

In agreement with the model, cicadas with life-spans of 13 and 17 years have synchronized emergences, and those with life-spans of 3, 4, and 7 years have balanced emergences. However, this model and analysis do not explain why the life-span of the periodical cicadas should be 13 or 17 years or why changes in the life cycle, such as 4-year accelerations, occur.

FRANK C. HOPPENSTEADT

JOSEPH B. KELLER

Courant Institute of Mathematical Sciences, New York University, New York 10012

References and Notes

1. R. D. Alexander and T. E. Moore, *Univ. Mich. Mus. Zool. Misc. Publ. No. 121* (1962).
2. J. White and M. Lloyd, *Am. Midl. Nat.* **94**, 127 (1975).
3. H. Bernardelli showed that, in a species whose reproductive window is short compared with its life-span, the birth rate can be a periodic function of time [cited by P. H. Leslie, *Biometrika* **33**, 183 (1945)].
4. M. Lloyd and H. S. Dybas, *Evolution* **20**, 133 (1966); *ibid.*, p. 466.
5. C. S. Holling, *Annu. Rev. Ecol. Syst.* **4**, 1 (1973).
6. The notation $(y)_+$ denotes y if $y > 0$ and 0 if $y \leq 0$.
7. Our model leads to the piecewise linear reproduction curve in Fig. 1. It is similar to, but simpler than, those used in studying fisheries and other ecological systems, where they are referred to as compensatory-compensatory (d-c) curves [P. A. Larkin, R. F. Raleigh, N. J. Wilimovsky, *J. Fish. Res. Board Can.* **21**, 477 (1964); (5)]. In addition, in our model the curve changes at each generation. Results similar to the ones presented can be derived for more general d-c reproduction curves. For example, Eq. 4 can be replaced by $x_n = F(x_{n-1}; P_n, K_n)$ where F is a smooth function satisfying $F(x) < x$ for $0 < K_n < x < P_n^*$ and $F(x) > x$ for $0 < P_n^* < x < K_n$. Such a function is given by $F(x) = [x - x(P_n^* - x)(K_n - x)]_+$. The threshold of extinction P_n^* and the residual carrying capacity K_n can be defined as in the present model.
8. Supported in part by National Science Foundation grant NSF-MPS75-09837. We thank M. Lloyd and M. Levandowsky for their comments and suggestions.

9 January 1976; revised 7 May 1976

Variations in Writing Posture and Cerebral Organization

Abstract. Two tachistoscopic tests of cerebral lateralization were administered to 73 subjects classified by handedness, sex, and hand orientation in writing. The results indicated that the direction of cerebral lateralization could be indexed from a subject's handedness and hand posture during writing. In subjects with a normal writing posture, the linguistically specialized hemisphere was contralateral to the dominant hand, and the visuospatially specialized hemisphere was ipsilateral; the reverse was true in subjects with an "inverted" hand position during writing. Females and subjects having an inverted hand posture manifested smaller degrees of lateral differentiation than males and subjects with a typical hand posture.

In the vast majority of right-handed persons, the left cerebral hemisphere is specialized for language integration and the right hemisphere is specialized for mental imagery and the understanding of spatial relationships (1). The association between the linguistically dominant left hemisphere and the dominant right hand seems to derive from the fact that the left side of the brain is organized not only for language integration but also for the programming of sequential manual movements. Unilateral lesions of the left hemisphere produce ideational and ideomotor apraxias as well as aphasia and agraphia (2).

However, the understanding of the association between handedness and brain organization has been inadequate because of the complexity of the relationship between the brain and the hand in the left-handed. The left-handed population is heterogeneous with respect to the direction of lateral specialization; some 60 percent have language functions in the left hemisphere and visuospatial functions in the right, and about 40 percent have the opposite organization (3). In addition, some small fraction, probably less than 1 percent, of right-handed

writers, have their main language functions in the right hemisphere and their visuospatial functions in the left (4). In left-handed writers with language functions in the left hemisphere or right-handed writers with language functions in the right hemisphere, control of the

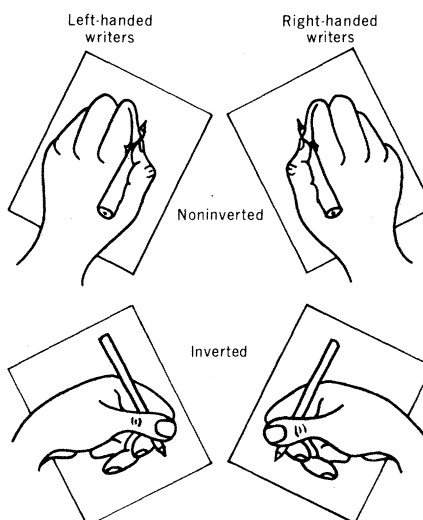


Fig. 1. Typical writing postures of dextrals and sinistrals who write with inverted and noninverted hand positions.

writing hand must be exercised either via the ipsilateral motor tracts, via commissural pathways, or, possibly, through both systems.

We now report a simple measurement which, in association with handedness, can reliably predict which hemisphere is predominantly linguistic and which primarily "spatial" in the left-handed and the occasional right-handed writer who is an exception to the normal relationship. Left-handed writers, in addition to being heterogeneous with respect to the direction of cerebral lateralization, also vary with respect to hand posture in writing. From our observations, more than 90 percent can be clearly classified as adopting either the "hooked" position, in which the hand lies above the line of writing, or the common right-handed position, in which the hand lies below the line of writing (Fig. 1). The hooked writing posture has been explained as a learned adaptation to the necessity of writing from left to right in our culture (5). Two observations make this interpretation unlikely. (i) We have observed several dextral writers who hold their hands above the line of writing in the inverted manner of a hooked left-handed writer. (ii) Writing in Hebrew proceeds from right to left, but in Israel, right-handed writers position their hands in the same way as Americans, but many left-handed Israelis display the hooked posture (6).

Results of a preliminary study by Levy and Mandel (7, 8) supported the hypothesis that writing position was related to cerebral dominance and indicated that the inverted position of left-handed writers was associated with an ipsilateral language hemisphere and the non-inverted position with a contralateral language hemisphere. However, sources of noise in the data left other possible interpretations open.

We have now tested 73 subjects, all university undergraduates, for cerebral lateralization with two tachistoscopic tests, one measuring visuospatial dominance and one measuring language dominance. There were 24 right-handed writers with the noninverted position (RN), 24 left-handed writers with an inverted hand position (LI), 24 left-handed writers with the noninverted position (LN), and one right-handed writer with the inverted position (RI). Half of each group was male and half, female. Subject RI was a female. Hand position was classified according to two criteria: (i) whether the hand was held below (noninverted) or above (inverted) the line of writing, and (ii) whether the point of the pencil pointed toward the

top (noninverted) or bottom (inverted) of the page. Two potential subjects whose hand positions could not be unambiguously classified were not included in the study. In a preliminary study, we were in complete agreement on classifications.

With tachistoscopic presentation of tests that require the specialized functions of one hemisphere, superior performance is seen for stimuli presented in the contralateral visual half-field (8). Thus, for right-handed subjects, the right visual field (RVF) is superior for verbal tests and the left visual field (LVF) is superior for visuospatial tests (9). If hand inversion indicates an ipsilateral relationship between the dominant hand and the language hemisphere, group LI should display the same field superiorities. In contrast, group LN and subject RI should manifest a superiority of the LVF on verbal tests and of the RVF on visuospatial tests.

In each trial of our verbal test (syllable test), a dark field with a white fixation point (fixation field) was displayed, followed by a dark stimulus field in which a pronounceable, vertically oriented, nonsense syllable (consonant-vowel-consonant) printed in white letters was presented 2° to the left or right of the fixation point, with a white number replacing the fixation point. The stimulus field was presented for a period ranging from 90 msec for some subjects to 180 msec for others. The exposure duration was determined separately for each subject in preliminary tests to maintain performance at approximately 50 percent accuracy. Subjects viewed binocularly during all testing. Termination of the stimulus field coincided with the appearance of a masking field (white letter fragments on a black background), which lasted for 200 msec before the fixation field was returned.

Subjects were required to report (i) the number displayed at the fixation point and (ii) the laterally projected syllable. Performance for each field was measured as the proportion of correct syllable identifications (in 60 trials per field) multiplied by the reciprocal of the exposure duration and a constant. This score is an index of the amount of information correctly processed per unit time.

In the visuospatial test (dot location test), subjects were asked to determine the position of a white dot that was tachistoscopically flashed within a white rectangular frame on a dark background in the left or right visual field. Subjects designated the position on a response card containing a 5 by 4 array, representing the

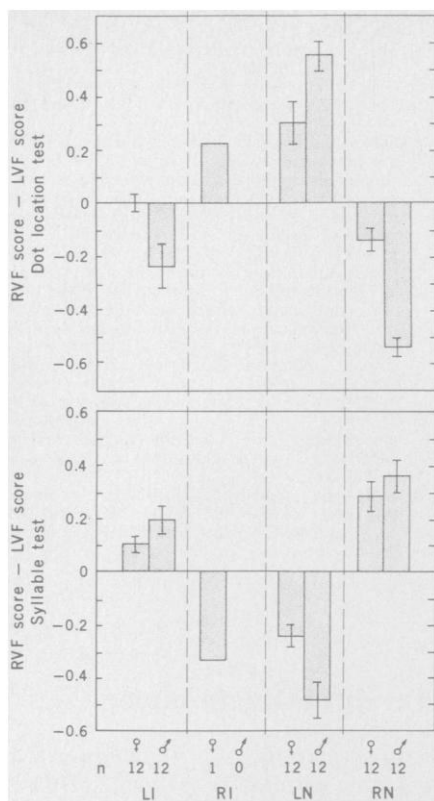


Fig. 2. Visual half-field difference scores ($\pm$ standard errors of the mean differences) for the syllable and dot location tests. Positive differences indicate superiority of the RVF, and negative differences, superiority of the LVF.

20 possible locations of dot stimuli within one visual field.

Each trial consisted of the sequential display of the fixation field (a dark field with a white fixation dot located midway between two white rectangular frames), a stimulus field lasting from 25 to 100 msec and having a central fixation number, and a masking field lasting 200 msec. Exposure durations and scores for each field were determined as for the verbal test. For each field, 20 trials were given. Again, subjects viewed binocularly.

Constants for the two tests were so chosen that the average performance of group RN for the two fields for one test equaled that of the other test. This normalization permitted a comparison of performances on the two tests within the other groups, and within the two sexes, relative to the mean of group RN.

As hypothesized, groups RN and LI demonstrated a superiority of the RVF on the syllable test and of the LVF on the dot location test; group LN and subject RI displayed the opposite field superiorities (Fig. 2) (10). Only one of 25 right-handed subjects manifested both superiority of the LVF on the syllable test and of the RVF on the dot location test; this was the single right-handed sub-

ject with an inverted hand posture. These data, along with the known rarity of right-hemispheric dominance for language in dextrals, support the proposal that hand position in writing, when a subject's handedness is known, classifies the direction of hemispheric lateralization. When the direction of cerebral asymmetry was indexed by the average of the RVF score minus the LVF score for the syllable test and the LVF score minus the RVF score for the dot location test (a positive average indicated specialization of the left hemisphere for language and of the right hemisphere for spatial processing; a negative average indicated the reverse), 70 out of 73 subjects displayed the described relationship. The exceptions were (i) one LI female who displayed reversed field superiorities on both tests, (ii) another LI female who had RVF superiorities on both tests, the magnitude of the field difference being larger on the spatial than on the verbal, and (iii) one LI male who displayed LVF superiorities on both these tests, with a greater superiority on the verbal than on the spatial test. For LI subjects, however, and particularly for females, field differences were small; any unreliability in the tachistoscopic indices of lateralization can easily lead to the misclassification of such subjects.

Subjects with an inverted hand posture typically displayed smaller field differences than subjects in the other two groups (Fig. 2) (11). The conclusion that sinistrals are less completely lateralized than dextrals seems to apply only to those with left-hemispheric specialization for language.

Brain organization varied as a function of sex. In all groups and for both tasks, the magnitude of field differences was smaller for females than for males (11). This is consistent with observations of other investigators (12).

The results of this study suggest that four neurologically meaningful categories of people are produced by the dichotomies of handedness and hand position. When total performance (averaged over both fields) of each group on both tasks is examined, group LI performed more poorly than either group LN or group RN, and females performed more poorly than males (10). Both being female and writing with an inverted hand position are also associated with less lateralization.

The variability of the LI males on the spatial test was significantly greater than that of the other groups ($P < .05$ for all comparisons). Three of these subjects outperformed all right-handed

subjects in the dominant LVF, but eight were inferior to all right-handed males, and only one was in the range of the right-handed males. It is possible that lowered lateralization, with possible dual representation of a function in both hemispheres, can lead to unusually good or poor performance, depending on the function measured.

The two traditional measures, handedness and sex, supplemented by our new measure of hand position, allow very simple, rapid, and reliable prediction of hemispheric specialization and lateralization. These observations allow us to meaningfully subcategorize left-handed writers and the method should be useful in lateralization research and in clinical medicine. Additional research is needed to determine how a dominant hand is controlled by an ipsilateral hemisphere, the sources of variability among individuals in the relationship between the brain and the hand, why manual control by an ipsilateral hemisphere leads to hand inversion and weak lateralization, the nature of the mechanisms underlying the association between performance measures and hand posture, and the possible cognitive correlates of handedness and hand position in writing.

JERRE LEVY, MARYLOU REID

Department of Psychology,
University of Pennsylvania,
Philadelphia 19174

References and Notes

1. H. Hécaen, in *Handbook of Clinical Neurology*, P. J. Vinken and G. W. Bruyn, Eds. (North-Holland, Amsterdam, 1969), vol. 4, pp. 291-311.
2. J. De Ajuriaguerra, H. Hécaen, R. Angelergues, *Rev. Neurol.* **102**, 566 (1960).
3. A. R. Luria, *Traumatic Aphasia: Its Syndromes, Psychopathology, and Treatment* (Moscow Academy of Sciences, Moscow, 1947); H. Goodglass and F. A. Quadfasel, *Brain* **77**, 521 (1954); H. Hécaen and J. De Ajuriaguerra, *Left Handedness* (Grune and Stratton, New York, 1964); O. L. Zangwill, *Acta Neurol. Belg.* **67**, 1013 (1967); A. Subirana, in *Handbook of Clinical Neurology*, P. J. Vinken and G. W. Bruyn, Eds. (North-Holland, Amsterdam, 1969), vol. 4, pp. 248-272; H. Hécaen and J. Sauguet, *Cortex* **7**, 19 (1971).
4. O. L. Zangwill, *Cerebral Dominance and Its Relationship to Psychological Function* (Thomas, Springfield, Ill., 1960).
5. E. A. Enstrom, *Elementary Engl.* **43**, 865 (1966).
6. R. E. Gur and R. C. Gur, personal communication.
7. Described by J. Levy, in *The Biology of Behavior*, J. Kiger, Ed. (Oregon State Univ. Press, Corvallis, 1972), pp. 158-180; J. Levy, in (8), pp. 121-183.
8. S. J. Dimond and J. G. Beaumont, Eds., *Hemisphere Function in the Human Brain* [Wiley (Halsted), New York, 1974].
9. D. Kimura, *Neuropsychologia* **4**, 275 (1966); *Can. J. Psychol.* **23**, 445 (1969); D. Hines and P. Satz, *Neuropsychologia* **9**, 21 (1971); M. Durnford and D. Kimura, *Nature (London)* **231**, 394 (1971); G. Geffen, J. L. Bradshaw, G. Wallace, *J. Exp. Psychol.* **87**, 415 (1971).
10. An analysis of variance was carried out, excluding subject RI, with three between-subject factors: (i) sex, (ii) group, (iii) task order, and two within-subject factors: (i) lateral field and (ii) task. Task order made no significant contribution to the variance, either as a main effect or in any of its interactions. The main effects of group [$F(2, 60) = 5.95, P < .005$] and sex [$F(1, 60) = 18.24, P < .001$] were significant; groups RN and LN had higher scores than group LI, and males were superior to females. The group by lateral field by task interaction was significant [$F(4, 120) = 80.35, P < .001$]; groups RN and LI had higher right visual field (RVF) scores on the syllable test and higher left visual field (LVF) scores on the dot location test, and group LN had the reverse. The four-way interaction among group, sex, lateral field, and task was also significant [$F(4, 120) = 10.38, P < .001$], which shows that females made a smaller contribution than males to the three-way interaction.
11. In a second analysis of variance for each task, superior/inferior field (SVF/IVF) was entered as a within-subjects factor instead of right/left field. The purpose was to compare the groups for degree instead of direction of lateralization. As a result of the definition of the field factor in this analysis, there must necessarily be a main effect of field. In both the syllable test and the dot location test, there was a significant group by field interaction [$F(2, 60) = 7.17, P < .005$, and $F(2, 60) = 9.16, P < .005$, respectively]. In both tasks, the interaction resulted from a larger difference between groups in the SVF than in the IVF; group LI was inferior to both groups RN and LN in the SVF but only marginally inferior in the IVF on the syllable test and not inferior on the dot location test. Thus, on both tests, the magnitude of the field difference was smaller for group LI than for groups RN and LN. Similarly, there was a significant sex by field interaction in both tests, with the field differences for females being smaller than that for males. Males surpassed females in both the SVF ($P < .001$) and in the IVF ($P < .05$).
12. M. P. Bryden [*Percept. Mot. Skills* **23**, 1127 (1966)]; R. Remington, S. Krashen, and R. Harshman (paper presented at the 86th annual meeting of the Acoustical Society of America, Los Angeles, 20 to 23 September 1973); D. A. Lake and M. P. Bryden [unpublished work (1975)]; and R. Harshman [unpublished work (1975)] all report smaller asymmetries of the ear for females than males on dichotic listening tasks. J. A. Wada, R. Clark, and A. Hamm [*Arch. Neurol. (Chicago)* **32**, 239 (1975)] found a smaller degree of anatomical asymmetry in adult female than in adult male brains.
13. We thank D. Kemler, P. Rozin, and J. Wishner for helpful comments and criticisms. We are also grateful to our 73 subjects who volunteered their time.

24 February 1976; revised 17 June 1976

The Biochemical High-Risk Paradigm: Behavioral and Familial Correlates of Low Platelet Monoamine Oxidase Activity

Abstract. A population of individuals potentially at risk for psychiatric disorders was identified by screening 375 college student volunteers for low platelet monoamine oxidase (MAO) activity levels. The lower and upper 10 percent in MAO activity were interviewed and family history data were obtained. Low-MAO probands reported more frequent psychiatric or psychological counseling and problems with the law. Families of low-MAO probands had an eightfold increase in the incidence of suicide or suicide attempts over those of high-MAO probands. This suggests that reduced MAO levels, reported previously in patients with affective disorders and chronic schizophrenia, may predict a vulnerability to psychiatric disorder.

The "high-risk" approach to the study of psychiatric disorders attempts to transcend the dilemma of whether the biological and psychosocial abnormalities observed in psychiatric patients are of etiological significance or result from the disorders. To do this, high-risk studies focus on individuals believed vulnerable to psychiatric disorders before the disorder appears. To select a pool of vulnerable individuals, nearly all high-risk studies have relied on familial models and have examined the offspring or relatives of a clearly defined patient sample. Biochemical studies of psychiatric disorders, on the other hand, have usually begun with patients in "known" diagnostic groups and searched for abnormalities. The present study integrates the usual biochemical paradigm with the high-risk one to produce a new biochemically-at-risk strategy. Here, the "proband" is established by a biological measure, not a clinical one. The use of this strategy reduces the heterogeneity of the sample; eliminates the hospitalization, labeling, and treatment factors that confound other biochemical studies; and rigorously tests the power of the biological factor under investigation.

The biochemical indicator chosen in our study to identify a population potentially at risk for psychiatric disorders is platelet monoamine oxidase (MAO) activity. We felt MAO activity to be especially promising for four reasons: (i) it has been reported in five out of seven studies to be lower in patients with chronic schizophrenia (1, 2) and bipolar (manic-depressive) affective disorders (3); (ii) it is consistent with two leading conceptualizations of biochemical abnormalities in the major psychoses—the transmethylation and dopamine hypotheses (2, 4); (iii) it is under genetic control (2, 5); and (iv) it is associated with some personality test differences in normal males (6) and with stable behavioral profiles in rhesus monkeys (7).

As is true of all promising biochemical leads, the significance of the finding of reduced MAO activities in psychopathologic groups is diminished in two respects. Low MAO activities are found in many but not all patients. More disturbing, there is a small percentage of "normal controls" whose MAO levels are well below the means of the patient groups.

Indeed, it was this group of presum-