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The Relation of Planum Temporale Asymmetry and Morphology of the Corpus Callosum to Handedness, Gender, and Dyslexia: A Review of the Evidence

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Asymmetry of the planum temporale in relation to handedness, gender, and dyslexia is reviewed. The frequency of rightward asymmetry is rather higher than are estimates of the proportion of right hemisphere speech representation in the general population. Conversely, the frequency of leftward asymmetry is lower than the proportion of the population with left hemisphere speech. Neuro-anatomic asymmetry may relate more to handedness than to language lateralization. There are suggestions that neuroanatomic asymmetry is reduced in females compared to males but the data are inconclusive. Reports concerning handedness and gender differences in callosal structure are conflicting but, as with planum asymmetry, any effect of handedness is as likely to relate to degree as to direction of handedness. It has been reported that the plana are more often symmetrical in size or larger on the right side among dyslexics than controls but this has not always been found. However, greater frequency of atypical (a)symmetry of the planum in dyslexia would be consistent with the absence of a factor which, when present, biases the distribution of planum asymmetry toward the left (and handedness towards the right) as hypothesized by Annett (1985). Studies of the size of the corpus callosum in dyslexia have produced conflicting findings.

The Geschwind–Behan–Galaburda (GBG) hypothesis of cerebral lateralization has attracted great interest and motivated a huge investment of research effort. The theory and associated findings were reviewed in detail by McManus and Bryden (1991) and Bryden, McManus, and Bulman-Fleming (1994), but these authors did not consider in any detail the anatomic postulates of the GBG theory. Briefly, the original version of the GBG hypothesis held that high levels of fetal testosterone or ''some other sex-related agent''

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produce a reduction in the neuroanatomic and functional development of the left cerebral hemisphere with a concomitant increase in left-handedness and incidence of dyslexia (Geschwind & Behan, 1982). More recently it was proposed that symmetrical brains, said to be characteristic of dyslexia, result from some interference with the process of involution whereby there is normally a greater reduction of cortex on the right than on the left side of the brain (Galaburda, 1993).

In this paper I consider cerebral anatomic asymmetry in relation to handedness, gender, and dyslexia. I also consider relevant research on the corpus callosum. The review is organized under three main headings: (a) anatomic brain asymmetry; (b) the corpus callosum, and (c) dyslexia. A final section draws together the earlier findings and conclusions.

ANATOMIC BRAIN ASYMMETRY

A great deal of research has focused on the measurement of structures including or surrounding the Sylvian fissure and in particular the posterior portion of the superior surface of the temporal lobe, the planum temporale. While asymmetries in other regions of the brain have been documented (Kopp, Michel, Carrier, Biron, & Duvillard, 1977; Weinberger, Luchins, Morihisa, & Wyatt, 1982; Falzi, Perrone, & Vignolo, 1982; Eidelberg & Galaburda, 1982; 1984; Jäncke, Schlaug, Huang, & Steinmetz, 1994), and some have been related to handedness (e.g., Le May & Kido, 1978; Bear, Schiff, Saver, Greenberg, & Freeman, 1986; Jancke et al., 1994; Habib, Robichon, Lévrier, Khalil, & Salamon, 1995; Snyder, Bilder, Wu, Bogerts, & Lieberman, 1995), it is asymmetry of the planum temporale that has received the most attention. I shall therefore concentrate on findings concerning the planum and related structures. For more extensive anatomical coverage, the interested reader is referred to reviews by Witelson (1980) and Witelson and Kigar (1988).

Post-Mortem Studies

Current interest in left–right asymmetry of the planum temporale stems from a report by Geschwind and Levitsky (1968), although related findings were published previously by Eberstaller (1890), Cunningham (1892), von Economo and Horn (1930), and Pfeiffer (1936). Among a series of 100 brains examined postmortem by Geschwind and Levitsky, 65 were said to have a longer planum on the left side, 11 had a longer planum on the right and the remaining 24 brains were approximately symmetrical. Wada, Clarke, and Hamm (1975) examined 100 adult and 100 neonatal brains. Using planimetric measurement of photographs of brains dissected through a section along the Sylvian fissure, they also found the planum in both the adult and the neonatal specimens to be greater in area on the left side than on the right. In the adult brains the plana were approximately equal in area in 8 cases and larger on the right in 10 cases. Corresponding figures for infant brains were 32 and 12. Chi, Dooling, and Gilles (1977) reported that the planum in 54% of 207 fetal brains (10–44 weeks gestation) appeared, on visual inspection, to be longer on the left and 18% appeared longer on the right.

An enduring difficulty in this area is that of measurement. One problem concerns how the anterior and posterior borders of the planum temporale are defined. It might be assumed that what one investigator calls the planum temporale is the same brain area that a second investigator calls the planum. In fact, investigators differ in how they define this region. The anterior border of the planum is usually defined with reference to the transverse gyrus of Heschl. The problem arises because not infrequently there are two transverse gyri and investigators have not all agreed upon whether the second gyrus should be regarded as lying within or outside the planum temporale. The problem is compounded by the fact that the number of Heschl's gyri may not be the same in left and right hemispheres.

In their seminal report, Geschwind and Levitsky (1968) do not state whether they included a second Heschl's gyrus in the area they defined as the planum. In referring to this paper, Witelson and Pallie (1973) state

> The previous work assumed, on the basis of the classical literature, that two transverse temporal gyri (that is, two Heschl gyri) may exist in the right but not in the left hemisphere and the planum was accordingly defined as the superior temporal surface posterior to the first transverse gyrus on the left, but the surface posterior to the first or second (if present) transverse gyrus on the right. (p. 642)

This could create a bias toward finding a larger planum on the left. However, Teszner, Tzvaras, Gruner, and Hécaen (1972), using area rather than linear measures of the planum, also reported that in 64 of 100 brains the planum was ''plus important à droite qu′ à gauche'' (p. 448). (From the context it is clear that this is an error and that they meant to write ''à gauche qu′ à droite''.) These authors defined the planum as posterior to the most posterior transverse gyrus of Heschl and there is nothing to suggest in their report that their definition was different for left and right sides. Of the 100 adult brains available to them, 5 were studied using a cut along the Sylvian fissure and 95 were examined from a plaster cast. In 64 cases the planum was larger on the left side, 10 were larger on the right side, and 26 were approximately equal on the two sides. Six of 8 neonatal brains were larger on the left. (Actual measurements of area were not given for either adult or neonatal cases.)

Galaburda, Corsiglia, Rosen, and Sherman (1987) carried out further analysis of the brains available to Geschwind and Levitsky (1968) (about which there is no information available concerning handedness or sex). Galaburda et al. confirmed (this time for measurement of area) that in the majority (63%) of specimens there was an asymmetry favoring the left planum but there was a continuum from such leftward asymmetry, through relative symmetry (16%) to rightward asymmetry (21%). In this reanalysis Galaburda et al. included a second gyrus of Heschl in their measurement. Inclusion of this second gyrus (which their Fig. 1 suggests is more frequent on the right) would tend to reduce the overall asymmetry favoring the left planum.

In the study by Galaburda et al. (1987), the correlation between combined cortical area (i.e., left plus right planum) and a measure of leftward asymmetry was statistically significant (the association between rightward asymmetry and total area was in the mirror direction but not significant). With decreasing leftward asymmetry (toward symmetry), the area of the right planum increased without significant change to the area of the left planum. In brains with rightward asymmetry there was little change in the area of the right planum in moving toward symmetry but an increase in the area of the left planum. Symmetrical brains were thus larger in total area of the planum temporale than were asymmetrical brains.

In brains with an asymmetry in the usual direction (larger planum on the left), the asymmetry is associated with a smaller right planum rather than a larger left planum. In the rat increased left–right cortical asymmetry is associated with a decrease in the number of callosal axon terminations (Rosen, Sherman, & Galaburda, 1989) as opposed to differences in cell packing density at the two sides. Galaburda and his colleagues therefore suggest that symmetrical brains result from a reduction in the loss of cortical cells during a particular stage of prenatal development (epigenetic involution). The implication is that in humans the usual asymmetry favoring a larger planum on the left arises as a consequence of greater involution on the right side (this represents some modification of the original Geschwind–Behan–Galaburda hypothesis which postulated that testosterone retarded the rate of development of the left hemisphere).

A second problem of measurement concerns the posterior end of the Sylvian fissure. The posterior portion of this fissure often angulates more sharply upward on the right side of the brain, which means that a knife blade inserted along the plane of the horizontal portion of the fissure at the two sides—the method employed by Geschwind and Levitsky—will exclude cortical tissue from the right side that should properly be included (Rubens, Mahowald, & Hutton, 1976), thereby introducing a bias in favor of the left side.

Using a higher cut so as to reduce the problem of unequal angulation of the Sylvian fissure on the two sides and using both linear and area measurements, Witelson and Pallie (1973) confirmed Geschwind and Levitsky's report of a larger area of planum on the left in a group of 16 adult brains and 14 neonatal specimens. Using comparable definitions of the borders of the planum for the two hemispheres, the asymmetry in area favored the left side in 69% of the adult cases. This rose to 94% if Geschwind and Levitsky's definition (in relation to Heschl's gyri) was used. The linear measure (as used by Geschwind and Levitsky) showed the planum to be longer on the left in 81% of adult cases. The number of cases in which it was larger on the right is not stated for any measure. No information as to handedness or gender relating to these specimens was available.

Recently, Aboitiz, Scheibel, and Zaidel (1992) estimated planum size from postmortem measurement of the length of the Sylvian fissure and concluded that 17 of 40 brains they examined had a larger right than left planum, with roughly equal numbers of each sex showing this ‘‘reversed asymmetry.’’ The proportion of right-biased brains (42.5%) is higher than that reported by other authors for more direct measures of the planum. It is thus possible that indirect measures give a picture of less extreme asymmetry than more direct measures.

The morphology of the Sylvian fissure varies quite considerably among individuals (Witelson & Kigar, 1988; Steinmetz, Rademacher, Jäncke, Huang, Thron, & Zilles, 1990). In many brains the horizontal fissure branches into two segments, the posterior ascending ramus (PAR) and the posterior descending ramus (PDR). Sometimes the posterior ascending and/or descending ramus is included in the measurement of the planum temporale. In the accompanying tables an indication is given where it was possible to discern from the report how the borders of the planum temporale were defined and measured. Table 1a summarizes postmortem studies of the planum temporale and related brain areas published since Geschwind and Levitsky’s paper in 1968. It does not claim to be exhaustive; rather, those studies most often cited and/or most relevant are included.

Handedness and Cerebral Anatomic Asymmetry

At the time of this writing there are no published papers on handedness in relation to postmortem measures of the planum temporale. However, Witelson and Kigar (1992) measured the length of the Sylvian fissure which of course is intimately related to the planum. Prior to their deaths, the individuals whose brains were studied by Witelson and Kigar had been tested for hand preference. Hand preference scores were available for 69 cases of whom 2 were excluded ‘‘due to neuropathology affecting the gross anatomy of SF (Sylvian fissure) regions.’’ The Sylvian fissure was divided into anterior, horizontal, and vertical segments. There was no difference between consistent right-handers and all other cases in asymmetry of any Sylvian fissure segment. In both groups the mean length of the vertical section was found to be greater on the right, which compensated for a longer horizontal section on the left. Among men but not among women the horizontal segment for both hemispheres combined was significantly greater in consistent right-handers than in nonconsistent right-handers. The findings cannot be attributed to a larger overall brain in consistent right-handers, since the results held up when overall brain weight was entered as a covariate in an analysis of covariance. Thus hand preference was related to a bilateral feature of Sylvian fissure morphology rather than to asymmetry.

TABLE 1a

Investigations of Postmortem Asymmetry of Planum Temporale and Related Areas

Authors	Subjects	Handedness	Age	Anatomical definition	Findings	Remarks
Geschwind & Levitsky (1968)	100 (sex NK)	NK	No details provided	Posterior to first transverse gyrus on left; posterior to second (if present) on right measured to ‘‘end of Sylvian fissure’’ (but no details).	65 longer on left 11 longer on right 24 equal Mean length significantly greater on left	No correction for overall brain size. Measurement details not provided in this paper.
Galaburda et al. (1987)	As above (sex NK)	NK	No details provided	Where present second Heschl’s gyrus included on both sides.	63 greater area on left 21 greater area on right 16 equal	Brains with asymmetry coefficients between 6 0.09 regarded as equal.
Teszner et al. (1972)	100 adults (sex NK)	NK	NK	Triangular area ‘‘Limitée en avant par le sillon de Heschl . . . , en arrière par la ligne de refléxion du cortex pariétal et temporal.’’	64 greater area on left 10 greater area on right 26 equal	No correction for overall brain size. Point to difficulty of determining the terminal point of the Sylvian fissure in a good number of cases.
	8 fetuses (sex NK)		28–38 weeks gestation			
Witelson & Pallie (1973)	16 adult (sex NK) 9 male infants 5 female infants	NK N/A	No details provided Median age 12 days	Area posterior to the first transverse gyrus, or, when present, to the second transverse gyrus (nonbiased measure). Also used as shown above for Geschwind & Levitsky (1968).	Adults 94% greater on left 81% longer on left 69% greater non-biased area on left Infants 86% greater area on left 86% longer on left 75% greater non-biased area on left	No correction for overall brain size. Area measured as per Geschwind & Levitsky (1968). Nonbiased area is same criteria for left and right planum.
Wada et al. (1975)	100 adults	NK (sex breakdown etc., not given)	17–96 yrs Mean: 69 yrs	Posterior to ‘‘gyrus or gyri’’ of Heschl and ‘‘in front of the posterior end of the Sylvian fissure.’’	Mean area of planum greater on left; greater on left in 55% of adults, 67% of infants.	
	100 infants	N/A	18 weeks gestation–18 months			
Kopp et al. (1977)	103 adults 103 infants (sex NK)	NK	NK	Definition not given	77% greater area on left 21.7% greater area on right 1.3% equal	
Chi et al. (1977)	207 fetuses (‘‘male to female ratio almost equal’’)	N/A	10–44 weeks gestation	‘‘Superior temporal surface area posterior to the first or second transverse temporal gyrus on either side, its posterior boundary being determined by the end of the Sylvian fissure.’’	On visual inspection longer planum on left in 54%; longer on right in 18%. No significant (sic) difference in 28%. No gender difference observed.	No correction for overall brain size. 60% sectioned in frontal plane; 20% in horizontal and 20% in sagittal plane.

Steinmetz et al. (1990)	3 male 7 female	NK	51–77 yrs	Anterior border ‘‘defined as the transverse sulcus lying behind the anterior transverse gyrus . . . referred to as Heschl’s Sulcus. Additional transverse gyri (H2, H3) thus belonged to the PT regardless of side. ‘‘The posterior border was defined as coinciding with the caudal end of the posterior horizontal ramus of the SF. The walls of the descending and ascending rami were thus excluded . . .’’ BUT also measured extended area of PT ‘‘as defined above plus the anterior and posterior walls of the posterior descending ramus of the SF and the posterior wall of the posterior ascending ramus of the SF until its upper end point.’’	Found significant leftward asymmetry using measure of exposed surface of PT but ‘‘extended measure’’ showed no asymmetry. The ‘‘excess’’ area [(PT 1) 2 PT] showed significant rightward asymmetry.	Also carried out MRI on cadaver brains.
Witelson & Kigar (1992)	24 males 43 females	13 CRH 11 NCRH 29 CRH 14 NCRH	25–70 yrs Mean: 53 yrs	Measured length of Sylvian fissure in segments; PAR but not PDR included in measurement of vertical segment of SF.	Horizontal segment of SF in both left and right hemispheres shorter among NCRH and CRH in males but not females. Horizontal SF segment longer in left than right hemispheres (males and females). Vertical SF segment longer on right than left side.	NCRH included at least one action performed preferentially by left hand.
Aboitiz et al. (1992)	20 males 20 females	Right-handers No details provided	Mean: 48.5 yrs Mean: 45.1 yrs	Measured length of Sylvian fissure ‘‘between the posterior end of Heschl’s first gyrus and the posterior end of the Sylvian fissure . . . We measured the superior and inferior branches of the Sylvian fissure, as well as the distance from Heschl’s gyrus to the point of bifurcation.’’	17 of the 40 brains were longer on the right than the left.	‘‘The only measurement that yielded interesting results was the distance from Heschl’s first gyrus to the end of the superior branch of the Sylvian fissure. The other two measurements are consequently omitted from this paper.’’ Also examined corpus callosum.

Note: NK, not known; N/A, not applicable; SF, Sylvian fissure; PT, planum temporale; PAR, posterior ascending ramus; PDR, posterior descending ramus; CRH, consistent right-hander; NCRH, non-consistent right-hander.

Neuroimaging Studies of Handedness in Relation to Cerebral Anatomic Asymmetry

Turning now to *in vivo* studies (see Table 1b), some radiographic and CT studies point to a relation between handedness and anatomic asymmetry. Hochberg and Le May (1974) reported that in right-handers the angle of the Sylvian arch as seen on X-ray films was greater (by 10 degrees or more) on the right than on the left side of the brain in 71 cases; angulation was approximately equal in 27 cases and greater on the left side in 8 cases. Among 13 individuals said to be left-handed, the corresponding figures were 6, 20, and 2. Thus the trend was for left-handers to show symmetry more often than right-handers. Since the angle of the Sylvian arch reflects the amount of tissue of the parietal operculum, the results suggest that greater equality of cortical tissue at the two sides of the brain is more frequent in left- compared with right-handers.

Le May (1976; 1977) and Le May and Kido (1978) reviewed CT scan asymmetries in occipital and frontal width and length in relation to handedness, the general trend of which also was to show reduced asymmetry and a greater frequency of reversed asymmetry in left-handers. More recently, Bear et al. (1986) reported that 16 individuals with laterality scores below 70 on the Edinburgh Handedness Inventory (Oldfield, 1971) showed a reduction of the usual leftward occipital bias (but normal right frontal bias) in comparison with 50 individuals with scores from 71 to 100 inclusive. The latter score represents extreme right-handedness but the cut-off score of 70 would place many less extreme right-handers among frank left-handers. Koff, Naeser, Pieniadz, Foundas, and Levine (1986), also using CT scans, failed to find any significant relationship between handedness as defined by scores on the Briggs–Nebes modification of Annett's (1970) questionnaire.

The significance (if any) of frontal and occipital asymmetries for language-related behavior is not clear. Pieniadz and Naeser (1984) studied planum temporale asymmetry postmortem in 15 men (said by relatives to have been right-handed) for whom CT scans were available. There was a significant correlation between occipital length asymmetry as measured on CT scan and planum length measured postmortem but neither occipital nor frontal width asymmetry (nor frontal nor posterior parietal asymmetries) correlated with the postmortem measure. Planum measurements were made after making a horizontal cut through the Sylvian fissure and are therefore subject to the possible biasing effect of unequal slants and bifurcation of this fissure at the two sides. (Of the 15 brains examined, two showed two transverse gyri of Heschl—both on the right side—and were included in measurements of the planum.)

Although Pieniadz, Naeser, Koff, and Levine (1983) reported that reduced or reversed occipital length or width CT asymmetries were associated with better improvement in naming and in single word comprehension and repetition by 14 male right-handers recovering from global aphasia, the same group also reported in a separate paper (Henderson, Naeser, Pianiadz, & Chui, 1984) that reversed asymmetries could not predict the occurrence of crossed aphasia (resulting from right hemisphere lesions in right-handers). This casts doubt on the significance of CT occipital or frontal width asymmetry as an indication of the side of speech dominance. Furthermore, a recent report suggests that the reliability of measurements of occipital asymmetry is not high (Chu, Tranel, & Damasio, 1994). On the other hand, Burke, Yeo, Delaney, and Connor (1993) found that increasing leftward occipital width asymmetry on CT scan was significantly correlated with scores on a test of language recovery following aphasia. The opposite findings to those of Pianiadz et al. (1983) may be due to different lesion sizes in the two series of patients. Global aphasia (Pianiadz et al.) commonly follows very large left-sided lesions which may lead to recovery mechanisms over the longer term being mediated at least partly by the right hemisphere. More restricted lesions may be associated with reorganization of function within the damaged left hemisphere.

One study has shown a relationship not between handedness and radiographic asymmetry but between the latter and a putative index of language lateralization. As the middle cerebral artery emerges from the depths of the Sylvian fissure, its posterior branch courses downward to curve under the parietal operculum. The width of the temporal lobe was measured at this point on the CT scan and expressed as a proportion of the skull diameter. The right minus left difference in this value was correlated with dichotic listening asymmetry by Strauss, Lapoint, Wada, Gaddes, and Kosaka (1985), who reported a nearly significant (p , . 08, two-tailed) inverse correlation.

An even more specific relationship between handedness and structural brain asymmetry has been reported. Kertesz, Black, Polk, and Howell (1986) obtained a significant correlation between hand differences on a manual task (that of Tapley & Bryden, 1985) and a composite measure of anatomical asymmetry as revealed by MRI scan. The anatomical measures that were used relate to, but are not synonymous with, planum temporale measurement. Habib (1989) also reports finding a significant correlation between handedness score as measured by the Edinburgh Handedness Inventory (EHI) and an index of asymmetry of the area of the planum temporale as revealed by MRI, but in his report there is no clear indication of how the planum was measured. Kertesz, Polk, Black, and Howell (1990) reported finding a significantly larger left- than right-sided parietal area (corrected for total brain size) in right-handed males and left-handed females, but found no effect for the temporal lobe as reconstructed from coronal slices.

Steinmetz, Volkmann, Jäncke, and Freund (1991) measured the planum from sagittal MRI sections. The subjects were 26 right-handers and 26 left-handers by self-report with equal numbers of males and females in each group. Handedness was also measured by performance tasks. Estimates of

TABLE 1b
Neuroimaging Studies of Planum Temporale and Related Areas

Authors	Subjects	Handedness	Age	Anatomical definition	Imaging plane/ magnetic strength	Findings	Comments
Kertesz et al. (1986)	11 females 9 males	10 Right-handers 10 Left-handers	20–40 yrs	See comments	Axial 0.15T	Correlation between differences in skill between left and right hands on Tapley & Bryden task and composite measure of anatomic asymmetry.	Composite measure of anatomic asymmetry included asymmetry of anterior frontal width, parietal width and opercular sulcus demarcation.
Habib (1989)	20 (sex not given)	Measured by EHI but scores not provided	19–51 yrs Mean: 33	Measurement details not provided.	Axial and sagittal 0.5T	Handedness score significantly correlated with planum asymmetry.	
Kertesz et al. (1990)	25 males 27 females 26 males 26 females	Right-handed Non-right-handed	18–49 yrs Mean: 26.9 yrs	‘‘The line between the splenium and the optic chiasm, which is parallel to the Sylvian fissures, . . . was used as the plane for the axial (horizontal) slices. The coronal planes were perpendicular to the axial slices . . . The first axial slice above the third ventricle where the bodies of the lateral ventricles appear to touch in the midline was used for linear and area measures of the hemispheres.’’	Axial and coronal 0.15T	Significantly larger left than right sided parietal area in right-handed males and left-handed females.	
Kertesz et al. (1992)	As above	As above	Mean: 26.9 yrs	The axial cut above the third ventricle was used to measure hemispheric sagittal length and area. The longer sagittal length was divided at 10% and 30% anteriorly and posteriorly, creating anterior frontal, posterior frontal, parietal and occipital widths.	As above 0.15T	Linear measure: all females with REA had longer hemispheric sagittal length on right side; only 2/3 of those with LEA did so. Area measure: Right-handers with REA and left-handers with LEA had larger structures than those in whom hand and ear dominance were in opposite direction.	

Steinmetz et al. (1990)	7 females 3 males	NK	51–77 yrs	See postmortem studies	Sagittal 1.5T	See postmortem studies	See also postmortem studies.
Steinmetz et al. (1991)	13 males 13 females 13 males 13 females	R. handers R. handers non R. handers non R. handers (see text)	Mean: 24.9 yrs Mean: 26.4 yrs	''The anterior border of the PT was defined as the bottom of Heschl's sulcus . . . The posterior border of the PT was defined as the point of transition of the posterior descending ramus of the Sylvian fissure into the posterior ascending ramus of the Sylvian fissure. Thus, all cortex buried in the posterior descending ramus was included with the PT. Cortex buried in the posterior ascending ramus was excluded.''	Coronal 0.5T	Degree of leftward asymmetry significantly greater for right-handers but only (*n* 5 49) when defined by skill, not preference. No correlation between hand preference and anatomic asymmetry.	
Rossi et al. (1994)	13 males 10 females	Right-handers by EHI	Mean: 31.5 yrs	Anterior border ''was constituted by Heschl's sulcus i.e. the transverse sulcus bordering the anterior temporale gyrus or Heschl's gyrus posteriorly. . . The posterior border of the PT was identified as the posterior termination of the horizontal stem of the Sylvian fissure where it meets the supramarginal gyrus.''	Sagittal 0.5T	Area: 9 males, 6 females larger planum on left than right side; 3 males, 1 female longer on right side; 1 male, 3 females equal planum on two sides.	Authors say reduced asymmetry of plana (asymmetry coefficient) in females–but difference unlikely to be significant.
Kulynych et al. (1994)	12 males 12 females	Mean 5 94.0 6 10.00 Mean 5 94.8 6 9.2 Measured on EHI	Mean 5 25.9 yrs 6 4.1 Mean 5 25.0 yrs 6 3.5	''Surface posterior to Heschl's sulcus. . . . identified according to the criteria of Steinmetz et al. (1991).'' ''The posterior limit of the planum temporale is chosen. . . . so as to exclude tissue of the posterior ascending ramus of the Sylvian fissure.''	Sagittal 1.5T	Area of left planum significantly greater than right among males, no significant difference among females. Gender by hemisphere interaction significant.	Asymmetry coefficient used to control for overall brain size.

TABLE 1b—*Continued*

Authors	Subjects	Handedness	Age	Anatomical definition	Imaging plane/ magnetic strength	Findings	Comments
Jäncke et al. (1994)	53 males	Right-handers	Males mean 27.5 6 8.2 yrs	As Steinmetz et al. (1991)	Sagittal 1.5T	Mean coefficient of asymmetry (area) significantly greater in right- than in left-handers. No effect of gender.	Used asymmetry coefficient to correct for overall brain size. Also measured wall of PAR—area significantly greater on right side. No correlation between areas of PT and ‘‘planum parietale.’’
	53 females	Right-handers	Females mean 25.5 6 4.0 yrs				
	17 males 18 females	Left-handers Left handers (see text)					
Foundas et al. (1994)	6 males 6 females	11 Right-handers 1 Non-right-hander	17–55 yrs mean 5 34 yrs	‘‘Anterior border was defined as the transverse sulcus caudal to Heschl’s gyrus. The posterior border was defined as the caudal extent of the posterior horizontal ramus as it bifurcates into the posterior ascending and descending rami.’’	Sagittal 1.0T	Length of planum measured at maximal extent. All 11 right-handers had greater length of planum on left and left language lateralization. One right-hander had rightward asymmetry and right language lateralization.	Language lateralization determined by Wada testing. Patients were all epileptic—5 with left sided seizure foci, 7 with right sided foci.
Foundas et al. (1995)	4 males 4 females	Right-handed Right-handed Mean 23.08 6 0.35	Mean 5 34 6 9.7 yrs	‘‘Anterior border defined as the transverse sulcus, caudal to Heschl’s gyrus and the posterior border as the caudal extent of the P[osterior] H[horizontal] R[amus] as it bifurcates into the PAR and PDR.’’	Sagittal 1.0T	Among the right-handers, the planum was longer on the left in 6 subjects, reversed in one and equal in one. Among left-handers, the planum was longer in 4 reversed in 3 and equal in one.	Also measured length of the anterior speech region a portion of the third frontal convolution of the inferior frontal gyrus and was defined as the angle formed by the A[nterior] H[orizontal] R[amus] and the A[nterior] A[scending] R[amus].’’
	4 males 4 females	Left-handed Left-handed Mean 16.8 6 7.7 Scored according to Briggs–Nebes’ modification of Annett’s (1970) questionnaire.	Mean 5 38 6 10.0 yrs	‘‘The posterior limit of the PT excluded tissue along the PAR.’’ ‘‘When multiple Heschl’s gyri were present, the anterior border of the PT was defined as the transverse sulcus of Heschl (first transverse sulcus).’’		Left-ward asymmetry of PT said to be significant among right-handers but not among left-handers.	Results for this region are similar to those for PT Used asymmetry quotient as well as measure of length alone. No tests of significance. No test of hand-by-hemisphere interaction.

Habib et al. (1995)	23 males 17 females	CRH NCRH French translation of EHI–idiosyncratic scoring method. CRH . 80 NCRH , 79	18–51 yrs	Anterior border taken as ‘‘Anteriormost transverse sulcus’’; posterior border as ‘‘posterior end point of the Sylvian fissure.’’ ‘‘In cases where the caudal Sylvian fissure bifurcates into an ascending and a descending rami (sic), only the ascending ramus was taken into consideration.’’	Sagittal 0.5T and 1.5T	A greater asymmetry in area of the planum temporale reported for right-handers than for non-right-handers (but see text). No correlation between handedness scores and anatomic laterality coefficients.	
Schlaug et al. (1995)	30 Musicians 11 with perfect pitch 19 without perfect pitch 30 Non-musicians Gender breakdown not given	Right-handed ‘‘Consistent right-handedness defined as performance of all 12 tasks with the right hand with up to 2 ‘‘either’’ preferences being acceptable.’’ 6 subjects said to be nonconsistent.	Mean 27 6 0.5 yrs Mean 26 6 4 yrs	See Steinmetz et al. (1991).	Sagittal 1.5T	Those with perfect pitch showed greater leftward asymmetry in area of planum temporale than those without perfect pitch (significant orthogonal contrast).	Asymmetry coefficient used
Karbe et al. (1995)	13 males 2 females	10 Right-handers 4 Left-handers 1 Amidexter Measured by EHI ‘‘and standardized tests of skilled motor performance’’ but no scores or details provided.	Mean 40.4 6 12.3 yrs	Planum temporale ‘‘defined according to the criteria of Steinmetz et al.’’	Transaxial 1.0T	Larger volumetric measure of leftward asymmetry in 9 of 10 right-handers, 2 of 4 left-handers and in 1 ambidexter.	Used asymmetry coefficient. Also used PET to measure activation—found significant negative correlation between extent of PT asymmetry and metabolic activation in part of Brodmann’s area 22 on the left; there was a significant positive correlation between PT asymmetry and metabolic activation of another part of Brodmann’s area 22 on the right.

Note. EHI, Edinburgh Handedness Inventory; PT, planum temporale; REA, right ear advantage; LEA, left ear advantage; PAR, posterior ascending ramus; PDR, posterior descending ramus; CRH, consistent right-hander; NCRH, non-consistent right-hander.

the surface area of the planum were made by summing the length of planum on each sagittal slice multiplied by the thickness of the slice. The area on the left side was greater than that on the right side in both handedness groups, but the mean degree of this leftward asymmetry was significantly greater for right- than for left-handers. This significance was only found when subjects were classified by performance test (*n* 5 49) and not by self-report (*n* 5 52).

As the report by Steinmetz et al. is the most often cited *in vivo* study showing planum temporale asymmetry to differ as a function of handedness, it bears close examination. Brain asymmetry was measured using a method which reflected the entire convoluted surface area of interest, taking into account individual variability in cortical folding. The cortex buried in the posterior descending ramus of the Sylvian fissure was included but not that of the posterior ascending ramus. There is no mention of the existence of two Heschl's gyri in this paper so presumably this was not a complicating factor. Anatomical asymmetry in surface area was expressed in terms of the coefficient [R 2 L/0.5 (R 1 L)].

Handedness was classified by self-report and measured by asymmetry of performance on a finger-tapping task and, in a separate assessment, by a ''hand dominance test.'' The latter appears to include a pencil-and-paper hand dominance test plus ''3 dexterity tasks (tracing lines, dotting circles, and tapping on squares) each to be performed with maximal speed and precision over 15 s. Laterality coefficients (R 2 L/R 1 L) were determined for each test and rounded off to one decimal point''. It is not clear from the paper whether each task gave the same result or whether an overall assessment was made on the basis of all tasks combined. Whichever it was, subjects were classified as left- or right-handed according to whether their laterality coefficient was positive or negative, and anatomic asymmetry coefficients of left- and right-handers were compared using a series of Mann–Whitney *U* tests. Subjects were also classified according to the presence or absence of sinistrality within their first degree relatives. Thus comparisons were made of left- versus right-handers and, within each handedness group, of those with and without left-handed relatives. These comparisons were made for each of the three handedness criteria, namely self-report, tapping and ''hand dominance''. Of the 9 statistical comparisons reported (2 tails), only those for left-versus right-handers as classified by the finger tapping task (*p* , .023), right-versus left-handers classified by the hand dominance test (*p* , .012) and left-handers (as classified by the hand dominance test) with and without sinistral relatives (*p* , .045) were significant. However, the multiple testing procedure raises some doubt as to the ''true'' significance of these findings. Together with the uncertain nature of the assessment on the ''hand dominance test,'' a degree of skepticism in accepting these findings seems warranted. Furthermore, despite the wording of the abstract to the paper, no ‘‘correlation’’ was found between asymmetry in performance between the hands and anatomic asymmetry.

Foundas, Leonard, and Heilman (1995) used three-dimensional sagittal images to measure the length of the planum temporale. Their definition excluded the posterior ascending ramus. Subjects were eight right-handers (four males, four females) and four left-handers as assessed by the Briggs–Nebes modification of the Annett (1970) questionnaire. The authors report that the planum (measured at its greatest length) was longer on the left in six of the eight right-handers, equal in one case, and longer on the right in one right-hander. Among left-handers the planum was longer on the left in four cases, equal in one case, and longer on the left in three cases. Mean leftward asymmetry was said to be significant in the right-handers but not in the left-handers, but no analysis of variance was reported so the interaction between handedness and asymmetry was not tested; nor is the association between handedness and direction of asymmetry significant by chi-square. Even if these results were significant, it is not clear what they would show. The right-handers all had scores of 23 or 24 out of a maximum of 24; left-handers’ scores ranged from 2 1 to 2 24. Although scores of 23 and 24 can only be achieved by strong and consistent right-handers, scores close to zero can be achieved in a number of different ways, and it is not clear that individuals achieving such scores would necessarily be classified as left-handed by other scoring methods. Any difference between left- and right-handers in this study could as well be a function of degree as of direction of handedness.

Habib et al. (1995) measured the area of the planum from sagittal sections juxtaposed on an axial cut in 23 males and 17 females who were all normal volunteers. The definition of the planum included only the posterior ascending ramus ‘‘in cases where the caudal Sylvian fissure bifurcates into an ascending and a descending rami [sic]’’. (p. 241). Measurements were converted into an asymmetry coefficient. The authors write ‘‘using Steinmetz’s handedness classification and planum definition yielded no significant brain/handedness correlation’’ (p. 249). They refer to the Steinmetz definition as concerning only ‘‘the horizontal segment of the Sylvian fissure’’ whereas Steinmetz et al. in fact included the posterior descending ramus. Habib et al. excluded this but did include the posterior ascending ramus. Using a definition of handedness based upon a French translation of the 10-item version of the EHI, Habib et al. found that the ‘‘asymmetry coefficients were on the average significantly different between consistent right-handers and non-right-handers.’’ No statistical evidence for this ‘‘significant’’ effect is provided. Fortunately, Habib et al. provide detailed data for each of their subjects. I have calculated the *t* value between their right-handers (laterality quotient 80 or above) and left-handers (laterality quotient less than 80) and find that it is not significant.

The number of individuals showing a larger left than right planum was

25 (of 40). Of these, 19 were said to be consistent right-handers and the remainder (6) non-right-handers. Of the 15 cases with reversed asymmetry 10 were non-right-handers. Since there was no correlation between the anatomic asymmetry coefficient and handedness score considered both with and without regard to sign, Habib et al. argued that it is direction and not degree of handedness that was responsible for the association between direction of anatomic asymmetry and handedness. However, as only 5 subjects had a negative laterality index this does not necessarily follow.

In addition to measurement of the planum temporale Habib et al. measured the area of the parietal operculum. The two measures did not correlate significantly with each other but when both PT and opercular measures favored the left side of the brain, consistent right-handedness was found in approximately 90% of cases. This compares with 50% of cases with other combinations of asymmetry of the two regions.

Karbe et al. (1995) reconstructed volumetric measures of the planum from transaxial MR slices. They reported finding a larger left planum in 9 of 10 right-handed subjects, in 2 of 4 left-handers, and in one ‘‘ambidextrous’’ subject. At least one of the left-handers, it can be inferred from the article, showed a right-ward asymmetry. Handedness was apparently based on the EHI (but no criterion scores are given) and on ‘‘standardized tests of skilled motor performance’’; again, no details are provided.

Gender Differences in Cerebral Anatomic Asymmetry

As well as handedness differences in anatomic asymmetry, there have been occasional suggestions of a gender difference. Wada, Clarke, and Hamm (1975) reported that adult brain specimens showing a reversal of the usual left–right asymmetry of the planum temporale were more likely to be female than male. In a small group of neonatal specimens Witelson and Pallie (1973) noticed that the left–right difference was not as marked in males as in females. Contrariwise, Bear et al. (1986) found that 30 males showed significantly greater degrees of both frontal and occipital asymmetries on CT scan than 36 females.

Recently, Kulynych, Vladar, Jones, and Weinberger (1994) reported a significant gender-by-hemisphere interaction in MRI measurement of the planum from sagittal sections. In males the area of the left planum (which excluded tissue of the posterior ascending ramus) was found to be significantly greater than that of the right and, further, the left planum in males was larger than in females but there was no significant gender difference in the size of the right planum. These findings support those of Witelson and Kigar (1992) for the length of the horizontal segment of the Sylvian fissure (of which the posterior portion reflects the length of the planum temporale) and suggest that males may show greater anatomical asymmetry than females. Habib et al. (1995) reported that the mean leftward asymmetry of planum area was greater for females than for males but I have calculated from the data provided in their paper that the difference is not significant. Rossi et al. (1994) wrote ‘‘our findings suggest that females tend to have less PT asymmetry’’ but this was not significant on statistical testing.

In a study employing 70 normal males and 71 normal females (probably including those of Steinmetz et al., 1991), Jäncke et al. (1994) found no main effect of gender nor a handedness-by-gender interaction in asymmetry of the planum temporale (their definition included the posterior descending ramus whereas only the ascending ramus was included by Habib et al.). Since the nonsignificant gender difference in both Habib’s data and that of Jäncke et al. occurred in the context of significant effects due to handedness, it is unlikely that the negative effect for gender can be attributed to a lack of sensitivity in the method of measuring the planum.

Conclusions

There are relatively few studies of anatomic brain asymmetry (especially of the planum temporale) in relation to handedness or gender and fewer still which take into account other variables such as race (but see McShane et al., 1984) or adult age which conceivably is relevant. As far as handedness in relation to the planum temporale is concerned, the only postmortem study reported at the time of writing is that of Witelson and Kigar (1992). In their study Witelson and Kigar (1992) found no difference between their handedness groups in asymmetry of Sylvian fissure morphology (although they did report a bilateral difference). The definition used by Witelson and Kigar was that any subject not using the right hand for all items of the questionnaire that was administered (requiring subjects to demonstrate actual use of the hands) was classified as a nonconsistent right-hander. This means that others would probably classify a good proportion of such subjects as right-handed. Witelson and Kigar’s subjects included (at best) one consistent left-hander.

From the studies reviewed above, it appears that handedness and planum temporale asymmetry are related in some way but the exact nature of the relationship is obscure. The much cited *in vivo* MRI study by Steinmetz et al. (1991) claimed to find a greater degree of leftward asymmetry of the surface area of the planum among ‘‘right’’ than ‘‘left’’ handers. The latter finding was only significant for certain performance measures of handedness and not when handedness was defined by self-report. Similar results were subsequently reported by Jäncke et al. (1994) and by Habib et al. (1995) and, for length of planum, by Foundas, Leonard, Gilmore, and Heilman (1995). The results of all these *in vivo* studies as well as the postmortem study of Witelson and Kigar (1992) raise the possibility that any difference in magnitude of planum asymmetry is related not so much to direction as to degree of handedness. This possibility is supported by the finding of Kertesz et al. (1986) of a correlation between the relative difference between hands on Tapley and Bryden's circle-filling task and a composite measure of anatomical asymmetry relating to the region surrounding the planum temporale. Direction and degree of handedness should be considered separately (see also Bryden, 1987) in future research.

The conventional assumption is that planum asymmetry relates to language lateralization rather than to handedness per se. Alternatively, it may be that there is no functional significance to planum asymmetry, ''heretical'' though it may be to suggest this (see also Witelson & Kigar, 1988). It is true that Ratcliff, Dila, Taylor, and Milner (1980) reported that in patients with left hemisphere speech, as determined by Amytal testing, the mean asymmetry in the angle of the arch made by the branches of the middle cerebral artery as they passed under the parietal operculum was smaller on the left than on the right side. In patients with other than left hemisphere speech (i.e., with right-sided or bilateral speech) the mean asymmetry in the angle of the arch at the two sides was reduced significantly in comparison with patients having typical left-sided speech. Unfortunately, the relation of arteriographic asymmetry to asymmetry of the planum temporale is not known (see also Strauss et al., 1985), and some patients showed a marked dissociation between the directions of functional and morphological asymmetry.

A study by Jäncke and Steinmetz (1993) also raises questions about the relation of planum asymmetry to language lateralization. These authors found no correlation between extent of asymmetry in entire surface of the planum temporale and degree of asymmetry on any of four verbal dichotic listening tasks. What is striking is that the same subjects were reported as showing an association between handedness and anatomic asymmetry (Steinmetz et al., 1991). It is always possible, of course, that none of the dichotic tasks did, in fact, measure language lateralization. While the dichotic listening procedure may well be *capable* of reflecting the hemisphere responsible for speech (Zattore, 1989), individual dichotic tapes need to be validated against some other index (such as interruption of speech during the Wada Amytal test.) Steinmetz and colleagues have also reported that the planum temporale was significantly larger in a group of musicians who had perfect pitch as compared both with 19 musicians without perfect pitch and 30 non-musicians (Schlaug, Jäncke, Huang, Staiger, & Steinmetz, 1995). According to Jäncke (1995) this might be taken ''as evidence for a stronger leftward language lateralization in absolute pitch musicians'' since ''absolute pitch is defined as the ability to assign verbal labels to any tone.'' Alternatively, it could be argued that absolute pitch is a reflection of superior perceptual discrimination of certain types of nonverbal sounds and has little to do with language. Binder, Frost, Hammeke, Rao, & Cox (1997) found in a functional MRI study that activation patterns in the area of the planum temporale were equivalent for words and tones during passive listening and higher for tones than words during active listening.

It needs to be appreciated that the planum temporale is defined purely in morphological terms. It is not a single architectonic area, nor is there at present any evidence that it functions as a single entity. Indeed, Galaburda, Sanides, and Geschwind (1978) and Galaburda and Sanides (1980) identified on architectonic grounds an area of cortex (Tpt) which

> Represents a transitional type of cortex lying between the specialized isocortices of the auditory region and the more generalized isocortex (integration cortex) of the inferior parietal lobule . . . . Area Tpt often extends beyond the caudal end of the temporal lobe to occupy variable amounts of suprasylvian cortex. (p. 60)

In three out of four brains studied by Galaburda, Sanides, and Geschwind (1978) (and in two of three in Galaburda & Sanides, 1980) there was marked left–right asymmetry of Tpt in the direction of a larger area on the left. The asymmetry was less marked but in the same direction for the fourth brain. It might be argued that asymmetry of area Tpt may be exist even when there is no asymmetry in the overall planum and that it is asymmetry of Tpt that is important. However, an increased extent of area Tpt on the left was in each case associated with a larger left planum temporale and the asymmetry was of corresponding magnitude (Galaburda, Sanides, & Geschwind, 1978).

In a recent study which attempted to determine the relationship between volumetric asymmetry of structure and asymmetry of function, MRI images were compared with PET scans from the same 15 subjects (Karbe, Würker, Herholz, Ghaemi, Pietrzyk, Kessler, & Heiss, 1995). Scans were taken while the subjects repeated (German) nouns and, on a separate occasion, during a rest condition. By superimposing MR and PET scans the investigators were able to look at regions of metabolic activation in relation to the planum temporale within each individual subject. No asymmetry was observed in extent of activation of the planum on left and right sides during repetition, although there was an asymmetric increase in activation during the repetition condition in Brodmann's area 22 (BA22). According to the authors, ''The left BA22 (sulcus) was the only region that showed a significant correlation between planum size and functional activation. . .morphological predominance of the left planum temporale was associated with a reduced metabolic activation in BA22 (sulcus)'' (p. 871). The implication is that an obsession with the size, as opposed to the significance, of the planum temporale may well be misplaced.

Handedness and Speech Lateralization

If direction of handedness were perfectly correlated with direction of asymmetry of the planum temporale, then left-handers should be those with a rightward asymmetry of the planum temporale. It is clear that this is not the case. Alternatively, if anatomic asymmetry is related to language lateralization then one would expect those with right hemisphere speech to have rightward asymmetry of the planum temporale. Foundas, Leonard, Gilmore, Fennell, and Heilman (1994) report some suggestive data. These authors used MRI to measure the size of the plana in 12 patients who had undergone

Wada testing. One of these patients was said to be a non-right-hander who had right-hemisphere speech and rightward asymmetry of the planum temporale. The remaining patients all had leftward asymmetry and left hemisphere speech. Since handedness scores were not provided, it is unclear whether the non-right-hander was in fact left-handed or merely showed a lesser degree of right-handedness than other patients.

One question that needs to be asked is what proportion of the population has right hemisphere speech lateralization and therefore what proportion of rightward anatomic asymmetry would one expect if in fact planum asymmetry relates to language lateralization? (For the present purposes the related question of bilateral speech representation will be ignored.)

Ignoring findings from experimental techniques used with normal subjects which are probably too inaccurate to be useful in this context, the data on right hemisphere speech lateralization come from two main sources. The first is the incidence of aphasia following unilateral cerebral lesion; the second source is provided by sodium Amytal studies.

With regard to the Amytal studies, figures reported from Montreal by Rasmussen and Milner (1975, 1977) have been much quoted. Of 134 right-handed patients, 6 (4.5%) had right-sided speech; of 122 non-right-handers, 18 (14.75%) had right-sided speech and 18 had bilateral speech. Assuming an incidence of about 10% left-handedness in the general population (Gilbert & Wysocki, 1992; Davis & Annett, 1993), this would indicate an overall proportion of right hemisphere speech in the population of roughly 5.5%. There are, however, certain difficulties with accepting Rasmussen and Milner's figures. Firstly, the relative frequency of right-hemisphere speech in right-handers was not determined by testing all right-handed candidates for brain surgery; rather, the Amytal test was administered only to those right-handed candidates for whom there was some reason to suspect that they showed atypical lateralization. This is likely to inflate the figure for right hemisphere speech in right-handers (Beaton, 1985). Conversely, the definition of non-right-handedness adopted by Rasmussen and Milner is such that many individuals would have been classified as right-handed by more conventional criteria (Bryden & Steenhuis, 1991). This would lead to a higher proportion of right hemisphere speech among right-handers than was actually reported.

The figures I have quoted from Rasmussen and Milner's paper are for individuals in whom the lesion occurred after the age of 2 years. Although there are indications that lesions occurring even after this age may lead to some interhemispheric reorganization of speech functions (Rey, Dellatolas, Bancaud & Talairach, 1988; Strauss, Wada, & Goldwater, 1992), the Rasmussen and Milner data fall within the range of figures reported by other investigators. These vary from 1.5% (Loring et al., 1990) to 7.8% (Strauss, Gaddes, & Wada, 1987) for right-hemisphere speech lateralization among right-handers; corresponding figures range from 8.3% (Woods, Dodrill, & Ojemann 1988) to 15% (Rasmussen & Milner, 1975; 1977) for non-right-handers. Results from different clinics may not be entirely comparable due to differences in dose and method of administration of the drug and the criteria used to determine language preservation or disruption (Snyder, Novelly, & Harris, 1990).

In general, the Amytal data suggest an approximate proportion of right-hemisphere speech representation in right-handers of anything from 1.5 to 7.8%. These values are not too dissimilar to the estimates of 1 and 4.5%, respectively, by Segalowitz and Bryden (1983) and Carter, Satz, and Hohenegger (1984) based on aphasia data, but are a little lower than Annett's (1975) estimate of 9.2% based on the entire population (left- and right-handers). The latter is roughly consistent with a recent Amytal study by Kurthen, Helmstaedter, Linke, Hufnagel, Elger, and Schramm (1994) who found complete right hemisphere speech representation in 15 of 173 patients (8.7%). Taken together the lesion and the Amytal data indicate that fewer than 10% of the population have right-sided speech lateralization. How does this compare with the distribution of asymmetry of the planum temporale?

Large scale postmortem studies of asymmetry of the planum are not common. Only those of Geschwind and Levitsky (1968), Galaburda et al. (1987), Teszner et al. (1972), Wada et al. (1975), and Kopp et al. (1977)—each of approximately 100 brains—come anywhere near providing a good estimate of the likely asymmetry and that only if their definitions are accepted. If so, then the occurrence of a rightward bias in the size of the planum (11% in Geschwind & Levitsky for their linear measure and, for area measures, 10% in both Teszner et al. [1972] and Wada et al. [1975]; 21.7% in Kopp et al. [1977] and 21% in Galaburda et al. [1987]) is either just as common as or rather more frequent than right hemispheric speech lateralization (depending upon whose figures are accepted). On the other hand, the postmortem studies arguably overestimate the relative frequency of rightward asymmetry since they all excluded from measurement the terminal branches of the Sylvian fissure; inclusion of this tends to reduce the degree of asymmetry (Steinmetz et al., 1990).

In a report of a comparison of the largest number of right- versus non-right-handers in an MRI study to date, Jäncke et al. (1994) give only mean values of planum asymmetry separately for 106 right-handers and 35 left-handers. However, Steinmetz (1995) provides a figure based on results from (more or less) the same 121 right-handers and 33 left-handers (as usually defined by this group of researchers). It can be calculated from the figure that in 20 (16.5%) right-handers (and in 14 of 33 left-handers) the right planum was larger in area than the left. Based on these figures and those referred to above, a conservative conclusion would be that frequency of reversed anatomic asymmetry is rather higher than estimates of the frequency of right hemisphere lateralization of speech. Note, however, that the deficits associated with lesions of the upper surface of the temporal lobe tend to involve receptive rather than productive aspects of speech. It is therefore lateralization of speech perception and comprehension, as opposed to production, that might be expected to go with anatomic asymmetry of the planum.

Despite the apparent robustness of the finding of a larger planum temporale on the left side it is possible that left–right asymmetry as revealed in at least some MRI studies is an artifact of measurement. Loftus, Tramo, Thomas, Green, Nordgren and Gazzaniga (1993) used two algorithms to measure the planum. They found no left–right asymmetry in area of the region extending from the (first) transverse gyrus of Heschl and including the ''superior surface of the supramarginal gyrus lying along the inferior bank of the PAR (posterior ascending ramus)'' using an algorithm which ''took into account the folding and curvature of the cortical surface across adjacent coronal sections.'' Using an algorithm that did not do so (which is commonly employed in studies of this kind) there was a significant leftward asymmetry. ''Since the same contours were used for both . . . estimates, the different results obtained concerning hemispheric asymmetry were solely due to differences in the algorithms'' (p. 353). For discussion of other potential artifacts, the reader is referred to Glicksohn and Myslobodsky (1993).

In a combined postmortem and MRI study, Steinmetz et al. (1990) (see also Habib et al. 1995) found a significant leftward asymmetry of the exposed planum but a rightward asymmetry of total surface of cortex buried *posterior* to the planum and thus no significant left–right asymmetry in ''combined cortical surface area buried in whole posterior Sylvian fissure caudal to the first transverse gyrus.'' A similar point was made with regard to postmortem measurements by Witelson and Kigar (1992). As long ago as 1976, Rubens et al. wrote ''the planum temporale is longer on the left because the horizontal portion, but not necessarily the entire length, of the lateral fissure is longer on the left.'' If leftward asymmetry of the exposed planum may be balanced by a rightward asymmetry in the cortex of the depths of the Sylvian fissure, there may be little to justify considering only the planum as conventionally defined.

In summary, the uncertain situation with regard to both the functional significance of asymmetry of the planum temporale and its putative relationship with handedness needs to be borne in mind when attempts are made to interpret the significance of deviations from the presumed ''normal'' pattern of asymmetry as, for example, in dyslexia (see below).

THE ROLE OF THE CORPUS CALLOSUM

According to Galaburda and colleagues, ''Callosal connections are most certainly at the core of interhemispheric relationships and the phenomenon of cerebral dominance, and variability in this system of connections is likely to be reflected in variability in hemispheric specialisation. . .'' (Galaburda, Rosen, & Sherman, 1990, p. 530). They suggested on the basis of research in the rat (Rosen, Sherman, & Galaburda, 1989) that there is an inverse relation between magnitude of cerebral anatomic asymmetry (regardless of direction) and extent of commissural connections between the relevant cortical areas. Witelson and Nowakowski (1991) went further in arguing that ‘‘naturally occurring axon loss during early brain development may be a mechanism involved in determining hand preference and associated hemispheric asymmetries’’ (p. 328). It was proposed that the greater the loss, the smaller the corpus callosum and the greater the lateralization of function to the right hand. The evidence reviewed above suggests that the precise relation between cerebral anatomic asymmetry and handedness or gender has yet to be determined. What then of the relation of these variables to callosal morphology (as measured in the mid-sagittal plane either postmortem or *in vivo*)?

Gender Differences and Callosal Size

In the first of the studies suggesting sexual dimorphism in the human corpus callosum, De Lacoste-Utamsing and Holloway (1982) found the maximum width of the splenium (usually taken to be the posterior fifth of the callosum) to be larger in five female than in nine male brains examined postmortem. They reported that though absolute callosal area did not differ, it was greater in females relative to brain weight, but the statistical significance of this ratio was not presented. Since partial correlations between maximal splenial width and total brain weight, age, body weight, and height accounted for ‘‘very little of the variance’’ it was concluded that ‘‘the relationship between maximal splenial width and sex cannot be explained by these variables.’’ In an extension of their original study, Holloway and De Lacoste-Utamsing (1986) reported that the cross-sectional area and maximal splenial width were larger in females even though male brains were heavier overall. A comparable gender difference in splenial width was also found in fetal specimens aged 11–40 weeks (de Lacoste, Holloway, & Woodward, 1986). This result was not replicated by Clarke, Kraftsik, Van der Loos, and Innocenti (1989) who compared the brains of 16 male and 16 female fetuses of 20–42 weeks gestation.

Unlike Holloway and de Lacoste-Utamsing (1986) who reported a gender difference in the width of the splenium, Witelson (1989) found a proportionally larger isthmus in females than in males. The findings of a gender difference in callosal size have generally not been replicated in other postmortem studies (e.g., Bell & Variend, 1985; Bleier, Houston, & Byne, 1986; Weber & Weis, 1986; Demeter, Ringo, & Doty, 1988) which often failed to control for overall size of the callosum or brain, although one study (Clarke et al., 1989) found the cross-sectional area of the posterior fifth of the callosum to be proportionally larger in males while the maximal splenial width did not differ between the sexes. The total area of the corpus callosum measured postmortem by Aboitiz et al. (1992) was larger in males though not significantly so. The difference between the sexes for the isthmus alone was significant but not when overall brain weight or overall callosal size was taken into account.

Findings concerning gender differences in mid-sagittal total or regional callosal measures obtained from neuroimaging studies have tended also to be negative (Kertesz et al., 1987; Oppenheim, Benjamin, Lee, Nass, & Gazzaniga, 1987; Weis, Weber, Wenger, & Kimbacher, 1988; Allen, Richey, Chai, & Gorski, 1991). Byne, Bleier, and Houston (1988) emphasized the considerable degree of individual variation they found in their MRI study of 22 females and 15 males. These authors failed to find any gender difference in area of the splenium although there was a significant difference in the minimum width of the body of the callosum which was smaller in men (with no correction for total callosal or brain size). There was also a suggestion of an age-related sex difference in that men over 40 years of age, but not those under this age, had a smaller total callosal area than women of this age group. This may be relevant to the study by Holloway and de Lacoste (1986) since the age range of their male specimens was 35–81 years and for female brains 53–87 years.

Reinarz, Coffman, Smoker, and Godesky, (1988) found that whereas the ratio of total callosal area to overall brain did not differ between the sexes, the ratio of the first quarter of the callosum to entire callosal area was greater in males than in females. At the same time, the ratio of the posterior quarter to total callosum was greater in females. Casanova, Sanders, Goldberg, Bigelow, Christisin, Torrey, and Weinberger (1990) state that the corpus callosum was longer in 10 males than in 14 females among 12 pairs of monozygotic twins discordant for schizophrenia. However, no statistical test of this difference is reported. Total callosal area (whether ‘‘corrected’’ or not for total hemispheric sagittal area) did not differ between the sexes and diagnosis did not affect the callosal measures. Length of callosum (which did not correlate with hemispheric area) was larger in males. A gender difference in length but not area of the callosum suggests the possibility that the callosum was thinner in males. While no direct comparison of this is presented, the authors did report that the shape of the posterior callosum differed significantly between the sexes. Denenberg, Kertesz, and Cowell (1991) reported that the callosum was more circular in females than males.

In a retrospective MRI study of 24 children aged 2–16 years (12 males, 12 females matched for age) and 61 age-matched pairs of adults (one of each sex in each pair), Allen et al. (1991) found no convincing evidence of a sex difference in the total area of the callosum or in any subdivision. They did report, however, that the callosum differed in shape between the sexes, being more bulbous in females. They also reported that callosal area increased significantly with age in children (see also Schultz et al., 1994) and decreased significantly with age in adults.

Clarke and Zaidel (1994) reported MR findings with 60 subjects, 30 of each sex. Minimum width of the body of the callosum (both normalized and unnormalized for total callosal area) was larger in females as was the normalized isthmus area. Burke and Yeo (1994) measured the maximum length of the callosum and the mid-callosal width as well as the areas of seven callosal regions. With total cerebral volume as a covariate the genu, rostrum (and entire anterior half of the callosum) were each significantly larger in 38 females than in 59 males. Unfortunately neither Bonferroni nor other correction was applied to their data despite the use of multiple *t* tests. Burke and Yeo (1994) found a negative correlation between total callosal area and age to be significant for males but not for females.

Overall, then, there is little convincing evidence of a gender difference in total callosal size and conflicting data concerning individual callosal regions. Some authors have reported segments of the female corpus callosum to be relatively larger than in males (de Lacoste-Utamsing & Holloway, 1982; Holloway & de Lacoste-Utamsing, 1986; Witelson, 1989; Steinmetz et al., 1992; Burke & Yeo, 1994; Clarke & Zaidel, 1994); others have failed to replicate this effect or have reported the opposite (Aboitiz et al., 1992; Clarke et al., 1989). Kertesz et al. (1987) found no significant gender difference in callosal size unless callosal size was corrected for brain size. In this case there was a small but significant gender difference—the ratio of callosum to brain size was larger in females. For this comparison, a measure of the cross-sectional horizontal areas of both hemispheres was taken as an index of total brain size. However, when brain size was sagittal cross-sectional area of one hemisphere the difference was not significant. The dependence of a significant effect upon the particular value of the correction factor suggests that any genuine gender differences are likely to be fairly subtle. Moreover, Jäncke, Staiger, Schlaug, Huang, & Steinmetz (1997) have recently reported that as brains become larger, the callosa do not increase in the same proportion. Nonetheless, it is clearly important that overall brain size is considered when comparing callosal size between males and females.

Witelson (1989; 1991) reported that callosal size decreased with age in male but not in female postmortem specimens. These findings are supported by those of Burke and Yeo (1994) using MRI who found a greater decline in callosal area with age among males than among females. If these findings of gender-related changes in callosal size with age were confirmed (see also Byne et al., 1988) they would have obvious implications for comparisons between the sexes at different ages even if the sexes were otherwise well matched. It may be, for example, that Burke and Yeo's own finding of a larger anterior callosal area in females relates to the fact that their subjects were on the whole considerably older than those normally recruited for such studies. Clarke et al. (1989) compared males and females varying in age from 17 to 93 years so the apparent gender difference they reported may have been artifactually related to age (details for each sex separately are not provided). However, gender-related age changes could not explain the findings of Steinmetz, Jäncke, Kleinschmidt, Schlaug, Volkmann, and Huang (1992) who investigated the relationship among handedness, gender, and callosal size in the same sample of young healthy volunteers as they used to investigate planum temporale asymmetry. These authors found the area of the isthmus region to be relatively larger in 26 females than in 26 males but there was no difference in the splenial region.

Clarke and Zaidel (1994) found a significant negative correlation between the size of the isthmus and Sylvian fissure asymmetries and planum temporale asymmetry whether corrected or uncorrected for brain size and whether asymmetry was defined in absolute terms or in terms of an asymmetry coefficient (L 2 R/L 1 R). Since the isthmus connects ''the two perisylvian regions of both hemispheres'' this suggests reduced callosal connections between more asymmetric regions (as suggested by Witelson, 1985, 1989 and Galaburda et al., 1990). In males alone there was a strong negative correlation between the area of the anterior mid-body of the corpus callosum (whether corrected or not for total callosal area) and the length of the left Sylvian fissure and between the posterior midbody and the right Sylvian fissure. It was argued that together ''these findings suggest that a closer relationship between perisylvian areas and callosal structure may exist in males than in females.'' In their *in vivo* MRI study, however, Burke and Yeo (1994) found significant correlations between anterior and posterior left and right hemispheric volumes and callosal area in females suggesting that callosal anatomy and extent of other brain areas may be more closely linked in females.

Handedness and Callosal Morphology

The first report of differences in callosal morphology as a function of handedness was that of Witelson (1985) who reported that the area of the posterior region of the corpus callosum measured postmortem was larger in area in the brains of nonconsistent right-handers than in consistent right-handers (total *N* 5 42). This finding was replicated in an expanded study (*N* 5 50) inasmuch as the isthmus (immediately anterior to the splenium) was larger in male nonconsistent right-handers (Witelson, 1989). In a more recent study of 22 men alone (including those from the earlier samples), this finding was again replicated and a hand preference score (reflecting both magnitude and direction) was found to correlate significantly with area of the isthmus (Witelson & Goldsmith, 1991). The authors argue that the isthmus would be expected to show the greatest difference between handedness groups since it houses fibers from ''cortical regions particularly relevant to functional asymmetry.''

Kertesz et al. (1987) used reported writing hand to identify 52 right-handers and 52 left-handers and subsequently used a five-item questionnaire (weighted to reflect degree of use for each item including writing) to assess hand preference. They used a tapping task (Tapley & Bryden, 1985) to assess performance. There was no significant correlation between hand performance asymmetry and total callosal area as measured on MRI scan. No significant pairwise difference was found in callosal size of strong right-handers (*n* 5 50), strong left-handers (*n* 5 24), and mixed-handers (*n* 5 30), the largest size being that of strong right-handers followed by strong left-handers. (A single statistical test in relation to degree of handedness was not carried out.) The data of this study were reanalyzed by Denenberg et al. (1991) using a hand preference classification similar to that of Witelson; among men, nonconsistent right-handers had a larger isthmal area than that of consistent right-handers. This supports the earlier postmortem findings of Witelson (1985, 1989). No correction for overall brain size was carried out since there was no correlation between corpus callosum area or width of any region and a measure of ‘‘brain area . . . calculated from the total cortical surface digitized at the first horizontal section above the third ventricle.’’ Cowell, Kertesz, & Denenberg (1993) provide a further re-analysis of their MRI data and report a significant interaction between ‘‘consistency’’ and writing hand for certain callosal regions.

Using *in vivo* MRI in contrast to Witelson’s postmortem material, neither Reinarz et al. (1988) nor O’Kusky, Strauss, Kosaka, Wada, Druin, and Petrie (1988) found any difference in the size of the corpus callosum (or any specific callosal region) as a function of ‘‘handedness.’’ The measure of laterality used in the latter study was taken from Porac and Coren (1981) and confounded hand, eye, ear, and foot preference (but without including writing hand among the questions asked). Reinarz et al. state that they used the Edinburgh inventory but no details are provided.

Callosal areas in the mid-sagittal plane were measured by means of MRI by Hines, McAdams, Chiu, Bentler, and Lipcamon (1992) in 28 normal women. Hand preference was assessed by questionnaire which included the same items as those used by Witelson (1985). Subjects were divided into consistent right-handers and others. Again, no effect of handedness on callosal size was found.

Steinmetz et al. (1992) distinguished between consistent left-handers and mixed-handers using what they term Witelson’s questionnaire ‘‘based on the work of Annett.’’ Consistent left-handers (*n* 5 9) demonstrated left-hand use ‘‘with one or two either preferences’’ for all 12 items; consistent right-handers (*n* 5 19) were defined in an analogous way and mixed-handers were the rest (*n* 5 24). No handedness differences in callosal area were found in this study for any of the segments measured or in total callosal size.

Clarke, Lufkin, and Zaidel (1993) determined callosal area from MR images in normal young adults. There were 15 left-handers and 15 right-handers of each sex. All 30 right-handers wrote with the right hand and showed no left-hand preference for any of eight other actions; all 30 left-handers wrote with the left hand but ‘‘had varied hand preferences for the other right items.’’ Callosum measures per se did not differ between left- and right-handers, although these measures were not corrected for overall brain size.

Clarke and Zaidel (1994) found no significant effect of handedness on callosal size when subjects were categorized as left- or right-handed according to their responses on a modified version of the EHI. Right-handers were those who indicated no left preference for any of the nine items used. Left-handers were those who indicated a preference for the left hand for at least one of the tasks. Division of the left-handers into consistent left- (left hand preferred for all items) and mixed-handers (the remainder) still led to no effect of handedness (nor interaction with gender). However, exclusion of the consistent left-handers resulted in a significant gender-by-handedness interaction for the isthmus (normalized for total callosal area) which was larger in consistently right-handed females than in consistently right-handed males, while no gender difference was apparent for the mixed-handers.

The largely negative findings of the *in vivo* studies reviewed above would lead to the conclusion that there are no differences in callosal size between left- and right-handers. Recently, however, Habib, Gayraud, Oliva, Regis, Salamon, and Khalil (1991), using MRI and incorporating data reported earlier by Habib (1989), have to some extent supported Witelson's postmortem findings by demonstrating with healthy young adults an enlarged callosal region in nonconsistent right-handers, but this time for the area of the anterior body of the callosum just caudal to the genu and thus more anterior than Witelson's region.

The study by Habib et al. (1991) was carried out with 53 normal volunteers of whom 8 had a laterality quotient on the Edinburgh Handedness Inventory of less than 0 (indicating greater use of the left hand). For purposes of analysis, subjects were divided into two groups: those with an LQ of 80 or more were termed consistent right-handers and those with LQ less than 80 were termed nonconsistent right-handers (including left-handers). The former were found to have significantly smaller anterior callosal areas (corrected for total brain volume) than nonconsistent right-handers, at least among males. Among females, the posterior body of the callosum was larger among consistent than among nonconsistent right-handers. Habib et al. also looked at the degree of handedness without regard to direction. This measure correlated significantly with callosal measures; the greater the strength of handedness, the larger were several areas of the callosum. Their findings therefore suggest that callosal size is related to degree rather than direction of handedness.

In the largest study to date, Burke and Yeo (1994) measured the midsagittal area of the callosum in 97 subjects ranging from 56 to 90 years of age. They found that in males the area of the posterior callosum was significantly correlated with increasing right-handedness as measured by a 47-item handedness questionnaire. For females, both the anterior and posterior callosum area (as well as mid-callosal width) correlated inversely with hand preference scores. Age correlated differently with callosal area in males and females but was said to be unrelated to handedness (although no details were provided); thus, the correlations between size of the callosum and hand preference were not confounded by age.

Clarke and Zaidel (1994) correlated their measures of callosal size with a number of indices of behavioral laterality. It was argued that the correlational findings were consistent with the view that regional callosal size is related to functional interhemispheric inhibition (see Cook, 1984) and to hemispheric differences in arousal. O'Kusky et al. (1988), Hines et al. (1992), and Yazgan, Wexler, Kinsbourne, Peterson, and Leckman. (1995) all reported an inverse relationship between overall callosal area and extent of differences between the two ears on a dichotic listening task. Using a principal components analysis, Hines et al. (1992) obtained a significant negative relationship between the area of the posterior callosum and the degree of language lateralization (derived from absolute magnitude of dichotic ear asymmetry and the phi coefficient); the smaller the callosal area, the greater the degree of lateralization. This latter result was significant only on one-tail testing. Kertesz et al. (1987) found no relationship between callosal cross-sectional area and either tachistoscopic visual half-field difference scores or dichotic listening asymmetry.

Conclusions

From the studies reviewed above (summarized in Tables 2a and 2b) it is clear that there is considerable controversy regarding differences in callosal size as a function of both handedness and gender. For example, Witelson (1989), using postmortem material, and Habib et al. (1991), using *in vivo* MRI, reported handedness effects primarily in men; Burke and Yeo (1994), using MRI, found their effects to be more prominent in women. Steinmetz et al. (1992) and Hines et al. (1992), also using MRI, found no handedness difference at all. Even where sex or handedness differences have been found in either area or width there is little agreement as to the region of the callosum concerned, particularly in relation to the splenium and isthmus, or with regard to the nature of the ''handedness'' effect. It does not appear that disagreement hinges on the method of investigation that is adopted, postmortem versus *in vivo.*

Only the MRI studies of Kertesz et al. (1987), Steinmetz et al. (1992), and Clarke and Zaidel (1994) separated consistent left-handers from mixed-handers. Their failure to find a significant difference among handedness groups may be due to relatively small sample sizes, but an analysis of the Steinmetz data by Witelson (1992) suggests the possibility (as was suggested above for asymmetry of the planum temporale) that degree or consistency of handedness rather than direction may be important in relation to callosal morphology. A similar conclusion can be drawn from the results reported by Habib et al. (1991) and Burke and Yeo (1994).

Confirmation in neurologically undamaged subjects of the recent claim that IQ and the area of the posterior callosum are significantly correlated in epileptic subjects (Strauss, Wada & Hunter, 1994) would imply that future

TABLE 2a
Postmortem Investigations of Corpus Callosum

Authors	Subjects	Handedness	Age	Findings	Remarks
de Lacoste, Utamsing & Holloway (1982)	9 males 5 females	NK	Not reported	Average area of posterior fifth of callosum larger in females (p , .08)	No correction for overall brain size but partial correlation with brain weight accounted for very little variance
de Lacoste et al. (1986)	19 male fetuses 13 female fetuses	N/A	11–40 weeks gestation	Significantly greater splenial width in females	
Holloway & de Lacoste (1986)	8 males 8 females	NK	35–81 yrs 53–87 yrs	Total area of callosum greater in females; max. splenial width greater in females.	
Witelson (1985)	7 males 20 females	Consistent right-handers (CRH)	Mean: 50.3 yrs	CRH had smaller mid-sagittal area of callosum; significant for anterior and posterior halves separately, but not posterior fifth. No correlation between handedness score and callosal area in NCRH.	NCRH: Any action of 12 performed with left hand.
	5 males 10 females	Non-consistent right-handers (NCRH)	Mean: 48.7 yrs	No significant sex difference.	There were no consistent left-handers.
Witelson (1989)	9 males	CRH	Mean: 50.8 yrs	Larger isthmus (posterior mid-body) in NCRH but significant only for males.	Callosal size decreased with age in males but not females.
	23 females	CRH	Mean: 49.6 yrs		

	6 males	NCRH	Mean: 50.5 yrs	No sex difference in splenial size or in total callosal size. Isthmus proportionally larger in females.	Handedness scores as in 1985 paper.
	12 females	NCRH	Mean: 52.0 yrs		
Witelson & Goldsmith (1989)	13 males	CRH	51–69 Mean: 53.6 yrs	Total callosal size significantly larger in NCRH and isthmus significantly larger in NCRH.	Of the NCRH subjects, 8 wrote with the right hand; of these 3 were forced to do so when young. No correction for overall brain size.
	9 males	NCRH (see Witelson 1985; 1989)		Significant negative correlation between hand score and area of isthmus.	
Witelson (1991)	23 males		26–69 yrs Mean: 54 yrs	In males, callosal area decreased significantly with age; no correlation for women.	No correction for overall brain size.
	39 females		35–65 yrs Mean: 52 yrs		
Bell & Variend (1985)	28 males 16 females	No details provided	0–14 yrs	With age as covariate in ANCOVA, females had smaller maximum splenial width; not significant when age and brain weight both taken into account.	
Weber & Weis (1986)	18 males 18 females	No details provided	Mean: 72.85 yrs Mean: 76.58 yrs	No sex difference on any measure (total callosum and caudal $1/5$, $1/4$, $1/3$).	
Demeter et al. (1988)	22 males 12 females	N/K	23–91 Mean: 64 yrs 20–82 Mean: 58 yrs	No sex difference in maximum splenial width or in total area or of area of posterior fifth of callosum.	No correction for overall brain size. No correlation between callosal area and age or brain weight.

TABLE 2a—*Continued*

Authors	Subjects	Handedness	Age	Findings	Remarks
Clarke, S. et al. (1989)	27 males 19 females	No details provided	17–93 yrs	Posterior fifth of callosum proportionally larger in females; total callosal area greater in males—both effects are significant.	No correction for overall brain size. Also carried out MRI study of 5 males and 7 females (not included in postmortem material). (Larger callosum in men not found in MRI sample.)
	16 male fetuses 16 female fetuses		20–42 weeks gestation	No significant sex difference in maximum splenial width.	
	11 male infants 12 female infants		0–14 months	Pre-splenium thickness significantly smaller in females.	
	2 male children 3 female children		23 months–14 yrs	No sexual dimorphism in fetuses. Male infants had significantly larger total callosal area than female infants and significantly greater length.	
Aboitiz et al. (1992)	20 males	Right-handers (no details provided)	Mean: 48.5 yrs	No significant difference in size of callosal segments when corrected for total callosal area–otherwise isthmus sig. larger in males.	Also examined asymmetry of planum temporal—no significant sex differences were found.
	20 females		Mean: 45.1 yrs Combined range: 25–68 yrs	In males, significant negative correlation between area of anterior mid-body of callosum and length of left Sylvian fissure and between mid-body and fissure.	

Note. NK, not known; N/A, not applicable; CRH, consistent right-handers; NCRH, non-consistent right-handers.

studies of gender and/or handedness differences in callosal morphology should control for IQ as well as for age. Intriguingly, Schlaug, Jäncke, Huang, Staiger, and Steinmetz (1995) have recently reported that the anterior portion of the corpus callosum was greater among professional musicians who received training before the age of 7 years as compared with musicians who began training after this age. Since surgical section of the anterior callosum impairs performance on bimanual tasks (Preilowski, 1975), this finding suggests the possibility that experience (specifically bimanual training) can influence the size of the (anterior) callosum. If confirmed, this, too, would need to be taken into account.

SPECIFIC READING DISABILITY/DEVELOPMENTAL DYSLEXIA

The notion of specific reading disability rests upon the assumption that some individuals find learning to read (and to spell) disproportionately difficult. There is a problem in defining exactly what is to count as ‘‘disproportionate.’’ The well-known definition of specific developmental dyslexia adopted by the World Federation of Neurology was ‘‘a disorder manifested by difficulty in learning to read despite conventional instruction, adequate intelligence and sociocultural opportunity. It is dependent upon fundamental cognitive disabilities which are frequently of constitutional origin’’ (Critchley, 1970, p. 11). This definition begs the question as to what is to count as ‘‘adequate’’ intelligence and ‘‘fudges’’ the issue of etiology by referring to the origin of the disorder being ‘‘frequently’’ constitutional thereby allowing the possibility that it sometimes is not. Claims that there is something unusual about the brain organization of dyslexics are in general tacitly assumed to provide evidence in favor of a constitutional disability.

The central idea underlying the notion of specific dyslexia, namely that of a fundamental mismatch between an individual’s level of reading and the level to be expected on the basis of intelligence, education, and culture, has gained almost universal acceptance despite certain problems in defining dyslexia in terms of a ‘‘discrepancy’’ between IQ and reading ability (Siegel, 1988; Stanovich, 1994; McDougall & Ellis, 1994; Ellis, McDougall & Monk. 1996). There is, however, considerable controversy in the literature as to whether dyslexia represents the tail end of a normal distribution of reading ability (in which case there would be no theoretical reason to distinguish between so-called ‘‘garden’’ variety and dyslexic poor readers) or whether it represents some kind of anomaly (Miles & Haslum, 1986).

Rutter and Yule (1975) reported that ‘‘children [with specific reading disability] form a ‘hump’ at the bottom of the normal curve.’’ This work has been criticized by a number of authors (e.g., Rodgers, 1983; Thomson, 1982; Shaywitz, Escobar, Shaywitz, Fletcher, & Makuch, 1992a) and Stanovich (1988) states categorically that ‘‘There is in fact no hump in the distribution.’’ More recently Shaywitz et al. (1992a) (using a discrepancy definition

TABLE 2b
Neuroimaging Studies of the Corpus Callosum

Authors	Subjects	Handedness	Age	Magnetic strength	Findings	Remarks
Kertesz et al. (1987)	25 males 27 females	Right-handed writers	18–49 yrs Mean: 26.9 yrs		No gender difference in total callosal area (with handedness ignored).	
See also Denenberg et al. (1991) and Cowell et al. (1993)	26 males 26 females	Left-handed writers			No handedness difference (with gender ignored).	
	50 30 24	Strong right-handers Mixed handers Strong left-handers Measured by questionnaire Bryden (1977). No further details		0.15T	No association between gender or handedness and size of splenium relative to genu (on visual inspection). With horizontal measure of brain size, callosum-to-brain size ratio larger in females; no gender difference with sagittal cross-sectional area as measure of brain size.	
Oppenheim et al. (1987)	40 males 40 females	No details provided	No details provided	0.5T	No gender difference in any of 5 callosal segments, including posterior fifth.	
Weis et al. (1988)	20 males 20 females	No details provided	Mean: 44.1 yrs Mean: 48.9 yrs	0.5T	No gender difference in spenial width, total length or area.	No correction for overall brain size.
Byrne et al. (1988)	15 males	NK	14–68 yrs Mean: 46.5 yrs	1.5T	Significantly smaller width of body of callosum in males.	No correction for overall brain size. Also found age effect—length of callosum smaller in those over 40 yrs.
	22 females	NK	16–68 yrs Mean: 36.9 yrs		No gender difference in area of splenium.	
O'Kusky et al. (1988)	23 male epileptic patients 27 female patients 26 male controls 24 female controls	Handedness combined with other lateral preferences.	11–57 yrs 17–60 yrs	0.15T	Larger callosal area in those with right hemisphere speech compared with left or bilateral speech. Significant negative correlation between coefficient of dichotic ear asymmetry and callosal size (left ear advantage associated with greater callosal area).	No correction for overall brain size. Negative findings for laterality—no difference in total size or segment of callosum as function of laterality (but measure of laterality combines hand, foot, ear and eye preference).

Reinarz et al. (1988)	20 males 20 females 20 males 20 females	Right-handed Right-handed Left-handed Left-handed Assessed by EHI but details not provided.	Range 19–40 yrs	0.5T and 1.5T	No overall difference in callosal area/brain ratio between sexes or handedness groups. *But* Ratio of anterior quarter of callosum to entire callosal area was greater in males than in females; for posterior quarter (splenium), this ratio was greater in females than in males. No effect of handedness.	Differences said to be significant but statistical tests unclear.
Denenberg et al. (1991)	See Kertesz et al.	See Kertesz et al.	See Kertesz et al.	See Kertesz et al.	Factor analysis produced callosal width factors—sex by hand interaction was significant for certain of these. With handedness defined by writing hand, isthmus wider in males than females—no sex by hand interaction. With handedness defined by 5 items questionnaire, isthmus was significantly greater in NCRH than in CRH males and both groups of females.	No correction for overall brain size (but measure of brain area did not correlate with callosal area or width). Reanalysis of data of Kertesz et al. (1987). Items concerned writing, drawing, toothbrush, ball, scissors.
Habib et al. (1991)	35 males 18 females	26 CRH (19 males, 7 females) 27 NCRH (16 males, 11 females) EHI score 80–100 Of 8 with EHI score negative, 5 had scores between 2 80 and 2 100.	18–51 yrs Mean: 29 yrs	Not given	Significantly larger callosal area, especially in anterior half, in NCRH than CRH. Degree of handedness (without regard to direction) correlated positively and significantly with several segments of callosum.	
Allen et al. (1991)	61 males 61 females 12 males 12 females	Not Known	16–78 yrs Mean: 42.1 yrs 16–79 yrs Mean: 42.9 yrs 2–14 yrs Mean: 8.9 yrs 2–15 yrs Mean: 9.25 yrs	0.6T	No gender difference in overall size, or in any segment of callosum. Splenium significantly more bulbous in females. Among adults, size of anterior callosum decreased with age; in children, it increased with age.	No correction for overall brain size. Found one significant gender difference but this was attributed to multiple testing.

TABLE 2b—*Continued*

Authors	Subjects	Handedness	Age	Magnetic strength	Findings	Remarks
Hines et al. (1992)	28 females	16 CRH 12 NCRH Measured by combination of scales. Those responding ‘‘left’’ or ‘‘mostly left’’ to any one or more of 18 items were NCRH.	20–45 yrs Mean: 29.4 yrs	1.5T	No effect of handedness on callosal size. Correlation between hand score and dichotic listening asymmetry (absolute value without regard to direction). Also significant negative correlation between area of posterior callosum and dichotic listening asymmetry.	
Steinmetz et al. (1992)	13 males 13 females 13 males 13 females	Right-handers Left-handers 19 CRH 24 Mixed-handers 9 CLH	21–34 yrs Mean: 26.4 yrs 21–35 yrs Mean: 24.9 yrs	1.5T	Females had proportionally larger isthmus than males. No effect of handedness on total callosal size or segments.	Handedness measured in same way as Witelson (1985, 1989).
Clark et al. (1993)	15 males 15 females 15 males 15 females	Right-handers Left-handers (‘‘Modified’’ EHI)	Postgraduate students	0.3T	No overall difference between left- and right-handers in callosal measures. Significant negative correlation between dichotic right ear scores for males only (disregarding handedness) and for right-handers only (disregarding gender).	Not possible to assess whether there was any interaction between gender and handedness.
Clark and Zaidel (1994)	15 males 15 females 15 males 15 females All graduate students	Right-handed writers Left-handed writers	Range 21–43 yrs Mean: 28.2 yrs	0.3T	Minimum body width of callosum significantly greater in females both for absolute measure and when expressed as proportion of total callosal area. On proportional measure area of isthmus significantly larger in females than males. No significant effect of writing hand. Classification into consistent right- and left-handers and mixed-handers led to no effect. However, excluding consistent left-handers gave significant interaction between gender and handedness. Females had longer area of isthmus in CRH but not in mixed-handers.	Since total callosal area did not correlate with mid-sagittal cerebral area, regional callosal areas were not ‘‘normalized’’ for cerebral area. Also examined correlations with behavioral data. (Probably same subjects as above.)

Strauss et al. (1994)	47 (sex not known) All epileptic–full scale IQ range 40–114 (mean 86.1 6 14.2)	NK	12–57 yrs Mean 29.49 yrs 6 10.16	0.5T	Significant correlation between area of posterior fifth of callosum and IQ (with and without total callosal area partialled out).	No correction for multiple testing. Positive but nonsignificant correlation between age and callosal areas.
Burke and Yeo (1994)	38 males	Right-handed (mean 5 205 6 45)	Mean 77.90 yrs 6 4.42 (range 68–69 yrs)	2.OT	Rostrum significantly larger in absolute terms in males than females.	Significance level not adjusted for multiple *t* tests. Greater age-related decline in callosal area in males. Also found significant positive correlations between regional callosal size and posterior and left hemispheric volume.
	59 females	Right-handed (mean 5 222 6 28) Scored on 47 item questionnaire: min. score 5 47 (left-handed) max. 5 235 (right-handed)	Mean 77.70 yrs 6 6.10 (range 56–90 yrs)		With total cerebral volume as a covariate the areas of rostrum, genu (and overall anterior callosum) significantly larger in females than males. For males, significant negative correlation between age and total callosal area. For males, the area of the posterior callosum significantly correlated with increasing right-handedness. For females, areas of anterior callosum, posterior callosum and the mid-callosal width negatively and significantly correlated with hand preference.	
Yazgan et al. (1995)	9 males 2 females	Right-handed Right-handed Assess by EHI–no details	Mean 5 34.2 yrs 6 8.9	1.5T	As dichotic REA decreased, overall callosal area increased (correlation significant).	Subjects were of high ability. No correction for brain size.
Schlaug et al. (1995)	22 male musicians 15 trained , 7 yrs 7 trained . 7 yrs 8 female musicians 6 trained , 7 yrs 2 trained . 7 yrs	All except 3 males said to be consistent right-handers	Mean 26.1 6 3.8 yrs	1.5T	Anterior callosal area significantly larger in musicians than controls. This was due to significantly larger anterior callosum in musicians with early training compared with those without who did not differ from controls.	Breakdown by gender is not provided.
	22 male controls 8 female controls	All except 3 males said to be consistent right-handers	Mean 26.5 6 4.6 yrs			

Note. EHI, Edinburgh Handedness Inventory; CRH, consistent right-hander; NCRH, non-consistent right-hander; CLH, consistent left-hander.

of dyslexia) argued that ‘‘dyslexia occurs along a continuum that blends imperceptibly with normal reading ability . . . . no distinct cut-off point exists to distinguish dyslexia clearly from children with normal reading ability; rather the dyslexic children simply represent the lower portion of a continuum of reading capabilities’’ (p. 148). However, these authors also write ‘‘although our data are consistent with the hypothesis that dyslexia follows a normal distribution, it is still possible that a small second mode may have gone unnoticed . . . we do not wish to rule out the possibility that some may, in fact, have a reading disorder of qualitatively different origin or a unique biologic deficit’’ (p. 149). As they point out in replying to commentaries on their paper (Shaywitz et al., 1992b), ‘‘the normal distribution model is entirely consistent with a biologic cause.’’

In the review which follows no attempt has been made to distinguish findings according to the authors’ definition of dyslexia or reading disability since in most cases it is not possible from the published details to identify relevant dimensions on which subjects might differ across studies.

Laterality and Dyslexia

The idea that specific reading disability is associated with unusual patterns of handedness has a long history, inspired no doubt by the early views of Orton (1937). For many years it was considered almost a truism that there is an elevated frequency of left-handedness in dyslexia. Many clinic-based studies of dyslexia have reported such an association but it is difficult to reject the notion that there is a referral bias since left-handers are more likely to be referred to clinics because of the belief that left-handedness and dyslexia are related. Thus the prophecy is self-fulfilling.

A number of authors have reviewed the literature on handedness, cerebral laterality, and dyslexia (Hardyck & Petronovich, 1977; Annett, 1985; Beaton, 1985; Satz & Fletcher, 1987; Bryden, 1988; Bishop, 1990; Eglinton & Annett, 1994). All bemoan the inconsistency in defining dyslexia and in classifying handedness which bedevils research in this area. In her review Bishop (1990) included only studies in which reading scores were at least 6 months below age level, there was ‘‘some indication that reading level was well below mental age as well as chronological age’’ and handedness was measured by objective criteria, not self-report. This led to a total of 21 studies. Bishop’s conclusion was that ‘‘on the most optimistic interpretation, the rate of left-handedness in dyslexics is twice that of controls’’ (p. 125) but only if negative data (Bishop, 1984) from the very large-scale National Child Development Study (undertaken in the United Kingdom) are excluded.

Whether or not a relationship is found to exist between handedness and reading disability (henceforth used interchangeably with the term dyslexia) may depend upon a number of factors other than the definition of ‘‘disability.’’ Annett and Turner (1974) collected data from school children and analyzed their data in two different ways. When the children were classified in terms of handedness there was no significant difference in level of reading performance (measured in terms of reading quotients) between different handedness groups. However, when children were selected for reading disability, defined as a reading quotient 30 points below their vocabulary score, a significant ‘‘excess’’ of sinistrals was found in this group. Thus whether a relationship was found between reading and handedness depended upon the method of analysis. More recently, Annett, Eglinton, and Smythe (1996) have reported that dyslexic children with relatively poor scores on tests of phonological processing included a higher proportion of left-handers than dyslexics whose phonological ability was not poor. Annett and her colleagues interpret their findings in terms of Annett’s (1985) Right Shift theory of the genetic mechanisms underlying cerebral lateralization and handedness (recently criticized by McManus, Shergill, & Bryden, 1993 and defended by Annett, 1993, 1995, 1996).

There is now a considerable body of evidence (Smith, Kimberling, Pennington, & Lubs, 1983; Pennington et al., 1987; Olson, Wise, Connors, & Rack, 1989; Pennington, 1990; DeFries, 1992; Cardon, Smith, Fulker, Kimberling, Pennington, & DeFries; 1994) to support the view that genetic mechanisms underlie variation in the phonological processes relevant to the acquisition of reading although according to McManus (1991) the evidence is ‘‘far from conclusive.’’ Nonetheless, it is becoming increasingly accepted that individual differences in learning to read are, to some extent, genetically determined although clearly there cannot be a gene (or genes) for reading, per se, but rather for speech-related processes which underlie reading acquisition. There is also increasing acceptance that handedness is at least in part under genetic control (Risch & Pringle, 1985; Annett, 1985; McManus, 1985; Neale, 1988). Given the association between handedness and language lateralization and the persisting notion that there is a raised incidence of left-handedness in dyslexia, it is unsurprising that people have looked for a link between reading and brain laterality.

Dyslexia and Anatomic Asymmetry: Postmortem Studies

Suggestions that reversals of the ‘‘normal’’ anatomic asymmetry in width of posterior parieto-occipital areas of the brain were unusually common in dyslexia (10 cases out of 24) were made by Hier, Le May, Rosenberger, and Perlo, (1978) on the basis of *in vivo* CT measurements. These findings were not replicated by Haslam, Dalby, Johns, and Rademaker (1981) but the latter did report a relatively high frequency of symmetric brains (11 of 26).

Subsequently Galaburda, Sherman, Rosen Aboitiz, and Geschwind (1985) reported postmortem findings on the brains of four male dyslexics which included the case reported by Galaburda and Kemper (1978). Humphreys, Kaufmann, and Galaburda (1990), reporting on the area of the plana in three female cases, stated that ‘‘like the five males, the three women with dyslexia had symmetrical temporal plana’’ (p. 734). As these cases have been much cited it is worth looking closely at them.

The report of Case 1 states (Galaburda & Kemper, 1978, p94) ‘‘the patient was clumsier than his siblings. Speech in full sentences was delayed until after the age of three years. . . . The patient developed nocturnal seizures at the age of 16 years . . . (and) was left-handed.’’ The suspicion arises that the dyslexia was due to some early cerebral insult. In the first four male cases exact measurements of the plana are not provided. In the case of the female patients, however, ‘‘The areas of the plana were calculated on computer-assisted reconstructions’’ and ‘‘A directional asymmetry coefficient (delta) was computed. . . . A value of between 2 0.05 and 1 0.05 was designated to be symmetrical’’ (Humphreys et al., 1990), but otherwise details for individual patients are not provided.

A second point concerns the ‘‘diagnosis’’ of dyslexia. In some cases there is insufficient detail provided to enable the reader to decide whether the label ‘‘dyslexic’’ is appropriate. Male Case 2, for example, was said by age 8 to have had ‘‘notable language difficulties.’’ In female Case 1 ‘‘an automobile accident at age 2 years caused significant head injury with coma and altered consciousness lasting approximately 10 days. . . . she was noted to be a very active child with a short attention span.’’ Female Case 2 (a left-hander) was diagnosed at the age of 25 by Samuel Orton but ‘‘no formal psychological assessment of the patient was ever performed.’’ Female Case 3 showed ‘‘easy distractibility’’ as a child and one (of three) ‘‘experts’’ apparently ‘‘considered her reading disability to be secondary to attention deficit disorder.’’

The concern has to do with the specificity of the ‘‘dyslexia.’’ If the reading deficit is associated with either developmental language impairment or with ‘‘attention disorder’’ then it is at least arguable that cerebral anomalies (including symmetry of the plana) relate as much to these conditions (see, for example, Jernigan, Hesselink, Sowell, & Tallal, 1991) as to dyslexia. Furthermore, it is possible that in some cases symmetry of the planum may be related to non-right-handedness (but see above) rather than, or in addition to, dyslexia. A final point of note is that ‘‘every one of our patients showed lesions in the inferior frontal gyrus’’ (and elsewhere) and most showed evidence of abnormalities of cell migration (Galaburda et al., 1985) which arguably were more important as far as dyslexia is concerned than symmetry or asymmetry of the planum temporale.

Galaburda (1993) writes: ‘‘The presence of symmetry in the planum temporale signifies that the usually smaller right side has grown big and not that the usually larger left side has failed to develop. Dyslexic brains therefore have an ‘excess’, not a deficiency, in the amount of the posterior language area, as represented by the planum temporale’’ (p. 164). This was said to be due to some interference with the process of epigenetic involution which

TABLE 3a
Postmortem Investigations of Asymmetry of Planum Temporale in Dyslexics

Authors	Subjects	Handedness	Age	Anatomical definition	Findings	Definition of dyslexia	Remarks
Galaburda & Kemper (1978)	1 male	Left-handed (no detail provided)	20 yrs	‘‘The region on the superior temporal plane lying posterior to Heschl’s gyrus.’’	‘‘The planum temporale. . . . was found to be approximately equal in extent in the two hemispheres.’’ ‘‘The left cerebral hemisphere, . . . was . . . consistently wider than his right.’’	Reading performance and spelling were much below expectation for his intellectual level, socio-cultural opportunities and educational exposure.’’	Seizures at 16 yrs, REA at 18 yrs. ‘‘Mild difficulties with right-left orientation and finger recognition were noted.’’
Galaburda et al. (1985)	4 males (1 as above)	1 Left-handed 1 ‘‘Ambidextrous’’ (no details provided) 2 Right-handed	20 yrs 32 yrs 14 and 20 yrs	‘‘The triangular region lying immediately caudal to the transverse gyrus of Heschl on the dorsal surface of the temporal lobe.’’	Patient 1–as above Patient 2–(R. handed ‘‘plana temporale . . . nearly symmetrical.’’ Patient 3–(R. handed). ‘‘plana . . . roughly symmetrical in size and shape.’’ Patient 4–(ambidextrous), ‘‘plana . . . clearly corresponded to the symmetrical type.’’	As above: ‘‘diagnosis of specific reading disability was made soon after school entrance.’’ ‘‘The diagnosis of dyslexia was made at an early age.’’ ‘‘His learning ability was noted at the age of 5.’’ ‘‘Diagnosed as dyslexic at an early age.’’	Other abnormalities present for all four cases. IQ and reading test scores provided for 4 cases.
Humphreys et al. (1990)	3 females	2 Right-handed 1 Left-handed (no details provided)	20 and 36 yrs 88 yrs	None given	Patient 1: ‘‘The areas of the temporal plana . . . were symmetrical.’’ Patient 2: ‘‘The planum temporale was symmetrical.’’ Patient 3: ‘‘The plana temporale were symmetrical.’’	‘‘Major difficulty in learning to read was evident during the early years of school.’’ ‘‘Diagnosed as having typical dyslexia by Samuel T. Orton.’’ ‘‘Review of test results by three independent experts led to conflicting impressions: two classified the patients as primarily dyslexic.’’	Case 1: ‘‘significant head injury at age 2.’’ Case 2: diagnosed (by Orton) without formal testing. Case 3: ‘‘dyslexia’’ said by one ‘‘expert’’ to be secondary to attention disorder.

normally brings about a reduction of cortical cells during prenatal development.

The above cases (summarized in Table 3a) are the only ones known to me of examination postmortem of the planum temporale of purportedly dyslexic individuals. However, the planum temporale has been measured *in vivo* in reading-disabled subjects using neuroimaging techniques (summarized in Table 3b).

Dyslexia and Anatomic Asymmetry: In Vivo Studies

Rumsey, Dorwart, Vermess, Denckla, Kruesi, and Rapoport (1986) studied 10 severely dyslexic males aged 18–28 all of whom were said to be strongly right-handed. On clinical evaluation 9 of the 10 subjects ‘‘showed apparent symmetry of the volume of the temporal lobes’’ but no measurements were taken. Hynd et al., (1990) reported that although there was no overall difference between dyslexics and controls in overall brain area, dyslexics (*n* 5 10) had a smaller mean length of the planum on the left than on the right side (as measured by extreme sagittal slices). This pattern was found in 9 of the dyslexic children compared with the reverse pattern of asymmetry in 7 normal (and 7 attention disorder/hyperactivity) controls. There was also a significant hemisphere-by-group interaction. Mean length of the planum on the right was equivalent in dyslexics and normal but was significantly smaller on the left in dyslexics. Three dyslexics but none of the normal or attention deficit control subjects were said to be left-handed according to the Oldfield (1971) Edinburgh inventory but the criterion of ‘‘left-handedness’’ was not specified. Two of the 3 left-handed dyslexics had reversed asymmetry and one had symmetrical plana.

Duara, et al. (1991) made area measurements from a horizontal section of the brain (at the level of the foramen of Munro or inter-ventricular foramen) in 21 adult dyslexic and 29 control subjects, all of whom were right-handed (mean LQ . 80) according to the Edinburgh inventory. In the brain region designated the mid-posterior segment, the area on the right side was larger than the left in dyslexics but the left side was slightly larger in normal controls leading to a significant hemisphere by group interaction (with total brain area used as a covariate to control for individual differences in total brain size). The posterior central segment ‘‘the region of the brain that includes most of the planum temporale’’ was found to be symmetrical for both groups of subjects in this study. Absence of (the usual) asymmetry in normals shows how dependent demonstrations of such asymmetry are on the precise region of the brain selected for measurement. The larger right than left side of the neighbouring mid-posterior segment in the dyslexic but not control brains is, however, consistent with the findings of Hynd et al. (1990).

A subsequent paper from the same group of researchers (Kushch, Gross-Glen, Jallad, Lubs, Rabin, Feldman & Duara, 1993) reported that the area of the superior surface of the temporal lobe measured on coronal slices and expressed as a laterality index was symmetrical in a group of 17 dyslexics but not in 21 control subjects. The posterior area of the region measured was larger on the right side in 12 of the 17 dyslexics and larger on the left in the remaining 5; for control subjects the corresponding figures were 3 and 18 respectively. ‘‘Symmetry’’, it may be inferred, was an artifact of averaging the measurements across subjects showing different directions and degrees of asymmetry (see their Fig. 2).

A relatively high frequency (70%) of symmetrical plana (reconstructed through coronal slices) was reported by Larsen, Hoien, Lundberg, and Ödegaard (1990) among dyslexic (*n* 5 19) teenagers compared with control subjects (*n* 5 17). Among the latter only 30% were symmetrical. Symmetry in dyslexia (*n* 5 13) was associated with smaller mean width of planum on the left side and larger planum on the right side than was true of cases in which the plana were asymmetrical (*n* 5 6). The symmetrical brains were virtually the same size on the left as symmetrical control (non-dyslexic) brains (*n* 5 5) but were on average a little larger on the right side among dyslexics; the symmetry was therefore associated with an unusually large right planum rather than a smaller left planum. Asymmetrical cases of dyslexia showed a slight exaggeration of the normal pattern of asymmetry (larger on the left) seen in the asymmetrical control brains (*n* 5 12). Classifying subjects into those with consistent hand preference (left or right) and those with less consistent preference (mixed-left and mixed-right) on the basis of Annett’s (1970) questionnaire revealed no obvious relationship between degree of hand preference and neuro-anatomic asymmetry.

In the above study all four dyslexic cases with ‘‘phonological dysfunction’’ (inferred from performance on a non-word reading task), together with seven of nine cases showing ‘‘phonological’’ and ‘‘orthographic’’ dysfunction, had symmetrical plana. The one dyslexic subject with ‘‘pure orthographic dysfunction’’ (defined as difficulty in reading tachistoscopically exposed words) had asymmetrical plana. Of the remaining four ‘‘dyslexic’’ subjects (without defícts on the experimental tasks), one had symmetrical plana. Among controls, 5 of 17 cases showed symmetry of the plana. The trend is therefore toward symmetrical plana being found in association with ‘‘phonological’’ deficits. However, a single test of nonword reading, though suggestive (see Rack, Snowling & Olson, 1992), is not convincing evidence of a phonological deficit; additional deficits on tests of phonological awareness would be more persuasive.

Leonard et al. (1993) distinguished between the temporal and parietal banks of the Sylvian fissure. They studied 9 dyslexics (aged 15–65 years), 12 reading control subjects, and 10 unaffected relatives of the dyslexics. Only 1 subject (relative) was said to be left-handed. The length of the planum was measured from thin sagittal sections, the posterior border being taken as the point of bifurcation of the horizontal segment of the Sylvian fissure

TABLE 3b
Neuroimaging Studies of Asymmetry of the Planum Temporale in Dyslexia

Authors	Subjects	Handedness	Age	Imaging plane/ magnetic strength	Anatomical definition	Findings	Definition of dyslexia	Remarks
Rumsey et al. (1986)	10 males (all said to be dyslexic)	Right-handed ‘‘Responded with their right hand to at least 10 of 11 hand preference commands.’’	18–28 yrs Mean: 22.6 yrs	Coronal and transverse 0.5T	Planum temporale not specifically measured.	On visual inspection 9 of the dyslexics had ‘‘symmetrical brains in region of temporal lobes.’’	‘‘DSM III criteria for developmental reading disability and the World Federation of Neurology’s criteria for developmental dyslexia.’’	No correction for overall brain size. No measurements made of planum.
Larsen et al. (1990)	15 male dyslexics 4 female dyslexics 15 male controls 4 female controls	Norwegian version of EHI but is classified as consistent R/L handers, inconsistent R/L handers	Mean: 15.1 yrs Mean: 15.4 yrs	Coronal 1.5T	‘‘The posterior border of the planum temporale was defined by the most caudal slice showing the Sylvian fissure. The anterior border was defined by identifying the ridge of Heschl’s gyrus.’’	Symmetrical plana in 13 of 19 dyslexic brains; 5/17 of control brains. No effects of handedness.	‘‘Selected by applying the conventional inclusionary criteria (poor word recognition and exclusionary criteria (poor intelligence, . . . poor education, . . . language deviation.’’	No correction for overall brain size. Symmetry evaluated visually.

Hynd et al. (1990)	8 male dyslexics 2 female dyslexics	3 Left-handers (based on EHI; no details provided)	Mean: 118.9 6 24.55 months	Sagittal 0.6T [reported as 0.5 by Semrud-Clikeman et al., 1991].	‘‘An axial slice transversing [region of planum temporale.]’’ ‘‘Extreme lateral sagittal slices were employed in obtaining the left and right planum temporale length measurements.’’	Dyslexics had smaller mean length of planum (as measured by extreme lateral slice) on left than right side. Symmetry or rightward asymmetry found in 9 dyslexics but only 3 in each of control groups. Dyslexics differed significantly from normal control group in length of left but not right planum.	‘‘Diagnostic criteria for developmental dyslexia included normal or better intellectual ability (FSIQ $ 85), a positive family history for learning problems, personality history of difficult learning to read, reading achievement significantly ($20 standard score points) below FSIQ on both the word attack and passage comprehension subtests of the WRMT-R and no symptoms of hyperactivity.’’	No correction for overall brain size (but overall area said not to differ between left and right hemispheres nor total brain area between groups). Reported subsequently that verbal comprehension scores were significantly lower in subjects with reversed or equal symmetry in comparison with subjects who showed leftward asymmetry (Semrud-Clikeman et al. 1991).
	8 male controls 2 female controls	R. handed	Mean: 141.20 6 24.07 months					
	8 male ADD 2 female ADD	R. handed	Mean: 120.60 6 40.43 months					

TABLE 3b—*Continued*

Authors	Subjects	Handedness	Age	Imaging plane/ magnetic strength	Anatomical definition	Findings	Definition of dyslexia	Remarks
Duara et al. (1991)	12 male dyslexics 9 female dyslexics	Mean EHI score: 80 6 0.2	Mean 35.3 yrs	Horizontal 1.0T and 1.5T	Planum not specifically measured.	Mid-posterior horizontal segment of right hemisphere larger than left in dyslexics; left side larger in controls. Group-by-hemisphere interaction significant.	‘‘All dyslexic subjects were of average or high-average intelligence. The diagnosis of developmental dyslexia was made if all the following conditions were met: (1) a 1.5 SD discrepancy on reading and/or spelling tests vs. IQ was verified; (2) there existed a history of childhood reading and spelling problems, and (3) there existed a family history of dyslexia in at least 2 generations.’’	
	15 male controls 14 female controls	Mean EHI score: 82 6 0.2	Mean 39.1 yrs					

Kushch et al. (1993)	9 male dyslexics 8 female dyslexics	mean 5 0.63 6 0.6 (3 had negative scores)	Mean 5 26.2 6 15 yrs (range 8–58 yrs)	Coronal 1.5T		Divided superior surface of the temporal lobe (SSTL) into anterior and posterior parts. ‘‘posterior half of SSTL, namely, most of the planum temporale, part of Heschl’s gyrus . . . Anterior half of SSTL, namely, the anterior horizontal plane of the superior temporal lobe, part of Heschl’s gyrus and a small part of the PT.’’	For posterior area of SSTL, 18 of 21 controls showed leftward asymmetry compared with 5 of 17 dyslexics. Among dyslexics, but not controls, correlation between comprehension score and posterior SSTL asymmetry coefficient significant—the higher comprehension scores the greater leftward asymmetry.	Sliding scale—increasing IQ versus reading score discrepancies as age increased.
	8 male controls 13 female controls	Right handed: mean 5 0.79 6 0.3 Handedness assessed using EHI	Mean 5 33.4 6 15 yrs (range 11–63 yrs)					

Note. ADD, Attention deficit disorder; EHI, Edinburgh handedness inventory; PT, planum temporale.

in to ascending and descending rami. Leonard et al. found a larger mean length of the temporal bank of the planum on the left side in all three of their subject groups; indeed, only 1 subject showed a reversal of this effect. In this study, therefore, dyslexics did not show symmetry of the temporal bank of the plana (which corresponds to the horizontal segment of the Sylvian fissure). Images were reconstructed from sagittal sections, unlike the studies of Duara et al. who used horizontal section and Larsen et al. (1990) who used coronal sections. Importantly, perhaps, Leonard et al. (1993) did show that bilateral anomalies of gyral development, such as omission or duplication of gyri, were more frequent among dyslexic than control readers.

Schultz et al. (1994) measured the surface area of the planum temporale using oblique coronal images in 17 dyslexic and 14 control children (aged 7 ½–9½ years): all subjects were ''consistently right-handed'' according to the Edinburgh inventory. The posterior boundary of the planum was defined as the termination of the ascending branch of the Sylvian fissure and, since Heschl's gyrus could not be reliably identified in many cases, the anterior boundary was defined as the rostral-most slice not including the insula of Reil. On this definition, 13 of the 17 dyslexics and 10 of the 14 control subjects had a larger planum on the left. Although there was a significant main effect of gender there was no interaction between gender and subject group in a measure of planum asymmetry which took into account overall brain size. Again, then, the dyslexics were not characterized by symmetrical plana even though inclusion of the posterior ascending ramus tends to reduce left-right asymmetry. It is perhaps worth noting, however, that despite the lack of a significant interaction between gender and group, the mean scores of female dyslexics did show more or less symmetrical plana whereas those of males did not (see their Table 4). The lack of a significant gender-by-hemisphere interaction is probably due to the fact that the variance of the female scores was more than twice that of the males and the mean left–right difference for females was in the same direction as that for males, though much reduced.

Work by Tallal and her associates has demonstrated that language-learning-impaired children have deficits in correctly specifying the order of very brief acoustic stimuli presented in rapid succession. Such auditory temporal processing deficits have been found in reading-disabled children and the degree of impairment has been correlated with the number of errors made on a test of non-word reading (Tallal, 1980). Language-learning-disabled children frequently have difficulty learning to read and write (Bishop & Adams, 1990). It is possible that difficulty in discriminating the sounds of speech contributes not only to a delay in general language development but specifically to learning the phonetic discriminations upon which reading development initially depends (see Snowling & Hulme, 1994). Developmental dyslexia and specific language impairment may lie on a continuum.

Language-learning-impaired children have been reported to show abnormalities in the ‘‘perisylvian areas’’ on MR imaging. Plante, Swisher, Vance, and Rapscak (1991) report that six of eight boys with specific language impairment had atypical asymmetry (i.e., symmetrical areas or right side greater than left) in comparison with only two of eight control brains (age not given). The area measured (in the axial plane) extended beyond, but was said to include, the planum temporale.

Conclusion

There have been repeated suggestions in the literature that asymmetry of the planum temporale is reduced or reversed in dyslexia (Rumsey et al., 1986; Duara et al., 1991; Larsen et al., 1990) but this has not always been found (Leonard et al., 1993; Schultz et al., 1994). Whether reversed or symmetrical plana are found does not appear to depend upon whether the planum is defined as including cortex lying within the terminal (vertical) segments of the Sylvian fissure.

The earlier work in this field was reviewed by Hynd and Semrud-Clikeman (1987) who pointed out that methodological problems characterize the literature, particularly in regard to diagnosis of dyslexia, assessment of handedness, and a failure to provide evidence that symmetry of the plana is unique to dyslexia. The more recent work is more methodologically sophisticated but certain problems identified by Hynd and Semrud-Clikeman persist. In particular, definitions of the planum and of dyslexia have varied, numbers of subjects have generally remained small, and control groups have not always been well matched for handedness and gender. The thorny issue of matching for IQ has rarely been addressed (but see Schultz et al., 1994) except to ensure that subjects are considered to be of at least average ability. There is still a need for a large-scale, well-controlled study in which dyslexic subjects can be considered to comprize a reasonably homogeneous group with regard to the nature of the underlying deficit.

It is pertinent to ask whether the atypical patterns of brain organization seen on MRI scans reflect innate patterns of neural organization present at birth or else the effect of a particular post-natal environmental history. Galaburda (1993, p. 169) writes, ‘‘There are no available data to shed light on the etiologic mechanisms of cerebral asymmetry. Genetic predisposition is probably the main factor’’ (Galaburda, 1993, p. 169). He further proposes that ‘‘the putative dyslexic individual begins with a familial predisposition to dyslexia, which is expressed through a propensity to develop symmetric temporal plana’’ (p. 170). In this conection it is interesting to note that work in the field of neural computation suggests that a network trained initially with a given number of units may, after a task has been learned, subsequently operate more efficiently with fewer units (Brown, Hulme, Hyland, & Mitchell, 1994). This could explain why an ‘‘excess’’ number of neurons in reading-disabled or language-learning-impaired children, if not pruned, leads to difficulty in learning language and in acquiring literacy skills.

Dyslexia and the Corpus Callosum

A long-standing suggestion in the literature on dyslexia is that the condition may be characterized by a deficit in interhemispheric transfer of certain kinds of information (Vellutino, Steger, Harding, & Phillips, 1975; Badian & Wolff, 1977; Wolff, Cohen, & Drake, 1984; Hermann, Sonnabend, & Zeevi, 1986; Wolff, Michel, & Ovrut, 1990; Davidson, Leslie, & Saron, 1990; Moore, Brown, Markee, Theberge, & Zvi, 1995). At its simplest, this view implies some impairment or abnormality of function of the corpus callosum in dyslexia. It is therefore interesting to note that Temple and her colleagues (Temple et al., 1989, 1990; Temple & llsley, 1993) have reported that individuals born without a corpus callosum show deficits in phonological processing and in reading nonwords. Moore, Brown, Markee, Theberge, & Zvi (1996) reported that subjects low in phonological ability performed proportionally less well on tests of cross-hand tactile transfer than subjects higher in phonological ability.

At least three studies have looked at callosal size in relation to dyslexia. Duara et al. (1991) found in their MRI study that the area of the splenium in 21 dyslexic subjects was significantly larger than that of 29 normal controls. Both the splenium and the genu were significantly larger in female than in male dyslexics (all subjects were said to be right-handed). Measurements were made of scans in the mid-sagittal plane and were corrected for total brain size. Because acquired defects of reading often involve the left angular gyrus, and the angular gyri at the left and right sides of the brain are connected by fibers coursing through the splenium of the callosum, Duara et al. suggested that their findings (together with those reported for horizontal brain sections, see above) suggest an abnormality in the region of the angular gyrus in developmental dyslexic subjects. In contrast to these findings, Larsen, Höien, & Ödegaard (1992) found no difference between dyslexic and control groups in total callosal area or in area of the splenium as a proportion of the total callosal area. Handedness was not reported and measurements were not corrected for overall brain weight. Hynd et al. (1995) reported finding a smaller area of genu in 16 dyslexic subjects than in 16 controls but the groups were not well matched for age, IQ, or handedness (see Strauss et al., 1994). Admittedly there was no significant correlation between either handedness or IQ and callosal area but the dyslexic subjects had a significantly lower full scale IQ and 6 of them had a co-diagnosis (such as attention deficit disorder, developmental language disorder).

On the basis of the present evidence it is clearly too early to draw firm conclusions regarding callosal morphology in dyslexia.

OVERALL SUMMARY AND CONCLUSIONS

Publication of the paper by Geschwind and Levitsky (1968) reawakened interest in asymmetry of the planum temporale at the two sides of the normal human brain. Studies carried out since then have confirmed an asymmetry favoring the left side in both adult and neonatal brains. However, the relevant studies have mostly ignored the tissue in the terminal branches of the Sylvian fissure. Recent MRI investigations suggest that a leftward asymmetry of what is usually described as the planum temporale may be balanced by a rightward asymmetry of the terminal branches.

There are a number of issues associated with *in vivo* measurement of the planum temporale. Sagittal cuts have the advantage that they allow the full extent of the antero-posterior tissue to be measured but can be problematic as far as measurement of the lateralmost surface of the planum is concerned since parietal tissue can appear to belong to the planum and be mistakenly included with temporal tissue (Galaburda, 1995; Habib et al. 1995). Coronal slices avoid this problem but if the planum inclines upward, as it often does, then it appears foreshortened; the greater the inclination, the greater the foreshortening. The solution is to reconstruct the planum from both sagittal and coronal slices. According to Galaburda (1995), ''The commonly employed horizontal (axial) plane . . . is particularly unhelpful . . . because it is too close to the planum itself, making visualization, if not reconstruction, difficult even for experienced eyes'' (p. 56). Whatever plane is chosen, those investigators who reconstruct the planum from multiple serial sections (e.g., Steinmetz et al., 1991; Habib et al., 1995) are likely to have more valid measures than those who use only a single slice or a limited number of slices of considerable thickness.

Researchers tend to measure (or estimate) either the length or the area of the planum temporale. Surface area is usually estimated by multiplying the value obtained on each image by the slice thickness of the image and summing across the number of images. Schultz et al. (1994) argue that ''simple summation of PT area across images and adjustment for slice thickness provide an inadequate solution for estimating an undulating surface area.'' While a number of solutions to this problem have been suggested (Steinmetz et al., 1990; Loftus et al., 1993; Schultz et al., 1994; Rossi et al., 1994), problems of accurate delineation and measurement remain. The question also arises as to whether a longer planum is equivalent to a larger planum in terms of area. To the extent that both linear and area measures indicate leftward asymmetry of the planum it would not be surprising to find a correlation between the two measures. Leonard et al. (1993) state that ''the length of the temporal bank between sagittal positions of 2.75 and 3.25 correlated well with the area'' (p. 464) but did not provide any further detail. This is not to say, of course, that the apparent extent of asymmetry will necessarily be equivalent for the two measures.

In vivo MRI techniques are unable to delineate different cytoarchitectonic areas so it is not possible, for example, to look specifically at subregions of the planum such as cytoarchitectonic area Tpt identified by Galburda, Sanides, and Geschwind (1978). Asymmetry in this specific area may turn out to be more important than asymmetry in the overall region of the planum temporale.

The frequency of reversed (rightward) anatomic asymmetry reported in the literature is rather higher than estimates of right hemisphere lateralization based on aphasia following unilateral cerebral lesion or the Wada sodium Amytal test. Conversely, the frequency of leftward asymmetry is somewhat lower than estimates of the frequency of left hemisphere language. To some extent this might reflect the willingness of some investigators to classify small differences between the two sides as symmetrical but it does question the notion that the planum temporale is relevant to language production mechanisms.

It is almost universally assumed that asymmetry of the planum temporale (as usually defined) relates in some way to functional differences between the hemispheres. Direct evidence of this is scant although there are suggestive data. The report by Foundas et al. (1994) that one individual with reversal of the usual direction of anatomic asymmetry also shows a reversal of the normal pattern of language lateralization (which may have been caused by an epileptic focus in the left hemisphere but details are not provided in the paper) is the only one to date to show a direct relationship. Even so, it remains possible that the anatomic asymmetry relates more to handedness than to language lateralization. Jäncke and Steinmetz (1993) found no relationship between size of planum and dichotic ear asymmetry but did claim to find a relationship between planum asymmetry and handedness. To the extent that asymmetry of the planum temporale (and of neighbouring parietal cortex–Habib et al., 1995; Jäncke, Schlaug, Huang, & Steinmetz, 1994) has been shown to relate to handedness, the extant data are compatible with the view that neuro-anatomic asymmetry relates to consistency or degree of handedness as opposed to direction.

It has been common for investigators to compare consistent right-handers with all others, which confounds direction and degree of handedness, and to rely heavily on certain handedness questionnaires, especially the Edinburgh inventory (Oldfield, 1971). While handedness questionnaires can give reliable measures of hand preference (Raczowski, Kalat, & Nebes, 1974; McMeekan & Lishman, 1975; Bryden, 1977; Steenhuis, Bryden, Schwartz, & Lawson, 1990), they are subject to a number of difficulties (Salmaso & Longoni, 1985; Bryden & Steenhuis, 1991). The practice of defining handedness by adding scores corresponding to consistency of hand use for each item of a questionnaire (as with the Briggs-Nebes (1975) modification of Annett's (1970) questionnaire) has face validity but there is no evidence that different overall scores reflect theoretically meaningful distinctions (Beaton & Moseley, 1984). Furthermore, Peters (1992) has observed that the proportion of individuals classified as left-handed varies dramatically as a function of questionnaire length, the nature of the response permitted to each item, and the criterion used to define the categories of handedness used. He notes that the ‘‘right-hander/non-right-hander dichotomy is singularly unsuited as a basis for classification when handedness is to be related to some other neuropsychological factor’’ (p. 208). As noted above, such a classification has often been used in the studies considered in this paper.

It is usual in the handedness literature to distinguish between hand preference and hand skill (Annett, 1985; Beaton, 1985; Bishop, 1989, 1990; Bryden, & Steenhuis, 1991). The frequency distribution for preference is J-shaped, whereas that for differences between the hands in skill is approximately normal with either a single mode (Annett, 1970; Borod, Caron & Koff, 1984) or two modes (Tapley & Bryden, 1985; Beaton, 1995) depending upon the task under consideration. The causal relationship between manual preference and proficiency has been considered by a number of authors and no clear consensus has emerged. Some view skill as determining preference (Annett, 1985) while others regard preference as primary (McManus, 1985; McManus; Murray, Doyle, & Baron-Cohen, 1992). Either way, a close empirical relationship between hand skill and scores on a particular questionnaire has been demonstrated only in a few studies (Annett, 1970, 1976; Peters & Durding, 1978; Chapman & Chapman, 1987; Bishop, 1989; Provins & Magliaro, 1993). In effect, such studies provide construct validity for the relevant questionnaire. This means that those questionnaires which have been validated are to be preferred to others for which the validity (in this sense) has not been demonstrated. I am not aware of any published report of the construct validity of the Edinburgh Handedness Inventory despite its widespread use.

An alternative to the use of questionnaires is to use a measure of relative hand skill. This has been done by Steinmetz and his colleagues although the method of scoring has been inadequately described. The question arises as to which task to use. The circle-filling task devised by Tapley and Bryden (1985) and used by Kertesz et al. (1986) yields a bimodal distribution of differences between the hands in skill. Annett’s peg-moving task (and tapping) yields a distribution with a single mode (Bryden & Steenhuis, 1991; Annett, 1992a; Beaton, 1995) and is perhaps to be preferred on that account though more particularly for the links that can be made with the results of Annett’s experimental work (see Annett, 1985; 1995 for reviews). For discussion of the correlations between performance on different tasks, see Annett (1992a).

Many studies of planum temporale asymmetry have employed too few subjects, and hence too little statistical power, to adequately confront issues such as handedness and gender differences. The latter issue, in particular, has rarely been explicitly addressed as the main aim of the investigation. As a consequence there is very little strong evidence one way or the other as to whether males and females differ in degree of planum asymmetry. Moreover, the research reviewed in this paper has generally been carried out in something of a theoretical vacuum although many authors have linked their findings to the Geschwind–Behan–Galaburda hypothesis. This emphasizes the putative role of testosterone in the production of ''anomalous'' dominance (that is, other than typical left hemisphere speech lateralization, right hemisphere spatial representation, and right-handedness) but the predictions it makes are imprecise and not easily quantified (see McManus & Bryden, 1991; Bryden et al., 1994).

Annett (1992b) has pointed out the remarkable similarity between asymmetry of the planum temporale reported by Galaburda and colleagues and asymmetry of hand skill found by herself and co-workers. Anatomical asymmetry was found by Galaburda et al. (1987) to be continuous and distributed approximately normally (see also Wada et al., 1975; Steinmetz et al., 1991; Rossi et al., 1994; Loftus et al., 1993) as is peg-moving asymmetry, the task used by Annett in a large number of studies. Increased asymmetry of the area of the planum temporale is associated with reduction of cortex on the right side rather than an increase in area of the left side. Greater asymmetry of hand skill is likewise associated with reduction in skill of the left hand rather than with increased skill of the right hand. Symmetry of the planum temporale is associated with large total area and symmetry of hand performance is associated with good performance by both left and right hands. According to Annett, ''The parallels between PT and hand skill imply that similar mechanisms are at work in the processes that produce asymmetries of PT and the processes that produce asymmetries of hand skill. . . . It certainly does not follow that asymmetries of PT cause asymmetries of handedness, or vice versa. Both may be influenced by a third variable.'' (p. 958). Such a variable could be genetic, hormonal, or even environmental and could be influential at a particular point in gestation. Findings that amniotic testosterone levels predict subsequent hand preference (Grimshaw, Bryden, & Finegan, 1995) and that handedness relates to current levels of salivary testosterone (Moffat & Hampson, 1996) are not incompatible with genetic theories of the origin of handedness.

Family studies of planum asymmetry would be useful in evaluating Annett's theory. It is therefore of interest that Steinmetz et al. (1991) divided subjects into left- and right-handers with and without sinistral first degree relatives. The distributions of planum asymmetry for both left- and right-handers were shifted in the direction predicted by Annett's theory (though not interpreted in such terms). In another paper from this group a reduction in mean planum asymmetry in left- compared with right-handers was reported in 10 pairs of monozygotic twins discordant for handedness (Steinmetz, Hertzog, Schlaug, Huang, & Jäncke, 1995). That is, among the left-handed members of the twin pairs the mean asymmetry coefficient was in the direction of a larger left planum but was not statistically significant from zero. Among the right-handed members of the pair leftward asymmetry was significant, as it was among 10 right-handed twin pairs concordant for handedness. Intra-pair correlations of degree and direction of planum asymmetry was not high. It was argued that the findings suggest that planum asymmetry is not under genetic control but is determined by environmental events or chance. Bartley, Jones, & Weinberger (1997) have also recently obtained evidence to suggest that brain size is, to a very large extent, genetically determined.

According to Annett's right shift theory, both handedness and cerebral dominance for language are determined independently and according to chance in the absence of some (genetic) factor which otherwise biases the distribution of hemispheric language lateralization toward the left and handedness toward the right. For monozygotic twins to be discordant for handedness they would need to lack the shift factor (which Annett argues is in any case expressed less strongly in twins than in singletons). The left-handed members of the twin pairs would thus be expected to show an approximately chance distribution of planum asymmetry with zero mean difference between the left and right sides. The right-handed members of discordant pairs would be expected to show the same while concordant right-handed twin pairs would be more likely to show a ''shift'' of the planum to the left. The observations of Steinmetz and his colleagues are therefore in part compatible with Annett's theorizing; only the data for discordant right-handers are in conflict with expectation. However, many more such observations are required to adequately test whether variations in planum temporale asymmetry fit with the postulates of the theory as far as handedness is concerned. (A lack of agreement would not of course necessarily invalidate the theory as applied to handedness).

Short of identifying Annett's hypothesized genotypes directly it is necessary to make inferences from the available data. One prediction that can be made is that individuals with symmetrical plana or who show rightward asymmetry (putatively rs—genotype) should show a mean between-hands difference of close to zero on Annett's peg-moving task.

Turning now to the corpus callosum, differences in its size and/or shape as a function of gender or handedness have been reported by some authors but the findings are controversial as regards both sexual dimorphism and variations with handedness. As with studies of the planum, handedness has been defined almost exclusively in terms of consistent right-handers versus all others of different degrees and/or direction of preference. Only Kertesz et al. (1987), Steinmetz et al. (1992), and Clarke and Zaidel (1994) distinguished between consistent left- and right-handers and mixed-handers (finding no difference between these groups in callosal size).

Witelson and Nowakowski (1991) suggested that ''the course of loss of callosal axons may have a genetic component which is associated with a sex related influence and which is modifiable by prenatal and early postnatal events.'' The sex-related factor was thought to be either genetic or hormonal. There is, in fact, some evidence in the animal literature relating callosal size to testosterone (Denenberg, Fitch, Scrott, Cowell, & Waters, 1991). There is also evidence to suggest that the size of the callosum is partly under genetic control. Oppenheim, Skerry, Tramo, and Gazzaniga (1989) measured the size of the corpus callosum in five pairs of human monozygotic twins (four female pairs) and ten unrelated control subjects (six females, four males). There was a significant correlation between twin pairs for a measure of callosal area but not for callosal length. Unrelated pairs of subjects showed no significant correlations. While these results suggest that callosal anatomy is under genetic control, to some extent at least, they are also consistent with the possibility that a similar uterine environment is responsible for similar callosal area. Evidence of the effect of the environment on callosal size has been reported for the rat by Jurasaka and Kopcik (1986).

The finding that the corpus callosum is enlarged in dyslexia (Duara et al., 1991) awaits replication. To the extent that the callosum has been implicated in the establishment of neuro-anatomical asymmetry (Galaburda et al., 1990; Witelson & Nowakowski, 1991), one might expect to see a difference in callosal size between dyslexics who have symmetrical plana and those who do not. However, Larsen, Höien, and Ödegaard (1992) found no difference in either total callosal area or relative splenial area between dyslexics with and without symmetrical plana as visualized on MRI. Unfortunately, no correction was made for overall brain size and only six subjects showed asymmetrical plana.

The postmortem studies of the brains of a small number of dyslexics by Galaburda and his colleagues were the first to call attention to symmetry of the plana. However, support from neuro-imaging investigations for the idea that this is common in dyslexia has been equivocal, some authors reporting such an effect (Rumsey et al., 1986; Larsen et al., 1990; Hynd et al., 1990) and others not (Leonard et al., 1993; Schultz et al., 1994). Where symmetry has been reported it may sometimes be attributed to an artifact of averaging (Kushch et al., 1993) or has also been found in control subjects (Duara et al., 1991). (This emphasizes the fact that authors should not simply present mean asymmetry coefficients but indicate the number of subjects showing symmetry as well as leftward and rightward asymmetry.) In relation to Annett's theory, those dyslexics with primarily or exclusively ‘‘phonological’’ deficits should show a chance distribution of planum asymmetry in favor of the left and right sides with, presumably, some subjects showing little or no asymmetry (Beaton, 1995).

Several recent studies have looked at functional activation of the brain in dyslexia (Hagman, Wood, Buchsbaum, Tallal, Flowers, & Katz, 1992; Rumsey et al., 1992; Schultz et al., 1994). A possibility recently suggested by Hynd, Marshall, Hall, and Edmonds (1995) is that functional imaging techniques could be used to delineate areas of activation that are then taken as the basis for MR measurement (see Karbe et al., 1995). In this connection it is of interest that recent PET studies with normal readers have suggested fairly widespread sites within the temporal lobe for different aspects of phonological processing (Demonet et al., 1992; Howard, Patterson, Wise, Brown, Friston, Weiller, & Frackowiak, 1992; Warburton, Wise, Price, Weiller, Hadar, Ramsay, & Frackowiak, 1996; Paulesu, Frith, Snowling, Gallagher, Morton, Frackowiak, & Frith, 1996). Such investigations may eventually reveal that undue attention has been given to the dimensions of the planum temporale.

Paulesu et al. (1996) for example have recently shown that the left insula was not activated at all in dyslexics whereas it was activated in the controls. It was proposed that normally the insula acts as an anatomical bridge between anterior and posterior speech areas of the left hemisphere and has a major role to play in translating between different codes within the phonological system.

It is often forgotten that the postmortem studies of Galaburda and colleagues found abnormalities of cortical microanatomy (ectopias—intrusions of cells from one layer to another and dysplasias—disorganisation of cells within a cell layer). Other abnormalities were found in some of the postmortem specimens. Livingstone, Rosen, Drislane, and Galaburda (1991) examined the lateral geniculate nucleus (LGN) of five dyslexic brains and five control brains. Cells of the magnocellular layer of the LGN were significantly smaller in the dyslexic than control brains but no difference was found for cells of the parvocellular layer. Livingstone et al. also recorded the visual evoked potential responses of a group of five (different) dyslexic subjects (about whom we know only that ‘‘all had been formally diagnosed’’) and a control group of normal subjects. The dyslexics’ pattern of response was consistent with an impairment in the functions of the magnocellular division of the visual system. The possible contribution of visual deficits to dyslexia is a matter of some dispute (Stein, 1991, 1993; Lovegrove, Martin, & Slaghuis, 1986; but see Hulme, 1988, and reply by Lovegrove, 1991) but a cogent argument can be made out for at least some influence of an impaired magnocellular pathway (Breitmeyer, 1993). Impairments to a system which is the auditory analogue of the magnocellular division of the visual system might relate to the phonological difficulties experienced by dyslexic persons.

The future is likely to see rapid advances in the study of brain–behavior relationships. Despite great interest in asymmetry of the planum temporale and morphology of the corpus callosum the functional significance of deviations from the ‘‘normal’’ in these aspects of cerebral anatomy is at present unclear. Deviations from the ‘‘typical’’ pattern have been observed not only among dyslexics but also among language- and learning-impaired children (Tallal & Katz, 1989; Jernigan, Hesselink, Sowell, & Tallal, 1991) and schizophrenics (Buckley, 1994; Crow, et al., 1989). Of course, not all dyslexics, learning-impaired, or schizophrenic subjects show abnormal asymmetry (or an enlarged callosum) and some proportion of normal individuals show attenuated or reversed asymmetry. This raises questions as to what asymmetry (or lack of it) ‘‘means’’ in any given case. There have been relatively few attempts to determine how variation in cerebral anatomy relates to levels of cognitive or linguistic functioning (but see Hines et al., 1992; Aboitiz et al., 1992; Semrud-Clikeman & Hynd, 1991; Leonard, Lombardino, Mercado, Browd, Breier, & Agee, 1996); measurement of behavioral as well as anatomic variables must be considered a priority in future research studies. Only in this way, and guided by neuropsychological theory, is significant progress likely to be made.

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