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hallucination A hallucination is a sensory perception without external stimulation of the relevant sensory organ. Hallucinations are therefore contrasted with *illusions*, which involve the misperception of real physical stimuli. In some cases the individual may believe the hallucination to be an event in the real world; at other times the hallucination may be embedded in a delusional context; and in still other cases the hallucination, while vivid, may be recognized as a purely subjective experience.

Hallucinations may occur with all types of cerebral pathology, most commonly in the context of confusion, dementia, delusions, or paroxysmal activity. There is, of course, debate about whether the hallucinations which characterize certain functional disorders, notably SCHIZOPHRENIA, have some form of organic basis, but there is a general observation that the hallucinations in functional states are more commonly auditory and somesthetic in character, while the hallucinations which accompany gross organic pathology are more likely to be visual or olfactory; but this is not universally the case. There may well be a bias towards the reporting of certain types of hallucination, in relation to given pathological states, in the literature.

Hallucinations may also occur in a relatively pure form in association with localized damage to elements of the visual system and this may be true for other sensory modalities; the visual system has been subject to more study in this respect. Visual hallucinations are reported to occur in around 2 to 3 per cent of patients with occipital lesions. Damage to the secondary visual cortex and to areas of the occipito-parietal region may result in hallucinations of objects, people, and animals which may be perceived as engaged in specific activities. While there is a tendency for unformed images to be reported with damage to the visual pathways and primary visual cortex, and for full

percepts to follow damage to secondary visual association areas, this is not invariably the pattern and there are reports of well-formed visual hallucinations following eye disease. Other visual impairments may contribute to the occurrence of visual hallucinations, as may a high-level deficit in the ability to distinguish between veridical and hallucinatory percepts and the confidence in determining true percepts. One current hypothesis suggests that some hallucinations may arise from the faulty momentary reconstruction of the feature fragments of images, a result which is more likely to occur when defects in the system of visual perception result in the distortion of features, which makes the correct perception of the stimulus events less likely.

Hallucinations are also important in association with the aura preceding certain partial epilepsy phenomena, where they may be not only visual or auditory, but are also commonly hallucinations of smell (*see* EPILEPSY, temporal lobe epilepsy). Hallucinations also occur in NARCOLEPSY and in HYPNAGOGIC PHENOMENA, although they may commonly occur in any acute organic reaction.

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handedness Humans differ from other animals in that nine out of ten of them prefer their *right* hand for skilled tasks. That alone is sufficiently surprising to merit detailed study. However, its association with cerebral language lateralization also makes handedness a useful surrogate for studying the far less tractable phenomenon of cerebral dominance. Research on handedness, and particularly its genetics, often therefore supposes that appropriate models for handedness may well also be appropriate models for language dominance.

Handedness is essentially very simple, and is probably best assessed, in the absence of known

social pressure, by the hand used for writing. Its measurement has sometimes been rendered overly complex while yet missing its full subtlety. Three principal problems arise: the distinction between *skill* and *preference*; the nature of the *distribution* of laterality scores; and the different *laterality measures* that can be derived.

A person can be right-handed in two distinct senses: given a moderately skilled unimanual task they *prefer* to use the right hand; and when tested in turn with right and left hands they are more *skilled* with the right hand. Handedness/skill and handedness/preference are generally highly correlated, although that is not always the case.

MEASUREMENT OF HANDEDNESS

Measurement of handedness/skill

Many tasks have been used for assessing skill in the two hands. One of the most frequently used is the Annett pegboard task which measures the time for each hand to move ten pegs in a board as quickly as possible from one row of holes to another. Although originally scored as $Time_{Left} - Time_{Right}$, a common form of scoring computes $100x(Time_{Left} - Time_{Right}) / (Time_{Left} + Time_{Right})$ which assesses proportional hand differences independently of overall ability. Although popular, in part because it requires few instructions and can be used even at age 3 or 4, the test cannot be administered in groups and shows only small between-hand differences of about 4 percent, with a large overlap in distribution of right- and left-handers. Group testing is better carried out using the Tapley and Bryden task, in which a pencil is used in each hand in turn to place dots in as many circles as possible in 20 seconds. The laterality index is calculated as $100x(N_{Right} - N_{Left}) / (N_{Right} + N_{Left})$. The test is quick and reliable, and produces larger hand differences (about 10–12 percent) with little overlap in performance of right- and left-hand writers. Nevertheless there is still substantial variation within right- and left-handers. Other useful tasks include Bishop's square-tracing task (Bishop, 1990), and the dot-making task of the National Child Development Study. Finger-tapping speed also differentiates right and left hands, but is not as useful for routine testing. Strength differences do not relate to handedness and do not assess skill. Practice affects overall performance on skill tests but even when intense has minimal impact on left-right differences; likewise extensive prac-

tice on asymmetric skilled tasks transfers little to other tasks.

Measurement of handedness/preference in adults

Hand preference in adults can be assessed using questionnaires, of which there are many in the literature, typically having 4 to 60 questions, asking about the preferred hand for a particular task on a three-, five-, or seven-point scale (e.g. always right, usually right, either, usually left, or always left). Questionnaires differ principally in length and appropriateness of items. The Edinburgh Handedness Inventory with 10 items is popular, although its original response method is eccentric, and is better used with the five-point scale described earlier (when perhaps it could be the standard questionnaire method for handedness research). The Annett questionnaire is similar in format but with 12 items on a three-point response scale. In recent years longer questionnaires have become popular, such as the Waterloo Handedness Questionnaire with 60 separate questions, a few of which are inappropriate outside North America. A laterality index from questionnaires is typically derived by scoring +2 for a response of "always right," +1 for "usually right," 0 for "either," -1 for "usually left," and -2 for "always left," summing responses across items (after reversing scores on questions for which right-handers normally use the left hand), and standardizing so that persons answering "always right" or "always left" to all items score +100 and -100 respectively; a complete lack of preference then scores as zero.

Questionnaires with less than 12 or so items typically show a J-shaped distribution of scores with many right-handers in particular scoring at maximum (e.g. Figure 42e). Such floor and ceiling effects invalidate many statistical analyses. Questionnaires with more than about 25 items show distributions closer to a mixture of two normal distributions, with less censoring at the top and bottom ends of the scale. The distribution of left-handers is typically shifted somewhat more towards zero than is the distribution of right-handers, usually due to items with cultural biases (e.g. using a screwdriver, winding a clock, holding a knife when eating with a knife and fork); exclusion of such items restores symmetry.

Measurement of handedness/preference in children

Hand preference in children from the age of 10

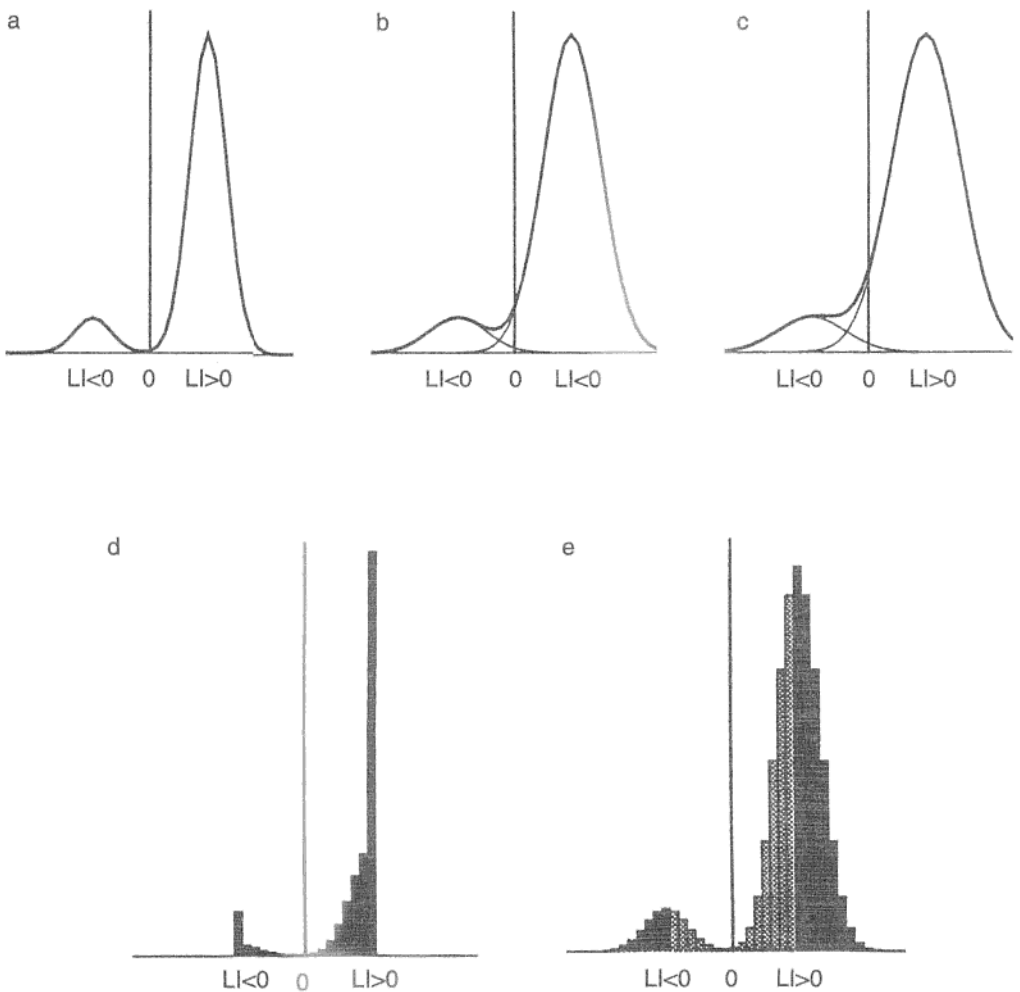


Figure 42 Laterality index distributions found for measures of handedness. a–c. Symmetric bimodal distributions with (a) almost no overlap, (b) mild overlap, and (c) moderate overlap, showing how the distribution can be bimodal or unimodal, according to the spread of the distributions. d. A typical J-shaped distribution of the type seen in handedness questionnaires, obtained by censoring the distribution of Figure 42a at the mean of each distribution. e. Arbitrary division of handedness into Left (left-hand distribution), Right (right-hand distribution), and “Mixed” (center distribution) showing how the “mixed” category confounds weak right-handers and weak left-handers.

can be assessed using questionnaires (Bryden & Steenhuis, 1991). With younger children, preference is usually assessed by performance measures in which it is observed which hand is used when the child carries out a number of simple tasks (such as drawing, hammering, taking a sweet). A laterality index can be derived by summing across measures as for questionnaires.

There are no standardized assessments of preference in infants, although many different measures show asymmetries.

Factorial structure of questionnaires

Several attempts have been made in recent years to use conventional methods of factor analysis for isolating different components of handedness.

Commonly two or more factors emerge, one of which appears to be "fine skill," involving the fingers in complex coordinated tasks, of which writing is the exemplar, and the other of which is "unskilled actions," often involving grosser, less subtle, more axial movements, as in carrying objects. The fine movement factor contains highly lateralized items and the unskilled factor the less lateralized items. These factors are probably artifacts due to violating the assumption in factor analysis that measures are multivariate normal. *Item scores tend to be bimodal*, with different proportions of right and left responses; factor analysis of such binomial measures results in artifactual "difficulty factors," and the factor structure should not therefore be trusted. Other multivariate techniques such as cluster analysis and association analysis may also produce artifacts with laterality data, and should not be relied on. At present handedness/preference is probably best conceptualized as unifactorial.

The distribution of laterality scores

Most measures of handedness/skill and handedness/preference consist of *mixture distributions*, usually of two normal distributions, one containing about 90 percent of the population and the other about 10 percent, placed approximately symmetrically about zero, and often censored at top and bottom ends (see Figure 42) – the *symmetric bimodal model*. The symmetry of such distributions makes it inappropriate to divide the distribution anywhere other than at zero.

Annett has claimed that her pegboard task is intrinsically unimodal, with the minor distribution centered at zero. Such a distribution is necessary in the right shift theory of the genetics of handedness (Annett, 1985), but is probably not supported by using appropriate statistical analysis (McManus, 1983) of empirical data, which finds a symmetric bimodal distribution even for the pegboard task. The apparent unimodal distribution is probably a result of the pegboard's particular task requirements (see Figures 42 a–c), and is not found for other tasks, even by Annett herself.

The four types of laterality measure

Bimodality of laterality scores has profound implications for the analysis of handedness and lateralization. Laterality scores should not be analyzed by statistical tests such as analysis of

variance, t-tests, or correlations, both because they are far from normal, and because they seriously confound variation *within* component distributions with variation in proportions of subjects *between* component distributions. If the component distributions do not overlap substantially then two separate scores can readily be calculated: *direction of lateralization*, which is a binary variable, "right" if the laterality index is greater than zero, and "left" if the laterality index is less than or equal to zero (zero usually being included as left-handed); and *degree of lateralization*, the absolute value of the laterality index (i.e. ignoring its sign), approximately normal in distribution, and interpreted as strength of lateralization. If the components of the mixture overlap substantially then advanced statistical techniques can separate effects of direction and degree (McManus, 1983).

Some studies divide subjects into three classes: *right*, *left*, and *mixed*. This practice has little justification. If measurement is to "carve nature at its joints," then Figure 42e shows that "mixed" handedness corresponds to no natural category; instead mixed handers are actually a mixture of weak right-handers and weak left-handers. If subjects are to be further subdivided then four groups are preferable (strong right, weak right, weak left, and strong left); alternatively the mean and SD of degree of lateralization should be reported separately for right- and left-handers. The problem is particularly serious in developmental studies if degree of lateralization increases with age, since the proportion of non-right-handers (i.e. mixed and left) will seemingly decrease with age, even though direction of lateralization is not truly changing.

In recent years the importance of distinguishing direction and degree of lateralization has been accepted. However, two other measures are as yet little used, despite one undoubtedly being important in understanding handedness. Consider a group of right-handers; their degree of lateralization is the mean lateralization score on individual questionnaire or performance items. Two different right-handers may have the same degree of lateralization and yet differ in *variance of lateralization* – one being moderately lateralized for all items, and the other showing strong lateralization for some items and no lateralization for other items. Although as yet hardly studied, variance of lateralization may be empirically important in distinguishing individuals.

The fourth measure, *ambiguous handedness*, requires that a set of items be administered twice to a subject. Two right-handed subjects may have an identical degree and variance of lateralization and yet one subject can be entirely consistent in hand usage *within tasks*, giving the same score on *both occasions*, whereas the other subject may be strongly right-handed on one occasion and subsequently weakly right-handed or even left-handed *at the same task*. This measure, of within-subject between-task unreliability, is called *ambiguous handedness* by Satz and his colleagues and differentiates children with autism from controls. In principle ambiguous handedness can be subdivided into *ambiguous direction of lateralization* and *ambiguous degree of lateralization*, although nothing has been published on that distinction. It should be noted that ambiguous handedness and degree of lateralization are inevitably partially confounded, although effects can be separated by analysis of covariance.

The interrelationship of handedness/preference and handedness/skill

For most subjects handedness/skill and handedness/preference are highly correlated, the preferred hand being more skilled on most tasks. An important exception finds a substantial minority of left-handers who, although more skilled at fine motor skills with the left hand, are more skilled at throwing with the *right* hand, are right-footed, and have stronger right hands. The origin of such *inconsistent left-handers* is not clear; neither is it clear if *inconsistent right-handers* exist in substantial numbers.

The association of skill and preference raises a causal question: Do right-handers prefer their right hand because it is more skillful, or is the right hand more skillful because of more practice due to being preferred? Cross-sectional studies in adults cannot answer that question. However, the finding that children with autism show population dominance for handedness/preference without the preferred hand being more skillful, implies that preference is causally prior to skill.

THE NEUROLOGICAL LOCUS OF HANDEDNESS

The anatomical locus of hand preference is not clear. The approximate, although not exact, bilateral symmetry of the bones, muscles, and nerves

of right and left arms points to handedness originating in the central nervous system. A cortical origin is often assumed, partly because of skill asymmetries between hands, and partly because of the existence of other large functional asymmetries, as in Broca's area. However, if preference is prior to skill then handedness may result from subcortical mechanisms. Anatomical studies of the basal ganglia find asymmetries correlated with hand preference in the globus pallidus, an area functionally active in skilled motor learning. Lower in the hierarchy, handedness may be best construed as a "turning tendency," which in rats is mediated via small asymmetries in nigrostriatal dopamine and modified by injection into the substantia nigra.

THE FUNCTIONAL LOCUS OF HANDEDNESS

In right-handers the right hand is more skilled even on simple tasks such as repetitive tapping, at which it is faster and less variable. Peters has suggested that the superiority is due to more precise force modulation, due principally to more precise timing. Suggestions that handedness relates to superior visual-manual coordination are probably falsified by the normal incidence of right-handedness in congenitally blind subjects. It is interesting that handedness means precisely that, rather than a more general "sidedness," measures of asymmetry being greatest for distal movements and less for proximal, axial movements; this probably reflects two motor control systems, one pyramidal, contralateral, and distal, and the other non-pyramidal, bilateral, and proximal.

THE INCIDENCE OF LEFT-HANDEDNESS

Studies have claimed widely different incidences of left-handedness, from 1 percent to 35 percent. A recent meta-analysis of 284,665 individuals in 100 populations found an overall incidence of 7.78 percent, with a higher incidence in younger populations. No evidence was found for geographical differences; nevertheless questionnaire measures find differences between cultures, with lower incidences in Muslim and Far Eastern societies where cultural taboos prohibit left-hand use for activities such as eating. That right-handedness does not originate in cultural asym-

metries due to writing is seen in a preliterate tribe of the Central Highlands of New Guinea of whom 10.3 percent were left-handed, a similar proportion to that elsewhere. Although anecdotes occasionally report populations with a majority of left-handers, none has been verified scientifically, and they are best viewed as modern myths.

Secular and age trends

Cross-sectional studies often find a lower incidence of left-handedness in older people. Interpretation is difficult because individual cross-sectional studies inevitably confound age effects and secular trends; thus, in a 1990 study, 30-year-olds were born in 1960 whereas 70-year-olds were born in 1920. Left-handedness has long been subject to social manipulation (Harris, 1990), particularly in the late nineteenth and early twentieth centuries, when schools forcibly prevented left-handed writing by children. Not surprisingly, that resulted in a lower manifest incidence of left-handedness. However, whether age trends can entirely explain secular trends is unclear, the effects not being disambiguated in a large meta-analysis. A study of 1,177,507 Americans showed no age effect in those aged under 41 (of whom 11.7 percent were left-handed writers), whereas above that age the incidence declined linearly. A far smaller age effect on throwing supported the existence of social pressure and secular trends. The point of inflection of the curve suggests that social pressures against left-handedness had ceased in the USA for cohorts born after 1945. Data on Victorian cricketers suggests that social pressure against left-handedness was absent in the early 1800s but present in the latter half of the century, only being lifted in the twentieth century.

Coren and Halpern (1991) interpreted age trends as evidence that left-handers have a reduced life expectancy. Their original data do not support that, since mean ages at death of right- and left-handers are not significantly different, and subsequent data relating age at death to handedness made serious epidemiological errors which ignored secular trends; neither have their data been replicated. Three causes for an increased mortality in left-handers were proposed: increased birth complications, auto-immune disorders, and accidents. The first two are considered below and rejected as unsupported by evidence. That accidents could be more common

in left-handers is very possible since in a complex, mechanical world their ergonomic needs are considered by few designers. Nevertheless, data claiming increased accidents in left-handers have yet to be replicated.

Sex differences

Sex differences in left-handedness have been controversial, although a meta-analysis shows clear evidence for left-handedness being more common in males than females, by about 27 percent; that is, for every five left-handed men there are four left-handed women. This ratio showed no secular or other changes, and in the recent very large US study is present at all ages; of those under age 41, 13.0 percent of males and 10.4 percent of females were left-handed writers.

The ontogeny of handedness

Handedness in young children is usually established between 18 months and 2 years of age. After that age, although direction seems fixed, degree of lateralization increases, probably throughout childhood and possibly throughout adulthood as well. Young infants show some evidence of predominant right-handedness, for instance, in how long they hold a rattle, although other asymmetries, the so-called turning tendencies such as the tonic neck reflex, do not seem to be obviously related to subsequent handedness. From 6 to 18 months infants pass through a "chaotic" phase of handedness, with direction of preference changing erratically, even from day to day, a phenomenon often causing confusion to parents. Despite such variability in infancy, ultrasonic observation of fetal behavior *in utero* suggests that even by 15 weeks of gestation about 90 percent of fetuses preferentially and consistently suck the right rather than the left thumb, with the direction related to subsequent head turning as neonates.

The phylogeny of handedness

That only a few people are left-handed has been recorded since ancient times, most notably in the Bible (Judges, 20: 15–16); and the associated symbolic differentiation of right and left into "good" and "bad" is prevalent in many geographically and temporally distinct cultures. Evidence for ancient handedness is necessarily indirect: during the past five millennia works of art

portraying unimanual actions consistently show the left hand use in about 7.4 percent of cases; Neolithic bone tools of 7,000 years ago show evidence of being right-handed, as do Upper Paleolithic bone scrapers of 8,000 to 35,000 years ago, and stone tool flakes from 150,000–200,000 years ago. Wear patterns on teeth which are at least 250,000 years old are compatible with right-handedness, as also are flake patterns on Lower Pleistocene stone tools of 1.5–2 million years ago. Since hominids first clearly appear in the fossil record at that time, the implication is that right-handedness is an ancient trait whose evolution is tightly linked to human evolution itself.

Handedness, footedness, pamedness, and clawedness in nonhuman species

Individual animals in many species, including rats, mice, dogs, cats, rhesus monkeys, chimpanzees, and gorillas, show hand, foot, paw, or claw preference in the sense of repeatedly using one side rather than the other for skilled actions. However, in almost all species precisely 50 percent of individuals prefer the right side and 50 percent the left side; that is, they show *individual handedness* but not *population handedness*. Although primate species have been claimed to show population handedness, the studies suffer from methodological and statistical problems; careful studies have found no evidence for population handedness in gorillas or chimpanzees. An exception to the general rule seems to be the parrot, in which there may be population footedness, as was noted by Broca; the association of left-claw preference for holding objects, vocal mimicry, and asymmetric control of the syrinx in vocalization in some birds has provoked suggestions of a causal link, although the mechanism is unclear.

THEORIES OF LEFT-HANDEDNESS

Explanations of left-handedness suggest either a genetic or an environmental origin. Environmental theories come in weak and strong forms, with the strong forms assuming that right-handedness is universally the natural form, with environmental insults or pressures reversing that situation (Harris & Carlson, 1988).

Pathological left-handedness

The concept that left-handers are neurologically damaged is a recurrent one in the twentieth

century, principally originating in the study of Gordon (1920). A particularly prevalent variant derives from the studies of Bakan, who suggested that left-handers showed an increased incidence of obstetric complications which caused minimal brain damage. Following the mathematical arguments of Satz, even if asymmetric damage randomly occurs in the right or left hemisphere, the consequence is necessarily increased left-handedness. Although mathematically correct the model fails empirically, a large number of studies failing to find increased obstetric complications in left-handers. An important exception is in extremely premature infants, weighing under 1 kilogram, in whom left-handedness is undoubtedly more common; however, that cannot be explained by Satz's model since laterality of lesions is unrelated to handedness. It is more likely that prematurity and left-handedness both result from developmental instability and fluctuating asymmetry caused by earlier developmental abnormalities. A similar explanation is necessary to explain the increased sinistrality found in much mental retardation, particularly in conditions such as trisomy 21 (Down's syndrome) with symmetric neurological damage: the implication in these cases is that individuals are not right-handers who have become pathologically left-handed, but rather that lateralization was never set up properly in the first place (primary rather than secondary pathological left-handedness). Bishop has assessed pathological left-handedness by measuring motor skill in the *non-preferred* hand. Brain damage causing transfer of hand dominance from right to left should result in the right hand of such pathological left-handers being substantially impaired compared with the right hand of "natural" left-handers; Bishop estimates that only 1 in 20 left-handers has secondary pathological sinistrality. That pathological left-handedness undoubtedly occurs is seen in children with a history of severe, acute, neurological illness in the first three years of life; twice as many are left-handed as in matched controls, although the differences are mostly explained by concomitant sensory, motor, and intellectual deficits.

The Geschwind-Behan-Galaburda model of lateralization

Geschwind and Behan (1982) published an influential and much cited theory, subsequently

handedness

extensively elaborated; the complex ramifications (McManus & Bryden, 1991) can only be summarized here. Essentially the theory is a strong pathological one, individuals normally being right-handed unless increased fetal testosterone levels retard left hemispheric development and cause left-handedness, atypical language lateralization, and a range of other conditions, of which the most surprising are immune disorders. The theory's most substantial evidence when first published was the highly counter-intuitive suggestion that immune deficits such as allergies, arthritis, asthma, diabetes, eczema, hay fever, migraine, myasthenia gravis, psoriasis, systemic lupus erythematosus, thyroid disorders, ulcerative colitis, and urticaria, were more common in left-handers. Many subsequent studies since have failed to replicate that suggestion, although a meta-analysis finds that although left- and right-handers are equally affected in most conditions, left-handers may be *more* vulnerable to ulcerative colitis, allergies and asthma, and *less* vulnerable to arthritis and myasthenia gravis. Such a pattern of results cannot be explained by the theory, and with a host of other failed predictions (Bryden et al., 1993) means that the Geschwind model does not provide the theoretical integration of disparate phenomena that was originally hoped.

GENETIC MODELS OF HANDEDNESS

The antiquity of human handedness, its seeming presence *in utero*, and the lack of major environmental correlates of handedness have suggested a genetic basis, a hypothesis supported by the undoubted tendency for handedness to run in families: in published data left-handedness occurred in 9.5 percent of children of two right-handed parents, 19.5 percent of children of one right- and one left-handed parent, and 26.1 percent of children of two left-handed parents (McManus & Bryden, 1992). The absence of an effect in adopted children makes a strong *prima facie* case for genetic causation. Nevertheless conventional Mendelian models have problems since neither right-handers nor left-handers "breed true." The difficulty is seemingly compounded by many studies showing substantial discordance in handedness of identical (monozygotic) twin pairs (McManus & Bryden, 1992), an effect which is not due to mirror-imaging, a phenomenon with no embryological foundation.

Discordance is not the problem it seems at first sight, since monozygotic discordance is more frequent among dizygotic twins, and discordance is predicted by some genetic models.

There have been a number of genetic models of handedness since Ramaley's first model in 1910. Most have failed because of not taking into account the biological basis of asymmetry (McManus & Bryden, 1992). In particular, models have ignored the phenomenon known in biology as *fluctuating asymmetry*, and results from developmental instability and hence random fluctuations in characteristics not under genetic control. Its role is undisputed in the genetics of *situs inversus*, the anatomical variant in which heart, lungs, and all viscera are mirror-reversals of their normal structures. This occurs in mice, due to the well-characterized *iv* mutation, and in humans, where it is also inherited. Handedness is not simply a further consequence of the same gene since humans with *situs inversus* have the same rate of left-handedness as do individuals with *situs solitus*, the normal anatomy.

Annett's Right-Shift (RS) model (Annett, 1985), and McManus' DC (Dextral-Chance) model have both integrated fluctuating asymmetry into their models. In each case there is one genotype (RS++ or DD) in which almost all individuals are right-handed, and a second genotype (RS-- or CC) in which 50 percent of individuals are right-handed and 50 percent left-handed. In both models heterozygotes (RS+- or DC) show additive inheritance, manifesting midway between the homozygotes. Both models predict that neither right- nor left-handers "breed true," and that monozygotic twins should show substantial discordance, since chance determination of handedness due to fluctuating asymmetry is independent in each twin.

Although superficially similar, the RS and DC models differ in many important respects. Phenotypically, the DC model argues that handedness/preference is primary, with handedness/skill differences being secondary, whereas the RS model invokes a primary role for handedness/skill differences (which are assumed to be normally distributed in genotypes), with handedness/preference being secondary and essentially arbitrary in incidence, depending on where a threshold is set in the continuous distribution of skill differences. The models differ in

their predictions about the distribution of between-hand skill differences (see above), and insofar as the symmetric bimodal model is a better account of those distributions, then the DC genetic model is also superior.

The models also differ in explaining two separate phenomena concerning sex differences: the increased incidence of left-handedness in males, and the maternal effect, whereby left-handed females have more left-handed offspring (of either sex) than do left-handed males (McManus & Bryden, 1992). The RS model explains the increased incidence of left-handedness in males by a single additional parameter, whereby males are shifted more to the right than females. Although that parameter explains the difference in incidence it cannot explain the maternal effect adequately. The DC model explains the sex differences by invoking a second modifier gene located on the X-chromosome. Since the modifier manifests differently in males and females it explains the sex difference, and its different transmission by mothers and fathers also explains the maternal effect. This latter advantage argues in favour of the DC rather than the RS model.

A final difference between the RS and DC models is that, although the DC model argues that twins and singletons are equivalent in their inheritance of handedness, the RS model can only explain twin data by invoking a reduced right shift in twins (Annett, 1985), a biologically surprising effect without validatory support. Once more this should be taken as evidence in favor of the DC model.

Familial sinistrality

Familial sinistrality (FS) is a common measure in neuropsychology. *Broad FS*, having any left-handed relative, is a flawed measure, confounded with family size, not least since in the limit all humans are related to one another. *Narrow FS*, having first-degree left-handed relatives (parents, siblings, or children), is a more defined measure. It is theoretically sounder not solely to assess the phenotypes of relatives, but to use a specific genetic model to calculate exact genotype probabilities for probands based on the entire family tree. Data on calculated genotype probabilities show narrow FS to be a better predictor of genotypes than broad FS, although each measure leaves much true genetic variance unexplained. Familial sinistrality has been

suggested as a criterion for distinguishing *natural* or inherited left-handedness from *pathological* or acquired left-handedness, only left-handers with sinistral relatives being assumed to be genetically left-handed. The argument is invalid since both RS and DC models predict that about 50 percent of genetic left-handers will show no FS. Similarly, although FS has been used to predict right hemisphere language dominance in left-handers, genetic modelling shows that it has minimal predictive power. However, FS is predictive of right hemisphere dominance in *right*-handers.

THE EVOLUTION OF HANDEDNESS

The reasons *why* handedness should have evolved, and why *right*-handedness in particular, are controversial. The latter can parsimoniously be explained by the gene for handedness being evolved from the gene for *situs*, affecting cerebral rather than cardiac tissue, and making the developing brain rather than the developing heart grow slightly more on the left side. The reasons for handedness at all are more contentious, and are complicated by being deeply intertwined with cerebral dominance, the causal interrelations being very unclear. Theorists have concentrated on the advantages of handedness for early humans for throwing or for feeding or on the cerebral dominance of generative grammars; and lateralization itself has been justified in terms of competition for limited neural space, and the need to prevent coordination problems between hemispheres. A final evolutionary problem concerns why some people are *left*-handed. If there are selective advantages to right-handedness then all individuals should be right-handed. The continued existence of left-handedness over many millennia suggests it must be advantageous; or to be more precise genetically, that there must be an overall heterozygote advantage. The precise advantage is unknown at present; but Annett's suggestion of an intellectual advantage for heterozygotes has severe theoretical and empirical problems.

HAND-CLASPING, ARM-FOLDING, LEG-CROSSING, EAR DOMINANCE, AND EYE DOMINANCE

Right- and left-handedness are sometimes confused with other related phenomena. When the hands are clasped with the fingers interlocked,

either the right or left thumb is on top; similarly, when the arms are folded together one wrist is on top, and when the legs are crossed while sitting in a chair one knee is on top. All three behaviors are stable within individuals, show evidence of running in families, and are uncorrelated with one another or with handedness. In contrast, footedness for skilled actions is partly although not entirely correlated with handedness. Ear and eye dominance are sensory preferences. Ear dominance is little studied, typically being seen only in telephone usage. Eye dominance, which in many studies is uncorrelated with handedness, has been much studied, mainly because of theories which are not well supported, which relate crossed eye-hand dominance to reading difficulties. It can be subdivided into three uncorrelated components: sighting dominance (the usual meaning of eye dominance), sensory dominance, and acuity dominance. Eye dominance, like hand-clasping, arm-folding, and leg-crossing, runs in families and its inheritance can be modelled by the DC genetic model.

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CHRIS MCMANUS

hematoma A hematoma is a local swelling or tumor filled with effused blood. Besides being a consequence of bleeding within the brain, it may result from a subdural hemorrhage (*see also* SUBARACHNOID HEMORRHAGE) of the veins between the cortex and the venous sinuses, often a consequence of increased vulnerability following shrinkage of the brain in the elderly, or from an extradural hemorrhage of the arteries between the bone and the dura following head injury.

hemiagnosia Literally, hemiagnosia is an agnosia which applies to only one lateral half of sensory space. An example would be a disturbance of body image (ASOMATOGNOSIA) in which the disturbance was restricted to one side of the body. Nevertheless, it would be more common to term this a unilateral asomatognosia. The term "hemiagnosia" is, however, used for a particular syndrome: hemiagnosia for pain. This is seen only in patients with a significant reduction in the level of consciousness, and consists of an apparent inability to detect the nature or location of a painful stimulus, even though appropriate facial gestures or even verbal responses indicate perception of the pain; the patient makes no effort to drive away the painful stimulus with the functional hand.

hemiakinesia Patients with unilateral NEGLECT may fail to orient their eyes or head to

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