosci* 24, 733-742.
42. Schofield B.R., & D.L. Coomes: Auditory cortical projections to the cochlear nucleus in guinea pigs. *Hear Res* 199, 89-102 (2005)
43. Finger S.: Origins of neuroscience: A history of explorations into brain function. Oxford University Press, Oxford (1994)
44. Denes P.B., & E.N. Pinson: The speech chain: The physics and biology of spoken language. Anchor Press, Garden City NY (1973)
45. Lindamood P., N. Bell, & P. Lindamood: Achieving competence in language and literacy by training in phonemic awareness, concept imagery and comparator function. In: Dyslexia: Biology, cognition and intervention. Eds: Hulme C. & Snowling M., Whurr, London 212-234 (1997)
46. Lauter J. L. & P. F. McKane: The Trimodal Brain and reading II: Preliminary data on the co-occurrence of

problems in phonemic awareness and eye-movement coordination. *J Develop Learn Disord* 7, 85-96 (2003)

47. Turnbull O. H. & H. E. Bryson: The leftward cradling bias and hemispheric asymmetry for speech prosody. *Laterality* 6, 21-28 (2001)

48. Damerose E., & J. Vauclair: Posture and laterality in human and non-human primates: Asymmetries in maternal handling and the infant's early motor asymmetries. In: Comparative Vertebrate Lateralization. Eds: Rogers L. J. & Andrew R. J., Cambridge University Press, Cambridge 306-362 (2002)

49. Tomaszycki M., C. Cline, B. Griffin, D. Maestriperi, W.D. Hopkins: Maternal cradling and infant nipple preference in rhesus monkeys (*Macaca mulatta*) *Dev Psychobiol* 32, 305-312 (1998)

50. Damerose E., & J. Vauclair: Development of hand asymmetry in Olive baboons (*Papio anubis*) Effects of the mother's posture and manual laterality. *Folia Primatol* 70, 208-209 (1999)

51. Levine, J.L., R.L. Kurtz, & J.L. Lauter: Hypnosis and its effect on left and right hemisphere activity. *Biol Psychiat* 19, 1461-1475 (1984)

52. Gruzelier J., & K. Warren: Neuropsychological evidence of reductions on left frontal tests with hypnosis. *Psychol Med* 23, 93-101 (1993)

53. De Pascalis V., & M. Perrone: EEG asymmetry and heart rate during experience of hypnotic analgesia in high and low hypnotizables. *Internat J Psychophysiol* 21, 163-175 (1996)

54. Pauk J., C.M. Kuhn, T.M. Field, S.M. Schanberg: Positive effects of tactile versus kinesthetic or vestibular stimulation on neuroendocrine and ODC activity in maternally-deprived rat pups. *Life Sci* 39, 2081-2087 (1986)

55. Schanberg S.M., & T.M. Field: Sensory deprivation stress and supplemental stimulation in the rat pup and preterm human neonate. *Child Dev* 58, 1431-1447 (1987)

56. Liu D., J. Diorio, B. Tannenbaum, C. Caldji, D. Francis, A. Freedman, S. Sharma, D. Pearson, P.M. Plotsky, M.J. Meaney: Maternal care, hippocampal glucocorticoid receptors, and hypothalamic-pituitary-adrenal responses to stress. *Science* 277, 1659-1662 (1997)

57. Kuhn C.M., & S.M. Schanberg: Responses to maternal separation: mechanisms and mediators. *Int J Dev Neurosci* 16, 261-270 (1998)

58. De Kloet E.R.: Hormones and the stressed brain. *Ann NY Acad Sci* 1018, 1-15 (2004)

59. Lauter J.L.: The challenge of individual differences: Notes toward a new neurotypology of human function based on functional asymmetries and brain/behavior

relations. Invited presentation to International Conference on Measuring Behavior 98, Groningen, The Netherlands (1998)

60. Lauter J.L.: The Trimodal Brain: Physiological correlates of phonemic awareness. Invited presentation to Lindamood-Bell Research Conference, Washington DC (1998)

61. Lauter J.L.: Neuroimaging, the Trimodal Brain, and developmental communication neuroscience. Invited Main Report presentation to 24th World Congress of the International Association of Logopedics and Phoniatrics, Amsterdam, The Netherlands (1998)

62. Lauter J.L.: Neuroimaging and the Trimodal Brain: Applications in developmental communication neuroscience. *Folia Phoniatr Logoped* 50, 118-145 (1998)

63. Lauter, J.L., H. Richey, S. Gilmore & O. Lynch: Putting the 'central' back in Central Auditory Processing. *J Develop Learn Disord* 2, 51-106 (1998)

64. Rogers L. J. & R. J. Andrew (Eds): Comparative vertebrate lateralization. Cambridge: Cambridge University Press (2002)

65. Ronnqvist L., & B. Hopkins: Motor asymmetries in the human newborn are state dependent, but independent of position in space. *Exp Brain Res* 134, 378-384 (2000)

66. Lhote M., & A. Streri: Haptic memory and handedness in 2-month-old infants. *Laterality* 3, 173-192 (1998)

67. Tan U., & M. Tan: Testosterone and grasp-reflex differences in human neonates. *Laterality* 6, 181-192 (2001)

68. Holowks S. & L.A. Petitto: Left hemisphere cerebral specialization for babies while babbling. *Science* 297, 1515 (2002)

69. Balaban, M.T., L.M. Anderson, A.B. Wisniewski: Lateral asymmetries in infant melody perception. *Dev Psychol* 34, 39-48 (1998)

70. Sininger Y.S., & B. Cone-Wesson: Asymmetric cochlear processing mimics hemispheric specialization. *Science* 305, 1581 (2004)

71. Molfese D.L.: Predicting dyslexia at 8 years of age using neonatal brain responses. *Brain Lang* 72, 238-245 (2000)

72. Knickmeyer R.C., S. Wheelwright, K. Taylor, P. Raggatt, G. Hackett, S. Baron-Cohen: Gender-typed play and amniotic testosterone. *Dev Psychol* 41, 517-528 (2005)

73. Knickmeyer R.C., S. Baron-Cohen, P. Raggatt, K. Taylor: Foetal testosterone, social relationships, and restricted interests in children. *J Child Psychol Psychiatry* 46, 198-210 (2005)

74. Grimshaw G.M., G. Sitarenios, J.A. Finegan: Mental rotation at 7 years: relations with prenatal testosterone levels and spatial play experiences. *Brain Cogn* 29, 85-100 (1995)
75. Sweeten T.L., S.L. Bowyer, D.J. Posey, G.M. Halberstadt, C.J. McDougle: Increased prevalence of familial autoimmunity in probands with pervasive developmental disorders. *Pediatrics* 112, e420 (2003)
76. Klimkeit E.I., J.B. Mattingley, D.M. Sheppard, P. Lee, J.L. Bradshaw: Perceptual asymmetries in normal children and children with attention deficit/hyperactivity disorder. *Brain Cogn* 52, 205-215 (2003)
77. Bellgrove M.A., S. Collinson, J.B. Mattingley, C. Pantelis, P.B. Fitzgerald, A.C. James, J.L. Bradshaw: Attenuation of perceptual asymmetries in patients with early-onset schizophrenia: evidence in favor of reduced hemispheric differentiation in schizophrenia? *Laterality* 9, 79-91 (2004)
78. Doody R.S., J.L. Vacca, P.J. Massman, T.Y. Liao: The influence of handedness on the clinical presentation and neuropsychology of Alzheimer's disease. *Arch Neurol* 56, 1133-1137 (1999)
79. Ghazanfar A.A., D. Smith-Rohrberg, M.D. Hauser: The role of temporal cues in rhesus monkey vocal recognition: Orienting asymmetries to reversed calls. *Brain Behav Evol* 58, 163-172 (2001)
80. Hopkins W.D., & C. Cantalupo: Individual and setting differences in the hand preferences of chimpanzees (*Pan troglodytes*): a critical analysis and some alternative explanations. *Laterality* 10, 65-80 (2005)
81. Csermely D.: Lateralization in birds of prey: adaptive and phylogenetic considerations. *Behav Processes* 67, 511-520 (2004)
82. Hunt G.R., M.C. Corballis, R.D. Gray: Animal behavior: Laterality in tool manufacture by crows. *Nature* 414, 707 (2001)
83. Sergent J., S. Ohta, & B. MacDonald: Functional neuroanatomy of face and object processing: A PET study. *Brain* 115, 15-29, 1992.
84. Bartholomeus B.: Effects of task requirements on ear superiority for sung speech. *Cortex* 10, 215-223 (1974)
85. McFadden D.: A speculation about the parallel ear asymmetries and sex differences in hearing sensitivity and otoacoustic emissions. *Hear Res* 68, 143-151 (1993)
86. McFadden D., J.C. Loehlin, E.G. Pasanen: Additional findings on heritability and prenatal masculinization of cochlear mechanisms: click-evoked otoacoustic emissions. *Hear Res* 97, 102-119 (1996)
87. McFadden D.: Masculinization effects in the auditory system. *Arch Sex Behav* 31, 99-111 (2002)
88. McFadden D., & C. A. Champlin: Comparison of auditory evoked potentials in heterosexual, homosexual, and bisexual males and females. *JARO* 1, 89-99 (2000)
89. Nyborg H: Hormones, sex and society: The science of physiology. Praeger, Westport CN (1994)
90. Nyborg H: The neuropsychology of sex-related differences in brain and specific abilities. In: The neuropsychology of individual differences. Ed: Vernon P.A., San Diego, Academic Press 60-113 (1994)
91. Lauter J.L. & R.L. Loomis: Individual differences in auditory electric responses: comparisons of between-subject and within-subject variability. I. Absolute latencies of brainstem vertex-positive peaks. *Scand Audiol* 15, 167-172 (1986)
92. Lauter, J.L. & R.L. Loomis: Individual differences in auditory electric responses: comparisons of between-subject and within-subject variability. II. Amplitudes of brainstem vertex-positive peaks. *Scand Audiol* 17: 87-92 (1988)
93. Lauter, J.L. & R.G. Karzon: Individual differences in auditory electric responses: comparisons of between-subject and within-subject variability. III. A replication, and observations on individual vs. group characteristics. *Scand Audiol* 19, 67-72 (1990)
94. Lauter J.L. & R.G. Karzon: Individual differences in auditory electric responses: comparisons of between-subject and within-subject variability. IV. Latency-variability comparisons in early, middle, and late responses. *Scand Audiol* 19, 175-182 (1990)
95. Lauter J.L. & R.G. Karzon: Individual differences in auditory electric responses: comparisons of between-subject and within-subject variability. V. Amplitude-variability comparisons in early, middle, and late responses. *Scand Audiol* 19, 201-206 (1990)
96. Lauter, J.L. & R.F. Oyler: Latency stability of auditory brainstem responses in children aged 10-12 years compared with younger children and adults. *Brit J Audiol* 26, 245-253 (1992)
97. Lauter, J.L. & S. B. Wood: Auditory-brainstem synchronicity in dyslexia measured using the REPs/ABR protocol. *Ann NY Acad Sci* 682, 377-379 (1993)
98. Lauter, J.L., R.F. Oyler & J.M. Lord-Maes: Amplitude stability of auditory brainstem responses in two groups of children compared with adults. *Brit J Audiol* 27, 263-271 (1993)
99. Phelps V.R.: Relative index finger length as a sex-influenced trait in man. *Am J Hum Genet* 4, 72-89 (1952)

100. James W.H.: Finger-length ratios, sexual orientation and offspring sex ratios. *J Theor Biol* 212, 273-274 (2001)
101. Peters M., K. Mackenzie, P. Bryden: Finger length and distal finger extent patterns in humans. *Am J Phys Anthropol* 117, 209-217 (2002)
102. Manning J.T., S. Baron-Cohen, S. Wheelwright, G. Sanders: The 2nd to 4th digit ratio and autism. *Dev Med Child Neurol* 43, 160-164 (2001)
103. McFadden D., & E. Shubel: Relative lengths of fingers and toes in human males and females. *Horm Behav* 42, 492-500 (2002)
104. Lutchmaya S., S. Baron-Cohen, P. Raggatt, R. Knickmeyer, J.T. Manning: 2nd to 4th digit ratios, fetal testosterone and estradiol. *Early Hum Dev* 77, 23-28 (2004)
105. McFadden D., J.C. Loehlin, S.M. Breedlove, R.A. Lippa, J.T. Manning, O. Rahman: A reanalysis of five studies on sexual orientation and the relative length of the 2nd and 4th fingers (the 2D:4D ratio) *Arch Sex Behav* 34, 341-356 (2005)
106. Divenyi P.L., & I.J. Hirsh: Identification of temporal order in three-tone sequences. *J Acoust Soc Am* 56, 144-151 (1974)
107. Friedman A., & M. C. Polson: Hemispheres as independent resource systems: Limited-capacity processing and cerebral specialization. *J Exp Psychol Hum Percept Perform* 7, 1031-1058 (1981)
108. Efron R.: The decline and fall of hemispheric specialization. Hillsdale NJ, Lawrence Erlbaum Associates (1990)
109. Sergent J.: Hemispheric contribution to face processing: Patterns of convergence and divergence. In: Brain Asymmetry. Eds: Davidson R.J. & Hugdahl K. Cambridge MA, MIT Press 157-182 (1995)
110. Sergent J.: The cerebral balance of power: confrontation or cooperation? *J Exp Psychol Hum Percept Perform* 8, 253-272 (1982)
111. Sergent J.: Role of the input in visual hemispheric asymmetries. *Psych Bull* 93, 481-512 (1983)
112. Lauter J.L., & E. Plante: Global brain asymmetries in regional cerebral blood flow (rCBF) during resting conditions with positron emission tomography (PET): Establishing a baseline for experiments on brain asymmetries and complex sounds in the CNS Project. *J Acoust Soc Am* 85: S69 (1989)
113. Lauter, J.L. & E. Plante: Quantitative electroencephalographic (qEEG) correlates of anatomical asymmetries in human auditory cortex studied in the CNS Project. Presented to Society for Neuroscience, Anaheim CA (1992)
114. Gusnard D. A. & M. E. Raichle: Searching for a baseline: Functional imaging and the resting human brain. *Nature Rev Neurosci* 2, 685-694.
115. Lauter J.L., S. Wood, O. Lynch & L. Schoeffler: Physiological and behavioral effects of an antihistamine in adults. *Percept Motor Skills* 88, 707-732 (1999)
116. Lauter J.L.: Otoacoustic emissions and the 'set of the center:' a new test battery linking cortex, brainstem and ear. *J Acoust Soc Am* 113, 2198 (2003)
117. Lauter J.L., & C. Ninness: AXS and SOM: a new statistical approach for treating within-subject, time-varying, multivariate data collected using the AXS Test Battery. *J Acoust Soc Am* 114, 25 (2003)
118. Lauter J.L.: The Handshaking Model and the AXS Battery: A new noninvasive approach for studying rostro-caudal relations in the human auditory nervous system. Presented to Association for Research in Otolaryngology, New Orleans LA (2005)
119. Lauter J.L., L.K. Hawkins, L. Gonzales, A. Boring: "Central neurolaryngology" 1: A new test battery for documenting links between the speech motor periphery and the central nervous system in humans. Presented to SouthWest and Rocky Mountain (SWARM) Regional Conference of the American Association for the Advancement of Science, Tulsa OK (2003)
120. Ninness C., & J.L. Lauter: "Central neurolaryngology" 2: A new statistical approach for treating within-subject, time-varying, multivariate data illustrating relations between the motor speech periphery and the central nervous system in humans. Presented to SouthWest and Rocky Mountain (SWARM) Regional Conference of the American Association for the Advancement of Science, Tulsa OK (2003)
121. Lauter J.L., J. Bonomo, S. Abbott: Co-variances in the physiology of cortex, brainstem, and vocal folds. Presented to Annual Conference of the SouthWest and Rocky Mountain (SWARM) regional division of the American Association for the Advancement of Science, Tucson AZ (2005)
122. Lauter J.L., J. Brand, V. Perkins, P. Messina: Individual differences in neural correlates of temporomandibular joint (TMJ) pain. Presented to Symposium on Current Concepts of Pain Mechanisms and Treatment, Oklahoma City OK (1998)
123. Lauter J.L.: Fetal nicotine syndrome (FNS): A new explanation for an old problem. Presented to Symposium on The Neurobiology of Addiction: Neural, Behavioral, and Clinical Features. Oklahoma City OK (1999)
124. Lauter J.L., F. Tucker, K. Hubner: Asymmetries in motor cortex during unimanual and bimanual activation demonstrated with PET. Unpublished laboratory report,

## **EPIC model of functional asymmetries**

University of Tennessee Medical Center at Knoxville  
(1988)

**Key Words:** Functional Asymmetries, Human, Individual Differences, Crossmodal, Multisensory, Touch, Physiology, Visual perception, Auditory perception, Motor control, Space perception, Personal space, EPIC Model of Functional Asymmetries, Trimodal Model of Brain Organization, Psychoimmunoneuroendocrinology, Review

**Send correspondence to:** Judith L. Lauter, Ph.D., Human Neuroscience Laboratory, Dept. of Human Services, 13019 SFA Station, Stephen F. Austin State University, Nacogdoches TX 75965, Tel: 936-468-1252, Fax: 936-468-7096, E-mail: [jlauter@sfasu.edu](mailto:jlauter@sfasu.edu)

<http://www.bioscience.org/current/vol12.htm>