

stage, that only males participate, and that the semen can be found on the dead bird (7). In similar experiments (2), we have found that *mated* males participate in these promiscuous copulations. We have observed that any heavy flying bird elicits this "rape" reaction. For example, on a few occasions when a just-released, newly color-marked bird had difficulty gaining altitude, it was pounced on by a group of birds who then attempted copulations. Similar reactions occur when the bird is flying with difficulty for natural reasons (for example, when it is sick). We think this may be related to the heavier flight of egg-carrying females. A final point is that although the female's reproductive system regresses throughout incubation, the male's does not: his testes contain sperm until well into the stage in which he is feeding nestlings (3).

Previously many aspects of the social behavior of animals have gone unnoticed, been misunderstood, or been ignored because of the failure to recognize their potential function of maximizing the individual's inclusive fitness (15). We suggest that much of the social behavior of bank swallows is understandable only when viewed in the context of an MRS. This aspect of social behavior among bank swallows is so prominent that we suspect that closer investigation of the natural history of other monogamous species living under the appropriate conditions may reveal that an MRS is indeed a relatively common pattern.

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5. Rape attempts have been reported in a number of duck species that are conventionally described as monogamous [D. P. Barash, *Science* **197**, 788 (1977); F. McKinney, in *Function and Evolution in Behavior*, G. Baerends, C. Beer, A. Manning, Eds. (Clarendon, Oxford, 1975), p. 331]. The male's reproductive strategy cannot be described as "mixed", however, at least in some of these species, since these males do not make any parental investment. The pair bond seems primarily to have the function, for the male, of enabling him to sequester the female. He does not help her build the nest, incubate the eggs, or feed or guard the young. Indeed, in duck species in which the male does provide some parental care, rape attempts are apparently rare [F. McKinney, in *Breeding Biology of Birds*, D. S. Farner, Ed. (National Academy of Sciences, Washington, D.C., 1973), pp. 6-21]. It seems probable, however, that in some of these duck species, field studies will reveal stable MRS's; for example, McKinney's study (1975) of green-winged teals in large pens is suggestive.
6. S. T. Emlen and N. J. Demong, *Science* **188**, 1029 (1975).
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8. One reason for the lack of data is the difficulty of sexing bank swallows. The only reliable basis for sexing is the brood patch, which only the female has. We capture the birds and color-mark them before pairing and then recapture them during incubation to determine (retroactively) the sex of the members of the pair.
9. We say pair formation has occurred when the pair is seen to move in and out together. Before this time both individuals may be seen at the nest, but they fly in and out independently of one another. Typically other females are present as well, and the male has no apparent favorite. We believe that copulation, occurring within the burrow, may be the key event in triggering the change from one state to the other.
10. Hoogland and Sherman (7) noted pairs leaving and entering the burrow together in the first part of the nesting cycle, which they interpreted as mate-guarding, as we do. Though they believed males guarded females, they were not able to determine who was guarding whom since they had no color-marked, known-sex pairs.
11. P. D. Sturkie, *Avian Physiology* (Springer-Verlag, New York, 1976), p. 388. Most of the available data are from domestic ducks and chickens. In addition, there has been no research on sperm competition, so it is impossible to make strong generalizations.
12. The data in Fig. 2 are not confounded with time since (i) day 1 represents different days for the different pairs (range May 14 through May 22), and (ii) it was an early subcolony. Other sub-

colonies arose at several points during the nesting cycle of the subcolony described in Fig. 2, so there were always females to be chased and males to chase.

13. We have no idea if these copulation attempts are successful. It seems unlikely that in this species the question can be directly answered. F. McKinney (personal communication) has described research with ducks directed toward direct assessment of the outcomes of "rape" attempts.
14. In this paper we have considered only the reproductive strategy of the male. The female's perspective is different, of course. We will consider it in detail elsewhere (2). We note here only that a promiscuous copulation entails a considerable cost to the female's mate but, generally, not to her since her offspring's relation to her is independent of who the father is. There can be indirect costs to her; for example, her mate might detect and not provide parental care to the "illegitimate" offspring. So far as we know there are no such indirect costs to the female in bank swallows.
15. S. Blaffer Hrdy has discussed this phenomenon [*The Langurs of Abu* (Harvard, Cambridge, 1977)] in connection with observations of infanticide in langurs and other primates.
16. We thank J. Alcock, C. Brown, S. Cohen, and P. Schwagmeyer for critical comments on the manuscript.

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Cerebral Specialization, Writing Posture, and Motor Control of Writing in Left-Handers

Abstract. *It has been suggested that the inverted hand position of left-handers during writing indicates the left hemisphere of their brain is linguistically specialized and that the writing of these left-handers may be controlled via ipsilateral pathways. Electroencephalograph alpha asymmetry measures at central and parietal leads, as well as dichotic tests, differentiated right-handers from left-handers, but not inverters from noninverters. Electroencephalograph differences between hand posture groups did appear, but only at occipital leads during reading and writing tasks. Regardless of hand posture or speech lateralization, the right central region of the brain is significantly involved in the control of left-handed writing.*

Left-handers vary in their pattern of hemispheric specialization. Most studies agree that at least half of the left-handed population processes language primarily in the left hemisphere, as do most right-handers. There is less agreement about the amount of right hemisphere participation in language in the remainder of the left-handed population, and this group is typically described as composed of individuals whose specialization for language is either "bilateral" or "reversed" (1-5).

Levy and Reid (6) have reported that hand posture during writing in left-handers "can reliably predict which hemisphere is predominantly linguistic and which [is] primarily 'spatial.'" They described two distinct commonly used hand postures: the inverted position (IHP) in which the hand is held above the line and the pencil points toward the bottom of the page, and the noninverted (NHP) in which the hand is held below the line and the pencil points toward the top of the page. By using tachistoscopic measures, they demonstrated that right-handed subjects (except for one right-

hander who used IHP) and left-handed IHP subjects showed a superiority of the right visual field on a verbal test (nonsense syllable recognition) and of the left visual field on a spatial test (dot localization). The left-handed NHP group showed the opposite field advantages. Levy and Reid conclude that the linguistically specialized hemisphere is ipsilateral to the writing hand in the IHP group and contralateral in the NHP group. Further, Levy and co-workers speculate that the writing hand of the IHP group is controlled via ipsilateral pathways (6, 7).

It would be very useful to have a simple noninvasive technique to identify the linguistic hemisphere. However, researchers do not completely agree that hand posture can be used as such a general index. Moscovitch and Smith (8) used Levy's tachistoscopic measure and replicated the results (6, 7), but on a dichotic test they found no difference between hand posture groups. They also found that IHP writers react faster to visual hemifield targets with the ipsilateral hand, suggesting ipsilateral motor control. However, they failed to obtain the

Table 1. Log right/left alpha values at central and parietal leads for all subjects; data are expressed as means $\pm$ standard deviations.

Group*	N	BLOCKS	READ	SPEAK	WRITE	LISTEN	SPEAK-BLOCKS
<i>Log C₄/C₃</i>							
RH	30	-.093 $\pm$.146	.013 $\pm$.135	.056 $\pm$.126	.159 $\pm$.147	.003 $\pm$.149	.149 $\pm$.128
IHP	33	-.061 $\pm$.149	.008 $\pm$.117	-.002 $\pm$.138	-.100 $\pm$.179	-.014 $\pm$.149	.059 $\pm$.185
NHP	13	-.043 $\pm$.100	.021 $\pm$.125	.032 $\pm$.130	-.089 $\pm$.161	-.001 $\pm$.146	.075 $\pm$.169
<i>Log P₄/P₃</i>							
RH	30	-.001 $\pm$.101	.016 $\pm$.097	.060 $\pm$.092	.130 $\pm$.108	.013 $\pm$.073	.061 $\pm$.117
IHP	33	-.031 $\pm$.096	.005 $\pm$.091	.016 $\pm$.116	-.050 $\pm$.107	.013 $\pm$.150	.047 $\pm$.148
NHP	13	.009 $\pm$.068	.024 $\pm$.113	.010 $\pm$.102	-.052 $\pm$.150	-.026 $\pm$.121	.001 $\pm$.117

*RH, right-handed; IHP, inverted hand position; NHP, noninverted hand position. IHP and NHP groups are left-handers.

same reaction time effect with auditory or tactile stimuli.

Similar but not identical tachistoscopic measures were used by Corballis (9) and McKeever and VanDeventer (10) in unsuccessful attempts to discriminate between IHP and NHP in left-handers. McKeever and VanDeventer also found no difference between the two groups using dichotic listening tests. Milner (11), using the Wada sodium amytal technique to indicate the hemisphere that controls speech, has not found any relationship between hemisphere and hand posture.

To determine what hand posture does index, we assessed hemisphere specialization in IHP and NHP groups by using dichotic listening tests and electroencephalograph (EEG) alpha asymmetry during a battery of cognitive tasks. In addition, EEG asymmetry during writing enabled us to determine whether the writing hand is associated primarily with ipsilateral or with contralateral hemisphere engagement.

In previous experiments (12) we measured EEG alpha power from homologous leads while right-handed subjects performed tasks believed to engage primarily the left hemisphere, such as writing, or primarily the right hemisphere, for example, a block design task. By comparing the value of alpha in the right and left hemisphere leads, we found that right/left (R/L) ratios during the block design task were significantly lower than R/L ratios during writing. In general, the alpha power is relatively lower in the hemisphere primarily engaged by the task. We compared two tasks, rather than one task, to a baseline because it is difficult to specify what the brain is doing during a "resting" or baseline epoch.

The hand posture analysis reported here is part of a larger study assessing task-dependent alpha asymmetry and handedness (6). Ninety normal subjects (45 males and 45 females) (13) were divided into three groups: 30 right-handed, 30 ambidextrous, and 30 "strongly" left-handed, according to their responses to a questionnaire on unimanual activities

(14). All subjects who wrote with the left hand (30 "strongly" left-handed and 19 ambidextrous) were classified as IHP if they held their hand above the line with the pen pointed toward the bottom of the page, or NHP if they wrote with their hand below the line with the pen pointed toward the top of the page. Hand posture was assessed while subjects wrote a sentence, slanting the paper or tilting their heads as they wished. Three subjects were deleted from analysis because they showed equivocal hand posture. We observed no right-handers with inverted hand position. Of the remaining 46 left-handed subjects, 72 percent used IHP and 28 percent used NHP. This incidence of IHP is slightly higher than that found in other hand posture studies and higher than the number of left-handers predicted by clinical studies to have speech control in the left hemisphere. Of the 33 IHP subjects, 64 percent were male and 36 percent female; of the 13 with NHP, 23 percent were male, 77 percent female. This distribution of male and female differs significantly from chance ($\chi^2 = 6.20$, $P = .013$) and is similar to the sex distribution found by Levy and Gur (7) and McKeever and VanDeventer (10).

The dichotic listening tape (15) contained six stop-consonant vowel syllables: ba, pa, da, ka, ga, and ta. Subjects were given 120 trials with two different syllables presented simultaneously, one to each ear. They reported both in any order (forced choice). The number of syllables correctly heard and reported at the left ear was subtracted from the number correctly heard and reported at the right ear, for a right minus left ear advantage score.

The EEG was recorded from C₃, C₄ (central), P₃, P₄ (parietal), and O₁ and O₂ (occipital) leads, referenced to C_z, with a Grass model 7 polygraph (0.5-A cutoff = 1 to 35 Hz). The EEG signal was led to an on-line hard-wired analysis system that filtered the narrow band (9.0 to 11.9 Hz) and summed the alpha power over 30-second epochs. All six channels

of the polygraph and analysis system were adjusted for equal output with a standard 120- μ V, 10-Hz signal and calibrated each day before and after testing. The EEG was recorded while the subject performed cognitive tasks: BLOCKS, READ, LISTEN, SPEAK, and WRITE (16).

The experimenter who edited the EEG record for artifact (17) was blind to the output of integrated alpha power from the analysis system. Complete data at central and parietal leads were obtained for 33 IHP and 13 NHP left-handed subjects and for 30 right-handers. Several tasks tended to cause muscle artifact at the occipital leads in some subjects, and therefore the number for occipital data was reduced to 21 IHP and 9 NHP left-handers, and 13 right-handers. To make comparisons between occipitals and the other lead pairs, we also examined this subset of subjects for whom the same artifact-free epochs were available at all leads for all tasks.

The basic data are the integrated alpha values for each task at six leads (18) and the log R/L ratios between homologous leads indicating relative hemispheric activation. All computations involving ratios were performed on logarithmic transforms of ratios because the log values are linearly and symmetrically distributed.

On the dichotic measure no difference in ear advantage was found between IHP (mean R - L = 5.2, standard deviation = 7.5) and NHP (mean R - L = 4.6, S.D. = 7.0) or between right-handers (mean R - L = 7.0, S.D. = 6.3) and either hand posture group. However, the dichotic measure did discriminate right-handers from the 30 "pure" (excluding ambidextrous) left-handed subjects (mean R - L = 3.2, S.D. = 7.6, $t = 2.07$, d.f. = 58, $P = .05$) (19).

The EEG R/L ratios for central and parietal lead pairs for the entire population ($N = 76$) of the three groups (right-handed, IHP, and NHP) are shown in Table 1. An analysis of variance of the three groups for five tasks was performed, and significant task-

Table 2. WRITE, SPEAK, and BLOCKS tasks, showing alpha values (in microvolts squared) at central leads; data are expressed as means $\pm$ standard deviation. Right/left log ratios are computed for each subject and then averaged over the group, whereas alpha values are averaged over the group for each lead. Thus there is a slight discrepancy between average ratios and the right/left ratios of average alpha values.

Group	N	WRITE		SPEAK		BLOCKS	
		C ₃	C ₄	C ₃	C ₄	C ₃	C ₄
RH	30	78 $\pm$ 44	120 $\pm$ 84	163 $\pm$ 137	188 $\pm$ 159	107 $\pm$ 70	83 $\pm$ 51
IHP	33	126 $\pm$ 106	91 $\pm$ 60	218 $\pm$ 165	211 $\pm$ 169	101 $\pm$ 63	89 $\pm$ 54
NHP	13	131 $\pm$ 109	94 $\pm$ 55	216 $\pm$ 150	227 $\pm$ 151	104 $\pm$ 67	94 $\pm$ 57

group interactions were found at both lead pairs (centrals: $F = 11.32$, d.f. = 8, 292, $P < .0001$; parietals: $F = 7.14$, d.f. = 8, 292, $P < .0001$). Simple effects and Newman-Keuls tests show that IHP and NHP subjects differ from right-handers in several ways but do not differ from each other at all. For example, the WRITE task ratio is dramatically higher in right-handers than in the other two groups. Right-handers also differ from the other groups in the relationship of SPEAK to BLOCKS. The comparison of SPEAK and BLOCKS ratios provides a rough index of the degree of specialization at each lead pair. The ratios show how strongly the left hemisphere is specialized for SPEAK compared to how strongly the right is specialized for BLOCKS. We examined this relationship in three ways. (i) For right-handers, the SPEAK ratio was significantly higher than the BLOCKS ratio at the central ($P < .01$) and parietal leads ($P < .05$), indicating relatively more left hemisphere participation during SPEAK and relatively more right hemisphere participation during BLOCKS. In IHP and NHP groups there was no significant difference between SPEAK and BLOCKS at central or parietal leads, suggesting that neither IHP nor NHP groups have a pattern of hemisphere specialization similar to right-handers at these leads. (ii) At the central leads, while only 10 percent of right-handers showed a SPEAK ratio lower than

BLOCKS, 33 percent of the IHP and 31 percent of the NHP groups showed this reversal of the usual right-handed pattern. (iii) At the central leads, the SPEAK-BLOCKS ratio (actually SPEAK minus BLOCKS because logs are used) was significantly higher in right-handers than in the IHP group ($t = 2.31$, $P < .05$) but not higher than the NHP subjects. However, SPEAK-BLOCKS ratios did not differ between IHP and NHP groups.

All three ways of looking at the relationship between SPEAK and BLOCKS show a difference between these tasks in right-handers, but not in left-handers, consistent with the common finding that left-handers show less lateral specialization. But the results for each hand posture group do not support the prediction from Levy's model that specialization in those with IHP would be similar to right-handers, and that those with NHP would show more "reversed" specialization. The conclusion is the same when we examine alpha values for individual leads instead of the R/L ratio. Table 2 shows alpha values at C₃ and C₄ for WRITE, SPEAK, and BLOCKS. There is no difference between IHP and NHP groups at either lead for any task; the means are almost identical. Thus, by EEG criteria at the central and parietal leads, each hand posture group contains the same mixture of individual patterns of specialization found in any group of unselected left-handers.

Because the studies that have demonstrated differences between IHP and NHP groups have used a visual (tachistoscopic) test, we examined the visual area recordings (O₁, O₂). The subset population with artifact-free occipital data (Table 3) was used for further task by group analysis of variance for each lead pair. We had focused our initial interest on the central and parietal leads because the occipitals do not seem to be as sensitive as the other leads to task differences. In Table 3, at the central leads for right-handers, BLOCKS differs from SPEAK and WRITE, but at the occipitals, the ratios of the three tasks are almost identical. For the subset, as for the larger population, significant task-group interactions, simple effects, and Newman-Keuls tests at central and parietal leads show that right-handers differ from IHP and NHP groups on the WRITE task and in the relationship of SPEAK to BLOCKS, whereas the IHP and NHP groups do not differ from each other in these areas.

However, at the occipital leads, significant differences involving IHP and NHP as well as right-handed groups are found. The mean log ratios for all tasks combined differentiate the three groups (main effect for group, $F = 4.12$, d.f. = 2, 40, $P = .024$) although no comparisons between pairs are significant. But simple effects tests do reveal differences among the three groups on individual tasks: WRITE ($F = 7.25$, d.f. = 2, 200, $P < .01$); READ ($F = 3.83$, $P < .05$); and BLOCKS ($F = 3.26$, $P < .05$). Newman-Keuls comparisons between pairs show that on the WRITE task, the NHP group has lower ratios than the IHP ($P < .05$) and the right-handed group ($P < .01$); IHP ratios do not differ from the right-handed group. The differences are similar, but smaller for READ: those with NHP have lower ratios than right-handers ($P < .05$) (20). Alpha values at individual leads O₁ and O₂ are presented in Table 4. Ratio dif-

Table 3. Data on all tasks for subset with log right/left alpha values at central, parietal, and occipital leads. Data are expressed as means $\pm$ standard deviation.

Group	N	BLOCKS	READ	SPEAK	WRITE	LISTEN	SPEAK-BLOCKS
<i>Log C₄/C₃</i>							
RH	13	-.043 $\pm$.135	.058 $\pm$.176	.108 $\pm$.159	.195 $\pm$.180	.061 $\pm$.176	.151 $\pm$.109
IHP	21	-.047 $\pm$.121	.020 $\pm$.105	-.009 $\pm$.151	-.087 $\pm$.178	-.007 $\pm$.164	.038 $\pm$.175
NHP	9	-.038 $\pm$.108	-.012 $\pm$.105	.003 $\pm$.136	-.102 $\pm$.171	-.027 $\pm$.166	.041 $\pm$.158
<i>Log P₄/P₃</i>							
RH	13	.032 $\pm$.063	.043 $\pm$.082	.079 $\pm$.107	.161 $\pm$.097	.020 $\pm$.099	.047 $\pm$.103
IHP	21	-.042 $\pm$.098	-.007 $\pm$.098	-.017 $\pm$.119	-.045 $\pm$.082	-.009 $\pm$.157	.025 $\pm$.156
NHP	9	.023 $\pm$.063	.017 $\pm$.117	.028 $\pm$.110	-.042 $\pm$.163	-.019 $\pm$.132	.005 $\pm$.112
<i>Log O₂/O₁</i>							
RH	13	.056 $\pm$.096	.042 $\pm$.087	.043 $\pm$.077	.058 $\pm$.082	.008 $\pm$.078	-.013 $\pm$.086
IHP	21	-.010 $\pm$.081	.018 $\pm$.080	.027 $\pm$.095	.001 $\pm$.083	.028 $\pm$.084	.037 $\pm$.100
NHP	9	-.019 $\pm$.033	-.044 $\pm$.061	-.010 $\pm$.065	-.064 $\pm$.055	-.044 $\pm$.094	.009 $\pm$.053

Table 4. Alpha values at occipital leads for READ and WRITE; data are expressed as means $\pm$ S.D.

Group	N	READ		WRITE	
		O ₁	O ₂	O ₁	O ₂
RH	13	555 $\pm$ 185	648 $\pm$ 345	357 $\pm$ 141	424 $\pm$ 197
IHP	21	555 $\pm$ 281	572 $\pm$ 272	343 $\pm$ 135	339 $\pm$ 123
NHP	9	539 $\pm$ 283	483 $\pm$ 243	345 $\pm$ 172	292 $\pm$ 123

ferences among groups at the occipital leads are due entirely to changes in the O₂ lead.

These results suggest that the right occipital area is engaged during READ and WRITE relatively more in persons with NHP than in right-handers and those with IHP. Thus at the occipital leads (over brain areas which process visual information) during visual language tasks, the relationship of hand posture to hemisphere participation in "language" predicted by Levy and Reid (6) is confirmed. Interestingly, this relationship is absent at the anterior leads where auditory processing and elements of language production occur. On the O₂/O₁ BLOCKS ratio, IHP and NHP groups are nearly identical (Table 3). This is contrary to the prediction suggested by Levy's tachistoscopic data, which implied that for the NHP group the left hemisphere would be more engaged in spatial tasks and for IHP and right-handed groups the right hemisphere primarily would be engaged. Thus, no difference between IHP and NHP groups in spatial specialization was seen at any lead pair.

It is not clear why the significant ratio differences between IHP and NHP appeared in WRITE and READ. The effect does not seem to be generalized to all verbal tasks (not to SPEAK) nor to all visual tasks (not to BLOCKS). Perhaps the effect depends on an interaction of visual and verbal cognitive demands.

The suggestion by Levy and Reid that in the IHP group the writing hand may be controlled via ipsilateral pathways (6) is not supported by our data obtained at the central leads during the WRITE task. These leads are presumably located close to motor control areas for the hand. If speech in the IHP group is controlled in the left hemisphere and writing is controlled via ipsilateral pathways, then one would expect as much left hemisphere engagement as is found in right-handers. IHP WRITE ratios would be similar to right-hander WRITE ratios and significantly higher than NHP WRITE ratios where one would expect the right hemisphere to be engaged. The central leads (Table 1) show dramatic group differences on the WRITE task ($F = 22.49$,

d.f. = 2, 365, $P < .001$) due only to the right-handers: right-hander WRITE ratios are significantly higher than both IHP and NHP ($P < .01$). The ratios in the IHP group do not differ significantly from NHP on the WRITE task. WRITE ratios are significantly higher than SPEAK in the right-handers ($P < .01$) and significantly lower than SPEAK in IHP ($P < .01$) and NHP groups ($P < .05$), suggesting that the motor control of the right hand requires more left central engagement, while control of the left hand requires more right central engagement.

To determine how activity in each hemisphere contributes to these R/L ratio differences in writing, we examined the alpha values for separate leads C₃ and C₄ (Table 2). Since no differences were seen between IHP and NHP the two groups were pooled as left-handers. A two group (right-handed versus left-handed) by two lead (C₃ versus C₄) analysis of variance (repeated measures on lead) was performed on alpha values during WRITE. There was no main effect of lead or group; however there was a highly significant lead by group interaction ($F = 24.69$, d.f. = 1, 74, $P < .001$). To explicate the interaction, t -tests were calculated. The left hemisphere (C₃) is engaged more than the right (C₄) during WRITE in right-handers ($t = -4.24$, d.f. = 29, $P = .0002$), and the right hemisphere is engaged more than the left in left-handers. ($t = 3.28$, d.f. = 45, $P = .002$).

Therefore, we conclude that the WRITE task engages primarily the central region on the hemisphere contralateral to the writing hand, and the right hemisphere central region is activated for left-handed writing regardless of hand posture.

To further examine the hypothesis that the left hand is controlled via ipsilateral pathways in left-handers whose speech is processed in the left hemisphere, we analyzed our WRITE data in a second way. On the basis of their SPEAK and BLOCKS log ratios at the central leads, we selected left-handed subjects whose speech appeared to be processed primarily in the left hemisphere. We chose all subjects for whom SPEAK minus BLOCKS

was greater than 0.00 (an arbitrary cutoff point indicating, in general, greater left hemisphere participation in SPEAK and greater right hemisphere participation in BLOCKS). If writing is controlled by the same hemisphere as speech in these selected left-handers, one would expect WRITE ratios to be the same as or higher than SPEAK ratios, as is the case in right-handers. Ninety percent of the right-handers ($N = 27$), 67 percent of the IHP ($N = 22$), and 69 percent of the NHP ($N = 9$) groups were selected with this criterion. We used these groups for the second analysis of the WRITE data. An analysis of variance on C₄/C₃ SPEAK ratios reveals no differences among the three groups ($F = .07$, not significant), while an analysis of variance on C₄/C₃ WRITE ratios shows that again the difference in WRITE is highly significant ($F = 18.56$, d.f. = 2, 55, $P < .001$): the WRITE ratio in right-handers is significantly higher than in the IHP or NHP groups (Newman-Keuls, $P < .01$), but IHP and NHP do not differ from one another. As with the unselected populations, the WRITE ratio is significantly higher than SPEAK in right-handers and significantly lower than SPEAK in both left-handed groups (21). Therefore, even in those left-handers selected by EEG criteria for processing speech primarily in the left hemisphere, writing with the left hand involves considerable right hemisphere participation.

Thus, our EEG recording during writing in normal left-handed subjects leads us to conclude that the right hemisphere is strongly engaged during left-handed writing regardless of hand posture or hemisphere specialization for speech. In left-handers whose speech is primarily controlled in the left hemisphere, this process is presumably mediated across the corpus callosum. The idea that control of a hand might be executed across the corpus callosum is not a new one. Since 1908 it has been recognized that in patients with callosal lesions, the "minor" hand is apraxic (it cannot carry out verbal commands) because it can no longer operate under the control of the language hemisphere. Heilman *et al.* (22) have presented an excellent discussion of this literature.

Our assessment of hemisphere specialization with EEG and dichotic measures suggests that the differences found between the two hand posture groups may be based primarily on visual rather than auditory or proprioceptive-motor specialization. This would explain the absence of significant differences between IHP and NHP groups at anterior leads and the presence of differences during vi-

sual language tasks at the occipital leads. The repeated failure to find a difference between the IHP and NHP groups with dichotic listening tests would also be explained if hand posture is related to visual processing. Levy's successful method is visual.

In conclusion, we find modest support for the inferences of Levy and Reid (6) and Moscovitch and Smith (8) that the two hand postures might indicate different patterns of brain organization among left-handers. However, it does not appear the hand posture can be used to indicate the "language hemisphere." Indeed, the assumption that language is unitary may underlie much of the conflict in the literature on lateralization. The left-handed population is often described as including individuals in whom "language" is represented in the left hemisphere, or the right, or bilaterally. Evidence for this conclusion has come primarily from clinical studies of patients with lesions or patients who have undergone presurgical anesthetization of one hemisphere by sodium amytal (1) and from studies of normal subjects using visual hemifield stimulation (2), dichotic tasks (3), or EEG measures of task-dependent asymmetry (4, 5).

The correlations between results obtained with these various methods are low (23), perhaps because they are not studying the same language behaviors. For example, clinical studies frequently include receptive or expressive language dysfunctions, or both, under the general heading of aphasia. The sodium amytal procedure tests only speech; the tachistoscopic paradigm, only reading; and the dichotic measure, only listening. Few EEG studies have explicitly examined asymmetry differences among several language tasks. With all of these methods, although specific language behaviors are tested, the results are usually generalized to indicate "the language hemisphere" as if any language task were representative of them all.

Language is not a unitary function. In left-handers, or groups such as learning-disabled and stutterers whose cerebral organization is alleged to be less lateralized than typical right-handers, it may be only particular components of language that are lateralized differently. The concept of a language hemisphere may be most useful when describing typical right-handers in whom all these behaviors are lateralized fairly consistently to the left hemisphere; it may be misleading when applied to left-handers or ambidextrous persons whose patterns of specialization might differ for specific aspects of language. Specific language

tasks depend on communication between specific organized regions in the cortex. Therefore, attempts to show differences in language lateralization between subjects should also analyze task and regional specificity.

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13. Subjects were 18 to 45 years old, Caucasian, English-speaking, with no history of neurological disorder; they were recruited by advertisement, paid \$2.50 per hour, and were naïve to the experiment's purpose.
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15. The tape was obtained from C. Berlin, Kresge Hearing Laboratories, New Orleans, La. Standard clinical audiometry (250 to 6000 Hz) was administered before the dichotic listening tests to ensure that all subjects had no more than a 30-dB hearing loss at any frequency in either ear and that ears were matched within 10 dB. The two channels of Tandberg recorder and AKG stereo headphones were matched and calibration was checked before every block of 30 trials. Earphones were reversed after the first 30 trials.
16. In BLOCKS, a two-dimensional geometric pattern (Koh's) was memorized for 1 minute; then the EEG was recorded while subjects constructed the pattern from memory with multicolored blocks using both hands. Additional designs were presented until 3 minutes of recording were obtained. In READ, subjects read a factual but not difficult 1000-word passage on biological rhythms, concentrating on facts and ideas to summarize later. For the LISTEN task, subjects listened to a tape of a similar passage. For SPEAK, subjects gave a 3-minute oral summary of what they had just heard or read. For WRITE, subjects wrote as many of the facts as they could recall from what they had just heard or read. Tasks were repeated twice in counterbalanced order.
17. Editing criteria as described in (11). If an artifact occurred in one lead, for example, C₄, that epoch for the homologous lead (C₃) was deleted, but if the other lead pairs had no artifact in that epoch, they were accepted. A task record had to contain at least 2 minutes of artifact-free data for both central and parietal leads.
18. Full tables of values at each lead are omitted for brevity; complete data may be obtained from the authors.
19. The relationship between EEG asymmetry and dichotic listening was reported by J. Herron to the International Neuropsychology Society, New York, February 1979.
20. Although a full analysis of sex differences was not possible due to the small sample of males in the NHP group, analysis of the O₂/O₁ ratios revealed differences between females with IHP and females with NHP for reading ($t = 1.91$, $P < .077$) and writing ($t = 2.16$, $P < .049$). Thus the differences seen between IHP and NHP for O₂/O₁ for these tasks are not because there are more males with IHP and more females with NHP.
21. The IHP writing ratio (-0.074) was significantly lower than IHP speaking (.060) ($t = -4.72$, $P < .001$). The NHP writing ratio (-0.081) was significantly lower than NHP speaking (.078) ($t = -3.69$, $P < .01$). The right-handed writing ratio (.159) was significantly higher than right-handed speaking (.063) ($t = 3.22$, $P < .01$) (t -tests are for paired observations).
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Pupillary Responses During Information Processing Vary with Scholastic Aptitude Test Scores

Abstract. *The magnitude of task-evoked pupillary dilations during mental activity has previously been shown to index the cognitive capacity utilized in the performance of the mental task. To determine the relation between "intelligence" and capacity demands during mental activity, task-evoked pupillary dilations were measured while two groups of university students differing in their scores on the Scholastic Aptitude Test solved mental arithmetic problems. Over three levels of problem difficulty, more intelligent subjects showed smaller task-evoked pupillary dilations than did their less intelligent counterparts. Thus, the more intelligent appear to possess more efficient cognitive structures of information processing. These data provide evidence that physiological differences between individuals of differing psychometric intelligence emerge during mental activity.*

The general (G) factor of intelligence was first described by Spearman in 1904 (1) as an explanation for the consistent positive correlations observed between tests of cognitive ability that differ wide-

ly in both content and modality. Spearman further suggested that G may correspond to the amount of general mental energy available to an individual and that specific abilities are brain structures or