Available online at www.sciencedirect.com
ScienceDirect
Brain and Cognition 66 (2008) 124–139
Brain and Cognition
www.elsevier.com/locate/b&c

Asymmetry and performance: Toward a neurodevelopmental theory

David B. Boles [a,*], Joan M. Barth [b], Edward C. Merrill [a]

[a] *Department of Psychology, University of Alabama, Tuscaloosa, Alabama 35487, USA*
[b] *Institute for Social Science Research, University of Alabama, Tuscaloosa, Alabama 35487, USA*

Accepted 12 June 2007
Available online 30 July 2007

Abstract

Hemispheric asymmetry implies the existence of developmental influences that affect one hemisphere more than the other. However, those influences are poorly understood. One simple view is that asymmetry may exist because of a relationship between a mental process' degree of lateralization and how well it functions. Data scaling issues have largely prevented such investigations, but it is shown that scaling effects are minimized after correction for ceiling and floor effects. After correction, lateralization–performance correlations are pervasive. However, while some correlations are positive, others are negative, with the direction depending on the underlying lateralized process. Two hypotheses are proposed that can account for these relationships by pointing either to individual differences in maturation of the corpus callosum or to developmental limits encountered at different ages of childhood. Their investigation should contribute toward a neurodevelopmental theory of hemispheric asymmetry.

Keywords: Lateralization; Hemispheric asymmetry; Scaling; Performance; Correlation; Visual field; Dichotic; Development; Maturation; Corpus callosum

1. Introduction

Cerebral lateralization research has played an important role in addressing fundamental questions in development. One question is how the developmental specialization of neural networks results in hemispheric asymmetries and another is whether specialization and asymmetries are due to nature or nurture. Implicit in such research is the assumption that performance in many perceptual-cognitive domains is related in an orderly way to the development of lateralization, and that deviations from normative lateralization result in a performance decrement. Across the literature, the most common hypothesis is that greater lateralization is a sign of a more developed brain and is therefore related to better performance. However research examining lateralization–performance relations, most of it performed some years ago, has not always found such relationships (Birkett, 1977; Bryden & Sprott, 1981; Springer & Searleman, 1978). Thus it is not necessarily the case that being highly lateralized provides a performance advantage.

We propose instead that the relation between lateralization and performance, while orderly, is complex. In our view orderliness is brought to these relations by considering the developmental timetable for the emergence and maturation of cognitive or perceptual processes, and how that timetable corresponds to the maturation and plasticity of the corpus callosum during development.

This paper uses a unique approach to develop an explanatory theory by letting the relation between adult performance and lateralization be our guide. A key assumption in our approach is that laterality–performance correlations found in adult populations are consistent with the developmental history of a particular process. Before presenting our research findings on the relations between adult performance and lateralization, we review earlier theories on the development of lateralization, and describe previous research correlating performance and lateralization. Because much of this research, including our own, relies on measurement of perceptual asymmetries we also provide a critical review of scaling issues in these measures.

* Corresponding author. Fax: +1 205 348 8648.
E-mail address: dboles@bama.ua.edu (D.B. Boles).

0278-2626/$ - see front matter © 2007 Elsevier Inc. All rights reserved.
doi:10.1016/j.bandc.2007.06.002

1.1. Invariant and progressive viewpoints on lateralization

One older view of the developmental process by which brain function becomes lateralized is the "invariant" viewpoint. According to this view lateralization unfolds in the same way for every normally developing individual, and is complete by the end of infancy. Thus in the past there was a belief that at birth, or at least very early in life, the human brain is lateralized for motoric functions, language, and emotion processing. It was acknowledged that this picture can be modified somewhat by plasticity, so that for example under special circumstances language processing may "relocate" to the right hemisphere (RH). However, plasticity was held to pertain only to a limited number of cases and to a short period of time in development. Lateralization by this view is essentially "fixed" rather than "progressive" over development (Bryden, 1982; Hiscock, 1988; Kinsbourne, 1997).

In contrast to the invariant viewpoint, the progressive viewpoint states that lateralization develops over time. Lenneberg (1967) maintained that the hemispheres are equipotential in infancy but are lateralized by age 11–14, the result of progressive development. Recent evidence provides support for the progressive viewpoint. For example, the left hemisphere (LH) specialization for speech perception appears to increase during infancy (Werke & Vouloumanos, 2001), and in the early years, there is RH involvement in language acquisition that is less apparent in adults (Bates & Roe, 2001). Other studies using the visual recognition of words have suggested that a developmental transition to LH recognition occurs between the ages of 8 and 10 (Butler & Miller, 1979; Carmon, Nachshon, & Starinsky, 1976; Miller, 1984) and is in place by age 11 (Adair, 2003; Miller, 1981). Additional research indicates that 5-year-old children show similar, but weaker, RH processing of emotions compared to adults (Barth & Boles, 1999; Levine & Levy, 1986).

Further evidence that contradicts the invariant hypothesis comes from the face processing literature. Although there is clear evidence that newborn infants prefer face-like stimuli to non-face-like stimuli, the RH bias in face processing typically found in adults has not been observed until infants are at least 3 months old (De Haan, 2001). Even then the infant system is less specialized than the adult system. ERP components for processing faces do not become adult-like until children are nearly 12 years old, and hemispheric specialization for some aspects of face perception (i.e., inverted faces) shifts as the face processing system becomes refined with development (De Haan, 2001).

Although taken together these studies support a "progressive" lateralization viewpoint, they vary widely on the age at which the brain reaches mature lateralized status. They also do not address whether progressive lateralization is good or bad for performance, or whether this should vary over mental processes, questions central to explaining variation of asymmetry–performance correlations in adults.

1.2. A modular view of brain development

One possible basis for the discrepancy between the invariant and progressive viewpoints is that most studies on brain lateralization development have focused on only one cognitive or perceptual domain at a time. Few studies have entertained the possibility that the developmental timing for lateralization may vary across domains. In particular, if cognitive and perceptual processes are modular in the neuropsychological sense of modularity (independent representation in the brain), lateralization might develop at different ages for different modules. In fact a modular view of brain development is supported by developmental theorizing (Johnson, 1997) and is backed up by extensive factor analytic research with adults showing that lateralized processes are generally independent of one another (Boles, 1998, 2002).

While we support a modular view of mental process representation, as used developmentally it is clear that the concept by itself is not adequate to explain variations across processes. At best it provides a rationale for why such variations might exist. It does not provide insight into their causes.

It seems clear that the invariant and progressive viewpoints, and the modularity viewpoint, suffer from a paucity of hypotheses that might explain how mental processes might vary in their ontogeny. The invariant viewpoint merely states that processes are lateralized at a very early age, not how different processes might be lateralized differently. The progressive viewpoint states that process lateralization can vary over time, and thus opens the door to possible differences between processes, but it provides no basis for predicting that any such developmental differences might systematically affect performance. The modular viewpoint more explicitly states that processes are independent in their lateralization, and opens the door to possible developmental differences, but it lacks specific developmental hypotheses.

We propose that brain lateralization is subject to modification by both experience and maturation and can be influenced by important biological constraints associated with development such as sensitive or critical periods. Therefore brain development can take a different course for different individuals, producing individual differences in lateralization. We also presume that the brain develops on a modular basis, with some processes lateralizing at later developmental periods than others. Hence, any relation between brain lateralization and ability is necessarily a complex one that we expect to vary across both processes and the ages at which processes develop.

1.3. Lateralization–performance correlation in adults

Is it empirically true that the degree of lateralization of a mental process relates to how well it functions? In principle, it should be easy to answer this question by correlating the size of performance asymmetries (e.g., visual field or ear differences in recognizing stimuli) to overall performance (e.g., overall accuracy or reaction time, collapsed over visual field or ear). The use of asymmetry and overall performance measures from the same task means that the same processes are involved in both, so that if lateralization confers a processing advantage, a relationship should be found between the measures.

In practice, however, empirical data on the question of whether lateralization is linked to performance are sparse. This may be because of the early recognition of a scaling issue that can make the measurement of lateralization ambiguous when accuracy measures are used (Birkett, 1977; Bryden, 1982; Colbourne, 1978; Marshall, Caplan, & Holmes, 1975). Although reaction time (RT) data, based on a rational scale, are usually presumed to be free of scaling concerns, studies using accuracy measures predominate in the literature.

1.3.1. Scaling considerations

The gist of the scaling issue is that accuracy measures are potentially subject to ceiling and floor effects, so that respondents who are largely accurate or largely inaccurate at identifying stimuli, cannot in principle show as large a subtractive asymmetry between visual fields or ears as can a subject who shows middling accuracy. A slightly different way to state this is that a given numerical difference between experimental conditions in percent correct is "really" larger or more meaningful when accuracy approaches either perfect or chance levels. For example a RVF – LVF difference of 5% seems highly meaningful when RVF accuracy is 100% and LVF accuracy is 95%, with all of the errors made in the LVF, and less meaningful when RVF accuracy is 53% and LVF accuracy is 48%, with substantial errors made in both visual fields.

Although the scaling issue has been subjected to substantial scrutiny in the lateralization literature, rarely has it been recognized that its actual effect may be more apparent than real. There are three arguments that its effect is often negligible. First, scaling only concerns the *size* of asymmetry, not its *direction*. If some individuals show a visual field or ear difference in one direction, and others show a difference in the other direction, then direction and not just size carries much of the variation between individuals. Another way to state this is that under any scaling system the range of variation within groups of individuals showing either a right-side or a left-side advantage will almost certainly be less than the range of variation between those groups. Thus if the direction of asymmetry is preserved during data analysis the majority of variance between individuals will be captured, and it may be an acceptable practice to simply ignore the scaling issue and to use as a measure of asymmetry a simple subtraction between sides: for example, right visual field (RVF) minus left visual field (LVF), also denoted as RC − LC with "correct" data; and LE − RE with "error" data (Birkett, 1977; Marshall et al., 1975).

Second, several indexes of asymmetry are available that do take into account ceiling and floor effects. The index that is easiest to comprehend is the laterality coefficient (LC; also known as *e*, *f*, and the laterality index), defined as (RCorrect − LCorrect)/(RCorrect + LCorrect) when overall accuracy is less than 50%, and as (RCorrect − LCorrect)/(RErrors + LErrors) when accuracy is greater than 50% (Birkett, 1977; Bryden, 1982). This defines asymmetry as a proportion of the maximum difference that can possibly be obtained at a given level of accuracy. Other indexes that similarly take into account both ceiling and floor effects include the lambda (Bryden & Sprott, 1981) and phi coefficients (Colbourne, 1978; Hellige, Zatkin, & Wong, 1981).

A third argument for discounting the scaling issue is that studies have repeatedly found high correlations among different asymmetry measures, at least when the direction is preserved (Birkett, 1977; Brysbaert & D'Ydewalle, 1990; Hellige, Bloch, & Taylor, 1988; Hellige et al., 1981). These studies have used a variety of measures, including the subtractive difference, LC, lambda, phi, and what have been termed "percent of correct" (POC; defined as RCorrect/(RCorrect + LCorrect)) and "percent of errors" (POE; defined as LErrors/(LErrors + RErrors)) measures. Table 1 reviews the results across the literature. Over studies, the mean correlation among asymmetry measures is in excess of +.90. Clearly, when the direction of asymmetries is preserved, the choice of measure should be of little consequence.

However, previous studies have failed to report the sizes of correlations among measures when direction is *not* preserved: that is, when the absolute value of asymmetry is taken as a measure of asymmetry magnitude. Such values are of interest when experimental hypotheses concern the degree to which an individual is lateralized, irrespective of whether lateralization is to the left or right. When absolute values are used, variability due to direction is removed, and any effects of the scaling method will likely become more important. It appears that only two previous data sets in the asymmetry scaling literature allow this issue to be addressed, those of Bryden (1982) and Birkett (1977). Both presented raw data from individuals that allow recalculations based on magnitude and not direction. In the case of Bryden's data, recalculation shows that the correlation between the subtractive difference and LC falls slightly from +.99 to +.94 when asymmetry direction is not preserved. In Birkett's data, it falls more substantially from +.88 to +.62.

What these considerations indicate is that scaling is not a serious issue when the direction of asymmetry is preserved in an asymmetry measure, as indicated both on theoretical grounds and in studies that have empirically examined correlations between measures. However, when the direction of asymmetry is not preserved, this conclusion is less certain. In such cases a conservative approach would be to avoid the subtractive difference score, which does not account for ceiling and floor effects, and to use one of the indexes that takes those effects into account.

Table 1
Published correlations (r) among asymmetry measures, with asymmetry direction preserved

Study	Measures	Mean r among measures
Birkett (1977)	Dif, LC, POC, POE	+.86
Bryden (1982)	Dif, LC, lambda	+.995*
Brysbaert and D'Ydewalle (1990)	Dif, LC, lambda, phi, POE, 1 other	+.86
Hellige et al. (1988)	Dif, LC, lambda, phi, POC, POE	+.91
Hellige et al. (1981)		
Dichotic task	Dif, LC, phi, POC, POE	+.91
Visual field task	Dif, LC, phi, POC, POE	+.90

Note. Dif, subtractive difference; LC, laterality coefficient; POC, percent of correct; POE, percent of errors.
* Calculated from data provided.

1.4. Previous research on lateralization and performance

Previous research on lateralization and performance has used a variety of asymmetry measures. To maintain a fairly consistent standard and allow comparisons between studies, the laterality coefficient (LC) measure is used here wherever possible. Some studies, however, have not reported LCs but have used measures that likewise take into account ceiling and floor effects, and those have been included as functionally equivalent. Such studies include those of Bryden and Sprott (1981, lambda measure), Springer and Searleman (1978, phi measure), and Wexler and Halwes (1985, POC, which in that particular study was functionally equivalent to LC since mean accuracies were much less than 50%).

Table 2 presents correlations between accuracy and asymmetry, preserving direction. It appears, first, that accuracy and asymmetry do sometimes correlate significantly, and at surprisingly high levels: for example, $r = +.62$ and $+.48$ (Wexler & Halwes, 1985), $r = +.45$ (Hellige et al., 1981), and $r = -.43$ (Birkett, 1977). Second, there appears to be some order to the results. Tasks using dichotic presentations of language-related stimuli, using what has been termed the "auditory linguistic process" (Boles, 1996, 1998; Boles & Pasquarette, 1996), frequently produce at least marginally significant positive correlations between accuracy and asymmetry (Hellige et al., 1981, 1988; Wexler & Halwes, 1985). Tasks using visual stimuli of any type have not produced positive correlations, and in the case of dot localization (using what has been called the "spatial positional process"; Boles, 1991, 2002) a significantly negative correlation has been reported (Birkett, 1977).

These outcomes are consistent with two alternative interpretations. One is that the direction and degree of relationship between lateralization and performance is process-dependent, so that (for example) tasks using the auditory linguistic process show a positive correlation and those using the spatial positional process show a negative correlation. Alternatively, there may be a modality difference such that auditory tasks tend to produce positive correlations and visual tasks null or negative ones. In either case, something important seems to be at work that has not been adequately investigated. Lateralization not only seems to relate to performance in some situations and not others, but there are suggestions that it does so in a lawful manner.

None of the previously reported results have dealt with absolute measures of asymmetry, however. Such measures, ignoring sign, are of particular relevance to the question of whether lateralization aids performance, because a logical hypothesis might hold that it is only the degree to which an individual shows lateralization that should affect performance, not whether lateralization is to the left or right.

This hypothesis is implied by several existing theoretical positions on the causes of lateralization. What might be called the "control hypothesis" states that lateralization came about to resolve hemispheric conflict over the control of unitary mechanisms, such as limbs (Orton, 1937), the vocal apparatus (Bryden, 1982; Segalowitz & Gruber,

Table 2
Correlations reported in previous studies between accuracy and asymmetry preserving direction

Study	Stimuli/task	r*	$p<$
Birkett (1977)	Visual dot localization	−.43	.05
Bryden and Sprott (1981)	Dichotic syllable recognition	−.13***	NS
	Visual nonword recognition	−.01***	NS
Hellige et al. (1981)	Dichotic syllable recognition	+.45	.005
	Visual word recognition	−.01	NS
Hellige et al. (1988)	Dichotic syllable recognition	+.17	.10
	Visual lowercase syllables	−.04	NS
	Visual uppercase syllables	+.06	NS
Springer and Searleman (1978)**	Dichotic syllable recognition	−.01	NS
Wexler and Halwes (1985)**	Dichotic word recognition	+.48	.01
	Dichotic syllable recognition	+.62	.001
	Dichotic nonword nonword	+.29	NS

Note. The laterality coefficient (LC) was used unless otherwise noted.
* + sign reflects increasing LH asymmetry as performance increases.
** Used a measure functionally equivalent to LC.
*** Calculated from data provided.

1977), or attention (Nottebohm, 1984). Presumably the conflict should be resolvable regardless of whether control falls to the LH or RH. Similarly, what can be called the "representational capacity" hypothesis states that lateralization came about to eliminate redundancies between the two hemispheres, such as in the representation of memories (Doty & Overman, 1977) or processes (Kertesz & Naeser, 1994). Here too the issue of whether lateralization is to the left or right seems irrelevant. And so it goes: the "cognitive incompatibility" hypothesis states that lateralization occurs because two sets of processes are incompatible with one another (Levy, 1974), and the "multitasking" hypothesis states that lateralization allows the simultaneous execution of different processes in the two hemispheres (Wickens, 1984). Again under these hypotheses the important aspect is the segregation of processes between hemispheres, not the assignment of a process to the left versus right.

All of these hypotheses, then, predict that better performance should accompany increasing lateralization in an absolute, not just a directional sense. Individuals who are highly lateralized to the left *or* to the right should show better performance than individuals who are less so. Yet in spite of the theoretical strength of this prediction, the literature is virtually silent on it.

What is needed to answer the lateralization–performance question more adequately is a large-scale study involving several lateralization measures and many participants. In addition, it would be desirable to include reaction time measures, for they should be less susceptible to the potential scaling problems seen in accuracy studies. Such a data set would allow the question to be addressed from the perspective of multiple tasks and measures, and it should make it possible to determine whether directional or absolute asymmetry is a better predictor of performance.

1.5. Basis for a large-scale study

As it happens, a large-scale data set with a large sample size is available which can be analyzed to address these issues. We have assembled a sample of 789 right-handed adults from a number of reaction time and correlational studies performed in our laboratory (Boles, 1991, 1992a, 1996, 1998, 2002), representing about two dozen tasks that show significant or marginally significant asymmetry. Sample sizes for individual tasks vary from less than 50 to nearly 600. Use of this large sample has proven useful in such applications as demonstrating a "clean" factor structure that accurately reflects patterns of correlations among paired asymmetries (Boles, 1998) and differentiating between multiple lateralized spatial processes (Boles, 2002).

Based on factor structure, it is possible to identify a Modular Asymmetric Process Set (MAPS) consisting of lateralized tasks that each tap into a particular modular process that is independent or nearly so from all other processes in the set (Boles, 1996, 2002). Table 3 shows a description of MAPS as presently constituted, and gives examples of tasks that appear to use each lateralized process.

A portion of these tasks are now directed to the question of the relationship, if any, between lateralization and performance. We show, first, that such relationships are in fact pervasive. However, they by no means always favor a positive relationship, and the direction of relationship depends on the lateralized module. Finally, we show that there seems to be a relationship between the direction of the lateralization–performance relationship and the age at which the module becomes lateralized. In accounting for these results, we suggest the involvement of a commonly ignored component of the developing brain, the maturing corpus callosum, in interaction with the timing of lateralization.

2. Method

2.1. Participants

The participants were 789 college-age right-handers, 76% male, reflecting the predominantly male population

Table 3
The modular asymmetric process set (MAPS)

Process	Hemisphere	Task examples
Auditory emotional	Right	Dichotic emotion recognition
Auditory linguistic	Left	Dichotic word, syllable, or digit recognition
Facial figural	Right	Forced-choice selection of chimeric faces based on resemblance or happiness
Facial motive	Right	Judged mobility of eye winks
Planar categorical	Left	Above–below judgment
Spatial attentive	Right	Visual line bisection
Spatial emergent	Right	Figure-ground judgment of overlapped forms
Spatial concentrative	Right	Forced-choice selection of chimeric high-density dot fields based on numerosity
Spatial positional	Right	Dot location recognition
Spatial quantitative	Right	Bargraph or dot cluster enumeration
Tactile figural	Right	Tactile form recognition
Visual lexical	Left	Visual word, letter, or multiple digit recognition
Visual phonetic	Left	Rhyme judgment
Visual temporal	Left	Onset judgment

of the institute from which most were recruited. In all cases the participants wrote with the right hand, and nearly all (728) completed the Edinburgh handedness inventory (Oldfield, 1971) that confirmed their right-handedness for a broader range of manual activities (except for 2 participants with a completely neutral preference on the questionnaire, and one with a slight left preference). The college students participated over a period of about 10 years in individual factor analytic and correlational studies in the first author's laboratory. Included were participants from all studies involving three or more tasks that produced significant or marginally significant asymmetry, which included nine previously published factor analytic studies (Boles, 1991, 1992a, 1996), five previously published correlational studies (Boles, 2002; Boles & Pasquarette, 1996), and one small unpublished correlational study.

The decision to focus on right-handers was made at the outset of the studies in order to allow the identification of tasks showing performance asymmetries in the majority of the population. Not including left-handers may reduce variability in asymmetry, resulting in somewhat lower correlations between asymmetry and performance than might otherwise be obtained. However, this effect is probably not very large given that left-handers comprise only about 10% of the population and show differences from right-handers in asymmetry that tend to be subtle (e.g., Boles, 1989).

2.2. Task selection

A large variety of lateralized tasks were included in the 15 studies. However, a number of these proved unsuitable for present purposes because they (a) failed to show a significant population-wise asymmetry, a possible sign of an invalid lateralized task, (b) showed low reliability, (c) had relatively small sample sizes, or (d) produced a preference or bias score with no corresponding performance measure (for example, the much-used chimeric faces test produces a preference for faces smiling on one side or the other, but preferring one side says nothing about the ability to detect smiles). Thus for present purposes, tasks were first selected to afford both a performance measure and significant population-wise asymmetry. Second, the asymmetry measures were screened for acceptable reliability, defined as in Boles (1998, 2002) as a *minimum* Spearman-Brown-corrected test–retest or odd–even reliability of 0.30. Third, the measure had to have a minimum sample size of 100 to be included, in order to provide adequate power for assessment of lateralization–performance correlation. Given a sample size of 100 and an alpha level of .05, there is 80% power to detect a population correlation of .28, and the 95% confidence interval around a sample correlation (r) of zero is approximately $\pm.20$. A total of 12 tasks, one asymmetry measure from each, were selected using these criteria.

2.3. Apparatus, stimuli, and procedure

Eight of the 12 tasks (Bargraphs, Crosslines, Locations, Naming, Occlusions, Typing, Visual digits, and Visual words) used stimuli presented visually in monochrome (usually in blue but sometimes in white) against a dark background, controlled by an Apple-II-series computer running the Apple-Psych system of experimental software (Barnes & Burke, 1988; Osgood, 1988). The computer collected responses and timed manual reaction times (RTs) with millisecond accuracy in tasks calling for it. For all RT tasks, the task instructions emphasized both speed and accuracy, and in manual RT tasks, the response keys were arrayed with one toward and one away from the subject, with one hand on each key and the hand assignments balanced across participants.

All 8 tasks used a central arrowhead ("<" or ">") pointing to one side of a bilateral display of stimuli, the stimuli being paired randomly within a task. This indicated to the subject which stimulus to recognize and respond to. Bilateral displays were used because they have been found to provide larger, more significant, and more reliable asymmetries than unilateral displays (Boles, 1983, 1987, 1990, 1995; Olk & Hartje, 2001; Rayman & Zaidel, 1991).

The remaining 4 tasks (Dichotic digits, Dichotic emotions, Dichotic syllables, and Dichotic words) used tape-recorded presentations of stimuli, with different simultaneous inputs to the two ears. A miniature stereo cassette player and stereo headphones were used to present the stimuli. For Dichotic digits and Dichotic words, the subject called out the recognized stimuli and the responses were manually recorded by the experimenter using prepared answer sheets. For Dichotic emotions and Dichotic syllables, the subject circled what they recognized on answer sheets showing the possible stimuli. Details of each task follow.

2.3.1. Bargraphs

Bargraphs showing whole numbers from 1 to 8 were used, except for a small study included in the sample that used whole numbers from 1 to 6 (Boles, 1991, Pilot study). A bargraph consisted of a vertically-oriented rectangle plotted against unlabeled horizontal reference lines at the 0, 4, and 8 levels (see Boles, 1986b, for an example). It subtended a visual angle of 2.7° by 7.9° horizontally by vertically, with eccentricity from fixation to the near edge of 2.6°. A trial consisted of a central fixation cross presented for 750 ms, followed by a 100 ms blank, and then a 100 ms stimulus display (50 ms in the pilot study). The subject decided whether the bargraph to be recognized represented an odd or even number, and pressed a RT key accordingly. Feedback consisting of the RT or the word "Error" was given. After 24 practice trials, 144 experimental trials were administered in 3 blocks of 48. This task provides a RT asymmetry for each subject, calculated as median LVF RT – median RVF RT using trials with correct responses.

2.3.2. Crosslines

The Crosslines task involved judging whether a laterally presented horizontal line segment was presented above or below the central fixation cross. The 1.1° by 0.2° line segment appeared either 1.6° above or below the center of the cross, with eccentricity of 2.1° as measured from the fixation meridian to the near edge. Trials presented a 750 ms central fixation cross and a 100 ms blank period, followed by a stimulus display for 100 ms, and the subject responded by pressing a key labeled "TOP" or "BOTTOM" to indicate the relative position of the line. After 24 practice trials, 144 trials were given in 3 blocks of 48. This task likewise provides a RT asymmetry for each subject, calculated as median LVF RT – median RVF RT using trials with correct responses.

2.3.3. Dichotic digits

The tape used (DK Consultants, Canada) presented 2 practice followed by 24 experimental trials, most of which consisted of 3 dichotic digit pairs per trial in rapid succession. Numbers from 1 to 10 were the stimuli. Following a trial the subject vocally reported as many digits as possible in any order. After the 24 trials, the headphones were reversed and another run was administered. Although the task provides both error and report order measures of asymmetry (Boles, 1991, 1998), here the error measure was judged more suitable since it is conceptually more closely linked to the total number of errors for purposes of the performance–lateralization correlation. It is calculated as left ear error percentage minus right ear error percentage, with errors defined as omissions.

2.3.4. Dichotic emotions

Stimuli were brief (approximately one second) sentences with neutral verbal content (e.g., "This is for you.") crossed orthogonally with angry, bored, distressed, or happy tones of voice. The tape consisted of 24 dichotic pairs, with a different emotion presented in each ear, and with the participant circling the emotions heard on a prepared response sheet. After a run, the headphones were reversed and the tape replayed. Responses were assumed correct if they matched emotions that were presented: for example, if bored and happy emotions were presented, and the responses were "bored" and "angry", it was assumed the bored emotion had been correctly perceived. Asymmetry was calculated as left ear error percentage minus right ear error percentage.

2.3.5. Dichotic syllables

Pairs of syllables (/ba/,/da/,/ga/,/ka/,/pa/, and /ta/) were presented dichotically, with 30 pairs constructed pseudorandomly. Participants listened to each trial and circled their answers on a prepared answer sheet. Following the 30 trials, the headphones were reversed and the tape replayed. Asymmetry was calculated as left ear error percentage minus right ear error percentage.

2.3.6. Dichotic words

Pairs of one-syllable words were presented dichotically, with four pairs presented per trial (DK Consultants, Canada). Participants attempted to recall all words orally, and the experimenter marked correct responses on a prepared answer sheet. After 10 trials, the headphones were reversed and the 10 trials repeated. Asymmetry was calculated as left ear error percentage minus right ear error percentage.

2.3.7. Flashes

A light patch was flashed on the computer screen, and participants pressed a key on the same side. The patch subtended 3.8° by 4.8°, at 3.9° minimum eccentricity. A trial consisted of a central fixation cross for 750 ms, followed by a 100 ms blank, and a 100 ms stimulus. After 24 practice trials, 144 trials were given in blocks of 48. RT asymmetry was calculated as median LVF RT – median RVF RT using trials with correct responses.

2.3.8. Locations

A lateralized dot was presented on the computer screen to each side of fixation, appearing in one of 12 locations per visual field, along with a central arrowhead indicating the location to be recognized. Participants subsequently attempted to locate it on a centrally presented grid, mapping each visual field onto it, and typed a corresponding letter code into the console. The 3×4 grid of possible locations in each field measured 4.5° by 5.9° horizontally and vertically, at 3.4° minimum eccentricity, with a dot measuring 0.3° square. A trial consisted of a central fixation cross presented for 750 ms, followed by a 100 ms blank, a 100 ms stimulus display, an approximately 800 ms blank, and then the central letter grid (which remained until response). There were 24 practice and 144 experimental trials. Asymmetry was calculated as left visual field error percentage minus right visual field error percentage.

2.3.9. Naming

A word name of a number (e.g., ONE) was presented in each visual field, with a central arrow head at fixation indicating the word to be recognized and pronounced aloud as quickly as possible. The numbers ONE through EIGHT were used. Words subtended 0.4° horizontally and between 2.0° and 3.3° vertically, at 1.6° minimum eccentricity. A trial involved the same timeline as the Crosslines task. One practice block of 24 trials was followed by 144 experimental trials. A voice recognition board (Boles, 1988) recognized and timed the subject's responses, having been pretrained to recognize them. Feedback was given, consisting of the trial's RT or the word "ERROR". Asymmetry was calculated as median LVF RT – median RVF RT using trials with correct responses.

2.3.10. Occlusions

After a 750 ms fixation cross and a 100 ms blank, a pair of bars were presented in each VF for 100 ms, simultaneously with an arrowhead at fixation indicating the pair to recognize. One bar in each pair was horizontal (3.9° × 1.6°) and the other was vertical (1.3° × 5.0°). One bar (selected at random) was blue while the other was red; and one (also selected at random) partially overlaid or occluded the other, thereby appearing to be the foreground bar in a cross (+) with the other bar in the background. The subject pressed one of two RT keys labeled "BLUE" or "RED" to indicate the bar appearing to be in the foreground. A block of 24 practice trials was used, followed by 144 total experimental trials. Asymmetry was calculated as median LVF RT – median RVF RT using trials with correct responses.

2.3.11. Typing

A 3-letter word from a set of 18 was presented vertically in each visual field, with an arrowhead at fixation indicating the one to be recognized. Words subtended 0.6° by 2.7° horizontally and vertically, with a 3.5° minimum eccentricity. A trial involved a 750 ms fixation box, followed by a 100 ms blank, a 133 ms stimulus display, another 100 ms blank, and then a masking display of Xs in the letter positions for 133 ms. The subject attempted to type the word into the console at their own pace. No practice preceeded the 72 experimental trials. All letters of a word had to be correctly typed in the proper order for a word recognition to be scored as correct. Asymmetry was calculated as LVF error percentage minus RVF error percentage.

2.3.12. Visual digits

This task was identical to the Typing task, except that strings of 3 digits were generated randomly, on a trial-wise basis, in place of the 3-letter words. Asymmetry was calculated as LVF error percentage minus RVF error percentage.

2.3.13. Visual words

This task was identical to the Naming task, except participants pressed one of two RT keys to indicate whether the number was "odd" or "even". A block of 24 practice trials was given, followed by 144 experimental trials. Asymmetry was calculated as median LVF RT – median RVF RT using trials with correct responses.

3. Results and discussion

As indicated in the introduction, the possibility that it is absolute and not directional asymmetry that correlates more highly with performance argues for avoiding subtractive asymmetries based on accuracy measures (e.g., LVF – RVF) in favor of an index that corrects asymmetry for ceiling and floor effects. Accordingly as an initial step in the data analysis, all asymmetries based on accuracy were converted to laterality coefficients (LC) as the easiest-to-understand (and probably most used) index. Asymmetries based on RT were not converted because ceiling and floor effects are presumably minimal for RT data, which are measured on an essentially unbounded ratio scale.

Next, asymmetries of either type (LCs or RTs) were correlated to performance collapsed over side of presentation. For accuracy measures, overall performance was the percent correct on the left and right sides. For RT measures, overall performance was the average of RTs on the two sides. Both directional asymmetries and absolute asymmetries (ignoring sign) were then checked for correlation to overall performance. The results appear in Table 4, showing the size of each correlation and its significance as well as a test of the difference between the absolute and directional correlations, using the z statistic for dependent samples provided by Glass and Stanley (1970, p. 313). Tasks and measures are organized in the table according to the lateralized process believed to underlie them (Boles, 1996, 2002).

Several generalizations emerge from the results. First, significant correlations between asymmetry and performance are the rule rather than the exception. Across the 13 measures, 11 correlations were significant based on absolute asymmetry, and 7 were significant based on directional asymmetry. Second, as implied by this count, there is strong evidence that absolute asymmetry is a better predictor of

Table 4
Correlations of absolute and directional asymmetry to overall performance

Process/task	Absolute *r*	Directional *r*	*N*	*Z*
Auditory emotional process				
Dichotic emotions task (%C)	+.13	−.04	162	1.40
Auditory linguistic process				
Dichotic digits task (%C)	+.19***	−.06	388	1.63
Dichotic syllables task (%C)	+.42***	+.31**	118	1.99*
Dichotic words task (%C)	+.25***	+.29***	404	1.12
Planar categorical process				
Crosslines task (RT)	−.36***	−.31***	165	.70
Spatial emergent process				
Occlusions task (RT)	−.56***	+.37***	161	3.69***
Spatial positional process				
Locations task (%C)	+.26***	−.18***	598	2.06*
Spatial quantitative process				
Bargraphs task (RT)	−.37***	+.16***	527	5.85***
Visual lexical process				
Naming task (RT)	−.18	−.14	106	.55
Typing task (%C)	−.14**	+.19***	405	.80
Visual digits task (%C)	−.25***	−.04	220	3.00**
Visual words task (RT)	−.28***	.00	495	3.88***
Process undefined				
Flashes task (RT)	−.30**	−.18	102	1.33

Note. *Z*-test is for the difference between absolute value and directional asymmetry (based on their absolute values). Positive correlations indicate performance improved either as asymmetry increased (absolute asymmetry), or as asymmetry shifted toward the LH/away from the RH (directional asymmetry).
* $p < .05$.
** $p < .01$.
*** $p < .001$.

performance than directional asymmetry. Thus in 6 of the 13 tasks, absolute asymmetry produced significantly higher correlations than did directional asymmetry, and in 11 there was at least a trend in that direction. Indeed, directional asymmetry was a significantly better fit in none of the tasks.

To test the sensitivity of these results to possible outliers, the correlations were rechecked after dropping up to 1% of cases from each end of the distribution of each of the performance, absolute asymmetry, and directional asymmetry variables. Values were dropped from each end up to the point that the 1% value would be exceeded. Reanalysis of these data indicated that in 4 of the 13 tasks, absolute asymmetry was a significantly better predictor while directional asymmetry was a better predictor in none. Furthermore all but one of the 11 trends (of 13) that favored absolute asymmetry continued to favor it, with the one exception resulting in a tied correlation between absolute and directional asymmetry. Thus while there was a small reduction of trends as might be expected from the restriction of range, the overall pattern remained very similar and lends confidence that the results are reasonably robust with respect to possible outliers.

A third generalization from the results is that in spite of widespread correlations between asymmetry and performance, they bear no *simple* relationship to one another. Taking the absolute correlations as being of primary importance (given the second generalization), some correlations were robustly positive while others were robustly negative. What this means is that one cannot assume that performance increases as lateralization increases; it may in fact decrease depending on the task and measure.

However, a fourth generalization is that the relationship between asymmetry and performance appears to be lawful if taken from the perspective of particular lateralized processes. Of the 3 tasks believed to use an auditory linguistic process, absolute asymmetry correlated to performance in a *positive* direction all three times, indicating that as asymmetry increases (toward either hemisphere), performance also increases. In contrast, of 4 tasks using a visual lexical process, absolute asymmetry correlated to performance in a *negative* direction all 4 times (3 significantly so). In these cases, as asymmetry increases, performance decreases. Thus it appears that if an explanation is to be sought for relationships between asymmetry and performance, the explanation needs to invoke the lateralized process as the basic unit determining the direction of a relationship.

To better visualize these relationships, scatterplots were made of asymmetry versus performance (Fig. 1, with the panels reflecting the order of tasks as given in Table 4). The asymmetry variables are shown in their directional form to allow more complete visualization. Nondirectional asymmetry can be visualized by imagining each figure folded left-over-right at the zero point on its X axis. In interpreting the figures, it should be kept in mind that many of the points represent multiple participants with one participant's point overlaying others. The points in the scatterplots generally support the notion that performance either decreases or increases, depending on the task and thus presumably the lateralized process, as lateralization increases in either direction from zero. The fitted curves shown in Fig. 1 are for descriptive purposes only and represent best-fitting second-order polynomial functions. This type of function was selected because it has reversing limbs that illustrate why absolute asymmetry values tend to perform better than directional ones. No representation is made that they necessarily fit better than other possible functions.

We should note that a number of design differences between the tasks bear only modest relationship to whether the absolute correlations were positive or negative. Thus positive correlations were found for both auditory and visual tasks (e.g., Dichotic syllables and Locations), for both "left" and "right" hemisphere tasks as defined on a population basis (e.g., Occlusions and Locations), and for both divided and focused attention tasks (e.g., Dichotic syllables and Locations). Negative correlations were found for both RT and accuracy measures (e.g., Occlusions and Visual digits), and for both bilateral and unilateral displays (e.g., Occlusions and Flashes). To be sure, some of these distinctions fit better than others, but none of the distinctions fit all of the data.

4. Integration of developmental and adult research: Toward a neurodevelopmental theory

The most striking aspects of the present results are the pervasiveness of correlations between absolute asymmetry and performance, and their variation in direction as a function of the underlying lateralized process. Thus while asymmetry–performance correlations are commonplace, they do not support the view that a high degree of lateralization inherently confers a performance advantage. Strong lateralization is associated with increased performance for some processes (e.g., the auditory linguistic and spatial positional processes), but not for others, where strong lateralization is associated with decreased performance (e.g., the planar categorical, spatial emergent, spatial quantitative, and visual lexical processes). While such negative correlations may seem surprising, there is a precedent in research on gifted populations, where high ability has sometimes been linked to reduced asymmetry in task performance (O'Boyle et al., 2005).

Yet the sheer pervasiveness of lateralization–performance correlations, even though they vary in direction, suggests they do provide important information regarding the *why* of hemispheric asymmetry. It is not that lateralization is irrelevant to performance. To the contrary it is quite relevant, but its relevance is to be sought at the level of specific lateralized processes rather than among all processes generally.

The question, of course, is why asymmetry correlates positively to performance for some processes in the MAPS battery, while other processes show negative correlations. Because such task design factors as modality, predominant hemisphere of representation in the population, type of attentional demand, dependent measure, and type of stimulus display bear only modest relationship to the direction of correlation, the answer probably lies less in design factors than in the nature of cerebral lateralization itself. In reviewing possible causes of this variation, we have identified a

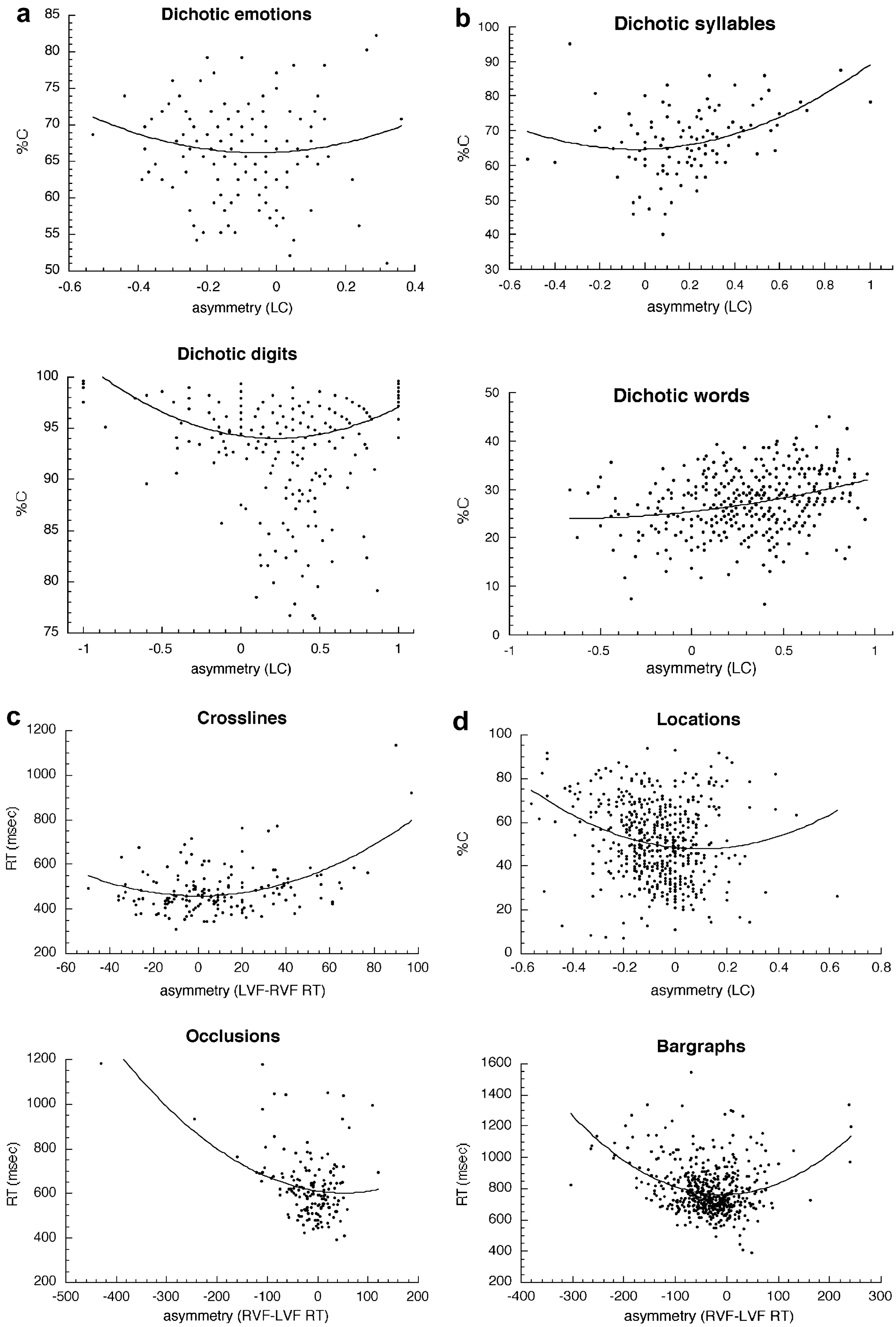

Fig. 1. Scatterplots of directional asymmetry versus performance, with best-fitting second-order polynomial functions. (a) Dichotic emotions and Dichotic digits; (b) Dichotic syllables and Dichotic words; (c) Crosslines and Occlusions; (d) Locations and Bargraphs; (e) Naming and Typing; (f) Visual digits and Visual words; and (g) Flashes.

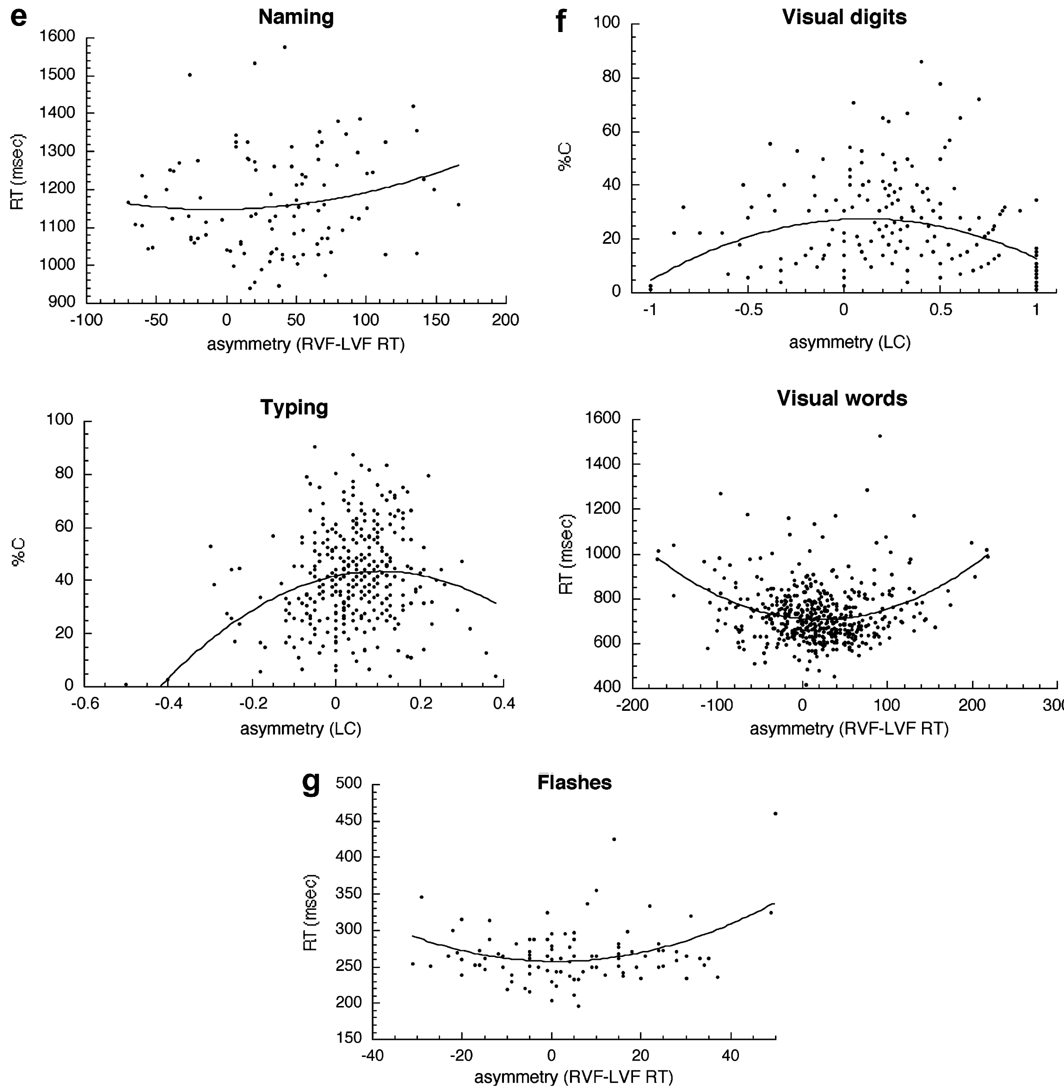

Fig. 1 (*continued*)

possible linkage to the age at which population-wise lateralization is experimentally detectable for particular processes or modules. The linkage in turn suggests a hypothesis for how the timing of neural development translates into differing patterns of process lateralization as well as lateralization relationships to performance. We first briefly discuss relevant developmental work and then present the hypothesis.

4.1. The development of modular lateralization

In this section we focus on the development of cerebral lateralization for those processes in Table 4 that show a significant correlation between absolute asymmetry and performance, whether positive or negative. Processes showing nonsignificant correlations are not included because it cannot be ascertained whether the corresponding population correlations are truly positive, negative, or null. We have also not included processes for which we can find no developmental literature on hemispheric asymmetry, such as the spatial emergent process. As an aid to exposition, Table 5 presents the included processes and for each, the major conclusion as to when lateralization is first detectable on a population basis.

Table 5
Developmental timing of lateralized process and absolute asymmetry–performance correlations

Process	When lateralization is first detectable	Correlation
Auditory linguistic	At birth	+.29
Spatial quantitative	By age 5 years	−.37
Planar categorical	By age 5 years?	−.36
Visual lexical	Between 8 and 11 years	−.22
Spatial positional	Between 14 and 18 years	+.26

Note. In cases where processes are represented by more than one measure correlations are means calculated using the *r*-to-*Z* transformation and back transformation.

4.1.1. Auditory linguistic process

Of the processes showing significant asymmetry–performance correlations, the auditory linguistic process may be the earliest to lateralize. Lateralization is typically measured with dichotic presentations of stimuli that have linguistic but not necessarily semantic content, for example digits and other words but also syllables. Such stimuli typically produce strong right ear or LH advantages in recognition (Boles, 1996, 1998), and as we have found in the current results, significantly positive correlations between absolute asymmetry and performance (Table 4).

Seminal work by Molfese (1977) and Entus (1977) demonstrated that language processing that is located in the LH on a population basis may be found for auditory linguistic materials in infancy, with Molfese finding it even in premature infants averaging 36 weeks of gestational age (Molfese & Molfese, 1980). While these conclusions were based on auditory event-related potentials (AERs), and in the case of Entus a measure of nonnutrive sucking, further research has reported right ear advantages in dichotic paradigms in children as young as can be tested, about 2–1/2 years of age (Hiscock, 1988).

Furthermore, the degree to which LH components are discriminable in AERs at birth predicts language performance 3 years later (Molfese & Betz, 1988). This may be a foreshadowing of the positive performance–asymmetry correlation found here in adults, and it yields some indication of developmental stability in interpreting experimental results from the earliest stages of life.

4.1.2. Spatial quantitative processing

Spatial quantitative processing has been investigated by laterally presenting bargraphs or dot clusters, typically with values of 1–8, with participants asked to recognize the value of the bargraph or the number of dots. In our work we have used two randomly-selected bargraphs presented bilaterally, with an arrowhead at fixation indicating the one to be recognized, followed by the subject responding on keys labeled odd or even. Under such conditions a LVF or RH advantage is usually found (Boles, 1991, 1998, 2002; Eviatar, 1997).

Developmental research on spatial quantitative processing is sparse, but there are suggestions of relatively early lateralization. Young and Bion (1979) used dot clusters with children ages 5, 7, and 11, and reported a general LVF (RH) superiority that did not interact with age. Adair (2003) used bargraphs with a middle school sample (ages 11–14) and similarly found a LVF advantage. Together the results suggest that lateralization of spatial quantitative processing is detectable by at least age 5.

4.1.3. Planar categorical processing

Categorical processing in the *X–Y* plane is usually investigated by asking participants to judge above–below or left–right relationships between two objects such as a dot and a line. Typically a RVF (LH) advantage is obtained in RT or accuracy (Hellige & Michimata, 1989; Kosslyn et al., 1989; Okubo & Michimata, 2002; Servos & Peters, 1990). We have found this effect when asking participants to judge the "above" or "below" relationship of a short line segment relative to the fixation point (Boles, 2002).

Koenig, Reiss, and Kosslyn (1990) conducted a developmental study of planar categorical processing and found some evidence of a LH advantage by age 5. Inclusion of results from an above–below judgment task with a distance-judgment task resulted in a significant task by VF interaction consistent with a RVF advantage in the categorical task and a LVF advantage in the distance-judgment task. However, neither asymmetry was significant when considered alone, and the interaction changed with practice. Although these results are not conclusive, they suggest that planar categorical processing may be left lateralized by age 5.

4.1.4. Visual lexical processing

Studies investigating visual lexical processing have typically presented words, multiple digits, or letters to one visual field, or bilaterally using different stimuli in the two fields, requiring recognition. We generally use bilateral displays with an arrowhead at fixation indicating which stimulus to recognize, and under these conditions find a robust right visual field or LH advantage (Boles, 1991, 1992a, 1996, 1998, 2002). Matching tasks, particularly those involving letters, are less useful in that they less often reveal asymmetries, probably because they can be performed by processes other than language ones (Boles, 1981, 1986a, 1992b; Boles & Eveland, 1983).

Developmentally, there are indications that visual lexical processing fails to show LH lateralization for the first few years of life. Using children as young as 5–1/2 years old, Carter and Kinsbourne (1979) and Kershner, Thomae, and Callaway (1977) showed that visual field asymmetry for multiple digit recognition was determined by the material (verbal or nonverbal) shown at fixation. Such effects are sometimes found in adults for lateral stimuli such as shapes that can be processed by both hemispheres (Hines, Glista, & Byers, 1985), but not for stimuli that call for asymmetric processing such as words or faces (Hines, 1978; Moscovitch & Klein, 1980), suggesting that the young children in the studies did not use an asymmetric process in performing the digit recognition task. Other studies using the recognition of words have suggested that a developmental transition to LH recognition of visual lexical stimuli occurs at about age 8–10 (Butler & Miller, 1979; Carmon et al., 1976; Miller, 1984) and is in place by age 11 (Adair, 2003; Miller, 1981).

4.1.5. Spatial positional processing

Presenting a dot in one VF and requiring that its location be subsequently stated or reproduced has typically resulted in a LVF (RH) advantage in college-age adults (Kimura, 1969; Levy & Reid, 1976). In our work dots are presented bilaterally with an arrowhead at fixation indicating the one to be localized, and the resulting LVF advantage is one of the most reliably replicated asymmetries that has emerged from our laboratory (Boles, 1991, 1992a, 1996, 2002).

Within this context, the one study that used younger participants produced strikingly different results. Adair (2003), working in our laboratory, found no tendency toward a visual field difference in her 11–14-year-old middle school students, either as a main effect or in interaction with group (control vs. ADHD). Though these results are obviously limited in scope, they suggest that spatial positional processing in the bidimensional X–Y plane is a late-lateralizing process.[1]

4.2. Two developmental hypotheses

Examination of the major conclusions of the developmental review in Table 5 suggests that both very early and very late-lateralizing processes evince positive correlations between absolute asymmetry and performance in adults. Thus the auditory linguistic process shows detectable lateralization at birth as well as a positive correlation between absolute asymmetry and performance. The spatial positional process appears not to show detectable lateralization until late adolescence or young adulthood, and likewise shows a positive correlation.

In contrast, processes lateralizing at intermediate ages show negative correlations between absolute asymmetry and performance in adults. This is most convincingly shown by the visual lexical process, which fails to show detectable lateralization until sometime between 8 and 11 years. Two other processes, the spatial quantitative and planar categorical processes, are potentially consistent with the conclusion in that lateralization has not been demonstrated for either before age 5, although it is also true that younger children have not been tested. It nevertheless is difficult to believe that lateralization would occur as early for these as for the auditory linguistic process, simply because the processes are not as developmentally urgent or emphasized.

What can account for the apparently U-shaped function relating age of lateralization to correlations between performance and absolute asymmetry? Although we have no additional evidence bearing on its cause, we can describe two possible mechanisms that may help advance the inquiry toward a neurodevelopmental theory.

The simplest mechanism we have been able to devise, which we refer to as *the maturity hypothesis*, is based on individual differences in rate of maturation of the corpus callosum. It assumes, first, that the extent to which a process becomes lateralized in an individual depends on the efficiency of commissural transfer of information. If the corpus callosum is immature, transfer will be slow and error-prone (Fagard, Hardy-Léger, Kervella, & Marks, 2001; Joseph, Gallagher, Holloway, & Kahn, 1984; O'Leary, 1980; Quinn & Geffen, 1986), making a highly lateralized process more efficient than one distributed between hemispheres. However, if the corpus callosum has reached a sufficient level of maturity, allowing rapid and accurate transfers, a process that is distributed across homologous locations between hemispheres may be more efficient than one distributed in fragments within a single hemisphere. The important part of the assumption is that an immature callosum results in a lateralized process, while a more mature callosum results in a less lateralized one.[2]

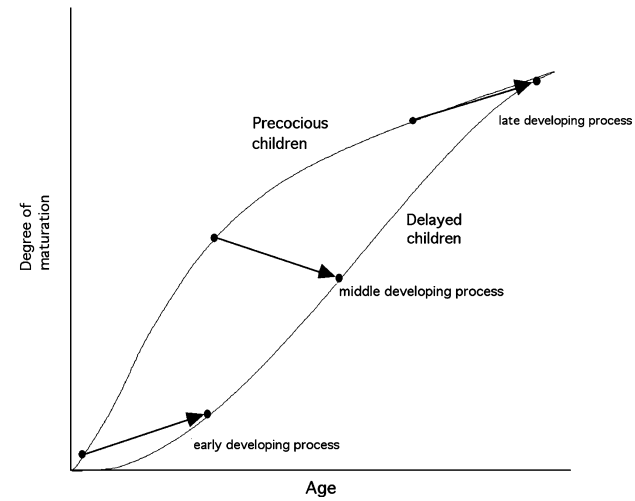

Fig. 2. The effects of delay in development according to the maturity hypothesis, showing the difference between advanced and delayed children. The degree of maturation of the corpus callosum is plotted against chronological age. Each arrow reflects a delay in development of a constant value, for early developing, middle developing, and late-developing processes.

The second assumption needed to generate the U-shaped pattern is that developmentally advanced children on the one hand, and developmentally delayed children on the other, are similar at both the beginning and end of development of the callosum, but differ in the rate at which the end points are reached. Fig. 2 illustrates this pattern, with the difference between curves exaggerated for the purpose of explication.

Now consider a process that develops very early (e.g., the auditory linguistic process), at an age where the two

[1] The distance-judgment results of Koenig et al. (1990), described under the planar categorical process, may not be relevant here because distance judgment does not necessarily require bidimensional localization. Thus it seems likely that distance can be estimated between two points without judging exactly where each point is on each of the X and Y dimensions.

[2] At first glance this assumption seems to predict that individuals with callosal agenesis will show greater lateralization than normal, a matter in which the research evidence is ambiguous (Chiarello, 1980; Jäncke, Wunderlich, Schlaug, & Steinmetz, 1997). However we do not propose that an immature but intact callosum is functionless. For example, it seems possible that an *unmyelinated* callosum could exert an inhibitory influence between hemispheres, providing a mechanism for increasing asymmetry that is not present in callosal agenesis. That a *myelinated* callosum is predominantly excitatory and not inhibitory in nature is supported by the aforecited developmental studies (Fagard et al., 2001; Joseph et al., 1984; O'Leary, 1980; Quinn & Geffen, 1986), and by an adult study indicating that functional asymmetry is negatively correlated with the size of the callosum (Yazgan, Wexler, Kinsbourne, Peterson, & Leckman, 1995).

curves are still fairly close together. A delay like the one illustrated in Fig. 2 represents a higher degree of maturation of the corpus callosum *at the time the process develops* in the delayed than in the advanced group. This is illustrated in the figure by an upward vector between the advanced and delayed groups. In other words, the advanced group has developed the process at an age when their callosum is less mature than that of the delayed group, with the result that for this early developing process, the advanced group is more lateralized than the delayed group. Furthermore, since earlier development compared to delayed development most often translates to greater ability in adulthood,[3] the asymmetry–performance correlation for the process in young adulthood should be positive.

In contrast, in middle childhood a process such as the visual lexical process will develop at a point where the two curves are farther apart. Now the same delay in development between the groups results in a downward vector, the advanced group developing the process when callosal development is more advanced than that of the delayed group. The process should be less lateralized in the advanced than in the delayed group, and again following the principle that earlier development generally translates to greater adult ability, the asymmetry–performance correlation in young adulthood should be negative.

By late childhood (e.g., during lateralization of the spatial positional process) the curves again squeeze together, with the result that asymmetry–performance correlations should again be positive for exactly the same reasons as in early childhood.

Furthermore, what is known of the development of the corpus callosum renders the growth curves represented in Fig. 2 rather plausible. Everyone begins development with zero accrued growth, and callosal maturity as indexed by myelination slows in late childhood yet continues (Yakovlev & Lecours, 1967). Together these observations make it quite plausible that there would be a greater separation between advanced and delayed children at middle ages of childhood, and that the curves would continue to ramp upward at a slower rate in later childhood. These features, paired with the two assumptions described above, are what allow the prediction of the U-shaped function.

A recent empirical study by Pujol et al. (2004) also lends some weight to the maturity hypothesis. A group of developmentally delayed children was found to lag a control group in cortical myelination by 3.2 years.

The strength of the maturity hypothesis is that it makes relatively few assumptions, principally that individuals differ in timing of the maturation of their corpus callosum and that this is reflected in strength of lateralization. The hypothesis does have a weakness, however, which may be adduced from Fig. 2: to produce the U-shaped function, the amount of delay in development must fall within a limited range of values that produces upward vectors in early and late childhood, but a downward vector in middle childhood. If the delay is longer, the middle childhood vector can shift upward, and if it is shorter, the early and late childhood vectors can shift downward. Of course part of the assumption is that the delay is sufficiently constant across ages that it can be modeled as illustrated. Without additional information it is impossible to judge whether the amount of delay illustrated in Fig. 2 is more (or less) plausible than others that would produce alternative outcomes.

The second hypothesis, what we call *the developmental limits hypothesis,* proposes that the U-shaped function is due to limits in development that differ at different ages. During early childhood the limit is the immaturity of the corpus callosum, yielding an account identical to that of the maturation hypothesis: for processes normally lateralizing at an early age (e.g., the auditory linguistic process), advanced children do not yet have fully functioning callosal mechanisms in place and therefore develop highly asymmetric representations, while delayed children develop less asymmetric representations because they have partially myelinated commissures that allow processes to spread between hemispheres. Therefore in adults, processes that normally lateralize at this age show positive performance–asymmetry correlations, because the most competent (least developmentally delayed) individuals have the most asymmetric representations.

The limit during middle ages of childhood, on the other hand, is proposed to be loss of plasticity. Delayed children, developing the process at a later age, have callosums that have lost some of their plasticity and are less able to support the spread of processes, producing relatively asymmetric representations. Advanced children, developing the process earlier, are not subject to loss of plasticity yet have myelinated callosums that do allow the spread of representations between hemispheres. This in turn produces less asymmetric representations, and because children who develop processes earlier are likely to be better performers as adults, a negative correlation is therefore found between lateralization and performance (as with the visual lexical process).

Finally, for processes that normally lateralize late in childhood, the limit is proposed to be impoverished development. Faced with a task requiring use of a late-developing process (e.g., the spatial positional process), delayed children who have had little opportunity to develop it are presumably forced to use more primitive strategies that result in poor performance. They are also unlikely to show evidence of lateralization for a process they have not developed. In contrast, advanced children who have had opportunities to develop the process develop it asymmetrically due to loss of plasticity of the corpus callosum, and they are competent at performing it. Therefore in adults, pro-

[3] IQ at age 6–8 predicts IQ at age 17–18 (Anastasi, 1968; Vernon, 1979), a straightforward indication that early intellectual development is reflected in later ability levels. Furthermore, Murray et al. (2006) note that while it is often assumed that the ages at which developmental milestones are passed are uncorrelated to later intellectual function, their own longitudinal data show a correlation between two behaviors involving frontal–niagral circuitry in the brain: the age at which an infant first learns to stand, and categorization ability in adulthood.

cesses that normally lateralize at this age show positive performance–asymmetry correlations.

The strength and weakness of the developmental limits hypothesis are complementary to those of the maturation hypothesis. Its strength is that unlike its competitor it does not depend on delays in development of any particular length, but only on the relative delay of some individuals compared to others. Its weakness is that it involves a larger set of assumptions than the maturation hypothesis, most notably that there are different developmental limits for each of the early, middle, and late stages of childhood. Whether this larger set of assumptions is more plausible than the smaller set made by the maturation hypothesis under more stringent developmental timing constraints, is something that can not be determined in the absence of additional information.

5. Conclusion

In conclusion the most striking feature of the present results is the pervasiveness of asymmetry–performance correlations, the breadth of which has not previously been recognized. Almost as striking is the extent to which the direction of the correlation depends on the nature of the mental process that is lateralized. We have argued that the direction of correlation appears to be related to the age at which lateralization for the process develops, in the form of a U-shaped function with early and late lateralizing processes showing positive correlations and those in the middle showing negative ones. Developmental hypotheses based on maturity or developmental limits are capable of accounting for the results. Our hope is that they will provide a useful framework for additional research that will ultimately contribute toward a neurodevelopmental theory of hemispheric asymmetry.

References

Adair, L. P. (2003). Patterns of hemispheric lateralization in children with attention-deficit/hyperactivity disorder. Master's Thesis, University of Alabama.

Anastasi, A. (1968). *Psychological testing*. London: Macmillan Company.

Barnes, S., & Burke, R. S. (1988). What is Apple-Psych? *Behavior Research Methods, Instruments, & Computers, 20*, 150–154.

Barth, J. M., & Boles, D. B. (1999). Positive relations between emotion recognition skills and right hemisphere processing. *Poster presented to the 11th Annual Convention of the American Psychological Society*, Denver.

Bates, E., & Roe, K. (2001). Language development in children with unilateral brain injury. In C. A. Nelson & M. Luciana (Eds.), *Handbook of developmental cognitive neuroscience*. Cambridge, MA: MIT Press.

Birkett, P. (1977). Measures of laterality and theories of hemispheric processes. *Neuropsychologia, 15*, 693–696.

Boles, D. B. (1981). Variability in letter-matching asymmetry. *Perception & Psychophysics, 29*, 285–288.

Boles, D. B. (1983). Hemispheric interaction in visual field asymmetry. *Cortex, 19*, 99–113.

Boles, D. B. (1986a). Confusion and visual field effects in rhyme and name letter matching. *Perception & Psychophysics, 39*, 123–128.

Boles, D. B. (1986b). Hemispheric differences in the judgment of number. *Neuropsychologia, 24*, 511–519.

Boles, D. B. (1987). Reaction time asymmetry through bilateral vs. unilateral stimulus presentation. *Brain and Cognition, 6*, 321–333.

Boles, D. B. (1988). Voice recognition with the Apple-Psych system. *Behavior Research Methods, Instruments, & Computers, 20*, 158–163.

Boles, D. B. (1989). Do visual field asymmetries intercorrelate? *Neuropsychologia, 27*, 697–704.

Boles, D. B. (1990). What bilateral displays do. *Brain & Cognition, 12*, 205–228.

Boles, D. B. (1991). Factor analysis and the cerebral hemispheres: Pilot study and parietal functions. *Neuropsychologia, 29*, 59–91.

Boles, D. B. (1992a). Factor analysis and the cerebral hemispheres: Temporal, occipital and frontal functions. *Neuropsychologia, 30*, 963–988.

Boles, D. B. (1992b). Fast visual generation: Its nature and chronometrics. *Perception & Psychophysics, 51*, 239–246.

Boles, D. B. (1995). Parameters of the bilateral effect. In F. L. Kitterle (Ed.), *Hemispheric communication: Mechanisms and models* (pp. 211–230). Hillsdale, NJ: Lawrence Erlbaum Associates.

Boles, D. B. (1996). Factor analysis and the cerebral hemispheres: "Unlocalized" functions. *Neuropsychologia, 34*, 723–736.

Boles, D. B. (1998). Relationships among multiple task asymmetries: II. A large-sample factor analysis. *Brain and Cognition, 36*, 268–289.

Boles, D. B. (2002). Lateralized spatial processes and their lexical implications. *Neuropsychologia, 40*, 2125–2135.

Boles, D. B., & Eveland, D. C. (1983). Visual and phonetic codes, and the process of generation in letter matching. *Journal of Experimental Psychology: Human Perception and Performance, 9*, 657–674.

Boles, D. B., & Pasquarette, S. J. (1996). Correlated auditory asymmetries in lexical and nonlexical tasks. *Cortex, 32*, 537–545.

Bryden, M. P. (1982). *Laterality: Functional asymmetry in the human brain*. New York: Academic.

Bryden, M. P., & Sprott, D. A. (1981). Statistical determination of degree of laterality. *Neuropsychologia, 19*, 571–581.

Brysbaert, M., & D'Ydewalle, G. (1990). Individual analysis of laterality data. *Neuropsychologia, 28*, 901–916.

Butler, D. C., & Miller, L. K. (1979). Role of approximation to English and letter array length in the development of visual laterality. *Developmental Psychology, 15*, 522–529.

Carmon, A., Nachshon, I., & Starinsky, R. (1976). Developmental aspects of visual hemifield differences in perception of verbal material. *Brain and Language, 3*, 463–469.

Carter, G. L., & Kinsbourne, M. (1979). The ontogeny of right cerebral lateralization of spatial mental set. *Developmental Psychology, 15*, 241–245.

Chiarello, C. (1980). A house divided? Cognitive functioning with callosal agenesis. *Brain and Language, 11*, 128–158.

Colbourne, C. J. (1978). Can laterality be measured? *Neuropsychologia, 16*, 283–289.

De Haan, M. (2001). The neuropsychology of face processing during infancy and childhood. In C. A. Nelson & M. Luciana (Eds.), *Handbook of developmental cognitive neuroscience* (pp. 381–398). Cambridge, MA: MIT Press.

Doty, R. W., & Overman, W. H. (1977). Mnemonic role of forebrain commissures in macaques. In S. Harnad, R. W. Doty, L. Goldstein, J. Jaynes, & G. Krauthamer (Eds.), *Lateralization in the nervous system* (pp. 75–88). New York: Academic Press.

Entus, A. K. (1977). Hemispheric asymmetry in processing of dichotically presented speech and nonspeech stimuli by infants. In S. J. Segalowitz & F. A. Gruber (Eds.), *Language development and neurological theory* (pp. 63–73). New York: Academic Press.

Eviatar, Z. (1997). Language experience and RH tasks: The effects of scanning habits and multilingualism. *Brain and Language, 58*, 157–173.

Fagard, J., Hardy-Léger, I., Kervella, C., & Marks, A. (2001). Changes in interhemispheric transfer rate and the development of bimanual coordination during childhood. *Journal of Experimental Child Psychology, 80*, 1–22.

Glass, G. V., & Stanley, J. C. (1970). *Statistical methods in education and psychology*. Englewood Cliffs, NJ: Prentice-Hall, Inc..

Hellige, J. B., Bloch, M. I., & Taylor, A. K. (1988). Multitask investigation of individual differences in hemispheric asymmetry. *Journal of Experimental Psychology: Human Perception and Performance, 14*, 176–187.

Hellige, J., & Michimata, C. (1989). Categorization versus distance: Hemispheric differences for processing spatial information. *Memory & Cognition, 17*, 770–776.

Hellige, J. B., Zatkin, J. L., & Wong, T. M. (1981). Intercorrelation of laterality indices. *Cortex, 17*, 129–134.

Hines, D. (1978). Visual information processing in the left and right hemispheres. *Neuropsychologia, 16*, 593–600.

Hines, D., Glista, J., & Byers, B. (1985). Perceptual interference and hemispheric specialization. *Brain and Cognition, 4*, 76–89.

Hiscock, M. (1988). Behavioral asymmetries in normal children. In D. L. Molfese & S. J. Segalowitz (Eds.), *Brain lateralization in children: Developmental implications* (pp. 85–169). New York, NY: The Guilford Press.

Jäncke, L., Wunderlich, G., Schlaug, G., & Steinmetz, H. (1997). A case of callosal agenesis with strong anatomical and functional asymmetries. *Neuropsychologia, 35*, 1389–1394.

Johnson, M. H. (1997). *Developmental cognitive neuroscience: An introduction*. Oxford: Blackwell.

Joseph, R., Gallagher, R. E., Holloway, W., & Kahn, J. (1984). Two brains, one child: Interhemispheric information transfer deficits and confabulatory responding in children aged 4, 7, and 10. *Cortex, 20*, 317–331.

Kershner, J., Thomae, R., & Callaway, R. (1977). Nonverbal fixation control in young children induces a left-field advantage in digit recall. *Neuropsychologia, 15*, 569–576.

Kertesz, A., & Naeser, M. A. (1994). Anatomical asymmetries and cerebral lateralization. In A. Kertesz (Ed.), *Localization and neuroimaging in neuropsychology* (pp. 213–244). San Diego: Academic Press.

Kimura, D. (1969). Spatial localization in left and right visual fields. *Canadian Journal of Psychology, 23*, 445–458.

Kinsbourne, M. (1997). Mechanisms and development of cerebral lateralization in children. In C. R. Reynolds, E. Fletcher, & O. Janzen (Eds.), *Handbook of Clinical Child Neuropsychology* (2nd ed., pp. 102–119). New York: Plenum Press.

Koenig, O., Reiss, L. P., & Kosslyn, S. M. (1990). The development of spatial relation representations: Evidence from studies of cerebral lateralization. *Journal of Experimental Child Psychology, 50*, 119–130.

Kosslyn, S. M., Koenig, O., Barrett, A., Cave, C. B., Tang, J., & Gabrieli, D. E. (1989). Evidence for two types of spatial representations: Hemispheric specialization for categorical and coordinate relations. *Journal of Experimental Psychology: Human Perception and Performance, 15*, 723–735.

Lenneberg, E. (1967). *Biological foundations of language*. New York: Wiley.

Levine, S. C., & Levy, J. (1986). Perceptual asymmetry for chimeric faces across the life span. *Brain and Cognition, 5*, 291–306.

Levy, J. (1974). Psychobiological implications of bilateral asymmetry. In S. J. Dimond & J. G. Beaumont (Eds.), *Hemisphere function in the human brain* (pp. 121–183). New York: Halsted Press.

Levy, J., & Reid, M. (1976). Variations in writing posture and cerebral organization. *Science, 194*, 337–339.

Marshall, J. C., Caplan, D., & Holmes, J. M. (1975). The measure of laterality. *Neuropsychologia, 13*, 315–321.

Miller, L. K. (1981). Perceptual independence of the hemifields in children and adults. *Journal of Experimental Child Psychology, 32*, 298–312.

Miller, L. K. (1984). Sources of visual field interference in children and adults. *Journal of Experimental Child Psychology, 37*, 141–157.

Molfese, D. L. (1977). Infant cerebral asymmetry. In S. J. Segalowitz & F. A. Gruber (Eds.), *Language development and neurological theory* (pp. 21–35). New York: Academic Press.

Molfese, D. L., & Betz, J. C. (1988). Electrophysiological indices of the early development of lateralization for language and cognition, and their implications for predicting later development. In D. L. Molfese & S. J. Segalowitz (Eds.), *Brain lateralization in children: Developmental implications* (pp. 171–190). New York: The Guilford Press.

Molfese, D. L., & Molfese, V. J. (1980). Cortical response of preterm infants to phonetic and nonphonetic speech stimuli. *Developmental Psychology, 16*, 574–581.

Moscovitch, M., & Klein, D. (1980). Material-specific perceptual interference for visual words and faces: Implications for models of capacity limitations, attention, and laterality. *Journal of Experimental Psychology: Human Perception and Performance, 6*, 590–604.

Nottebohm, F. (1984). Learning, forgetting, and brain repair. In G. Geschwind & A. M. Galaburda (Eds.), *Cerebral dominance: The biological foundations* (pp. 93–113). Cambridge, MA: Harvard University Press.

O'Boyle, M. W., Cunnington, R., Silk, T. J., Vaughan, D., Jackson, G., Syngeniotis, A., et al. (2005). Mathematically gifted male adolescents activate a unique brain network during mental rotation. *Cognitive Brain Research, 25*, 583–587.

Okubo, M., & Michimata, C. (2002). Hemispheric processing of categorical and coordinate spatial relations in the absence of low spatial frequencies. *Journal of Cognitive Neuroscience, 14*, 291–297.

Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia, 9*, 97–113.

O'Leary, D. S. (1980). A developmental study of interhemispheric transfer in children aged five to ten. *Child Development, 51*, 743–750.

Olk, B., & Hartje, W. (2001). The bilateral effect: Callosal inhibition or intrahemispheric competition? *Brain and Cognition, 45*, 317–324.

Orton, S. T. (1937). *Reading, Writing and Speech Problems in Children*. New York: Norton.

Osgood, G. (1988). Generalizing the Apple-Psych system. *Behavior Research Methods, Instruments, & Computers, 20*, 155–157.

Pujol, J., López-Sala, A., Sebastián-Gallés, N., Deus, J., Cardoner, N., Soriano-Mas, C., et al. (2004). Delayed myelination in children with developmental delay detected by volumetric MRI. *NeuroImage, 22*, 897–903.

Quinn, K., & Geffen, G. (1986). The development of tactile transfer of information. *Neuropsychologia, 24*, 793–804.

Rayman, J., & Zaidel, E. (1991). Rhyming and the RH. *Brain and Language, 40*, 89–105.

Segalowitz, J. S., & Gruber, F. A. (1977). What is it that is lateralized? In S. J. Segalowitz & F. A. Gruber (Eds.), *Language development and neurological theory*. New York: Academic Press.

Servos, P., & Peters, M. (1990). A clear LH advantage for visuo-spatially based verbal categorization. *Neuropsychologia, 28*, 1251–1260.

Springer, S. P., & Searleman, A. (1978). The ontogeny of hemispheric specialization: Evidence from dichotic listening in twins. *Neuropsychologia, 16*, 269–281.

Vernon, P. E. (1979). *Intelligence: Heredity and environment*. San Francisco: W.H. Freeman and Company.

Werke, J. F., & Vouloumanos, A. (2001). Speech and language processing in infancy: A neurological approach. In C. A. Nelson & M. Luciana (Eds.), *Handbook of Developmental Cognitive Neuroscience*. Cambridge, MA: MIT Press.

Wexler, B. E., & Halwes, T. (1985). Dichotic listening tests in studying brain-behavior relationships. *Neuropsychologia, 23*, 545–559.

Wickens, C. D. (1984). *Engineering Psychology and Human Performance*. Columbus, OH: Charles E. Merrill Publishing Co.

Yakovlev, P. I., & Lecours, A. R. (1967). The myelogenetic cycles of regional maturation of the brain. In A. Minkowski (Ed.), *Regional development of the brain in early life* (pp. 3–70). Boston: Blackwell Scientific Publications.

Yazgan, M. Y., Wexler, B. E., Kinsbourne, M., Peterson, B., & Leckman, J. F. (1995). Functional significance of individual variations in callosal area. *Neuropsychologia, 33*, 769–779.

Young, A. W., & Bion, P. J. (1979). Hemispheric laterality effects in the enumeration of visually presented collections of dots by children. *Neuropsychologia, 17*, 99–102.