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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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, C_4, that epoch for the homologous lead (C_3) 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 O_2/O_1 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 O_2/O_1 for these tasks are not because there are more males with IHP and more females with NHP.
21. The IHP writing ratio (−.074) was significantly lower than IHP speaking (.060) ($t = -4.72$, $P < .001$). The NHP writing ratio (−.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 widely 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 "mental engines" that draw upon this power reservoir. This forthright view of the biological nature of intelligence has since remained largely untested.

Spearman's concept of G as general mental energy has much in common with the concept of "processing resources" now prevalent in contemporary cognitive psychology (*2*). In this view, cognitive processing places demands on a limited supply of resources or capacity. Mental performance becomes resource-limited when the total demand for resources exceeds the available supply (*3*). The theoretical concept of momentary processing load seems to be reflected accurately in autonomic signs of central activation (*4*). Specifically, small task-evoked changes in the size of the pupil of the eye provide a sensitive autonomic index of the shifting demands of cognitive processing (*5*). This chain of reasoning suggests that the amount of "general mental energy" that is demanded in thinking can be measured with recently devised pupillometric methods. Thus, the dynamics of cognitive processing may now be compared among individuals who differ in psychometrically measured intelligence.

The hypothesis that task-evoked activation might be associated with general intelligence allows for three possible patterns of difference. An attentional or motivational view of intelligence would suggest that people who score high on intelligence tests apply themselves with more vigor to the task at hand. If that is true, larger pupillary responses should be observed for all types of problems in more intelligent individuals. A second possibility is that people differ in the efficiency with which they use their available capacity. This view is consistent with the notion that the component processes of any task might individually require less capacity if they are better learned or more automatic. Overlearned tasks elicit less autonomic activation responses in their execution (*6*). A third possibility is that more intelligent individuals have more capacity available and therefore can solve more demanding problems. This possibility is independent of the first two hypotheses, and was not tested by the experiment reported here.

To choose between the first two hypotheses, task-evoked pupillary dilations were measured in two groups of subjects of different psychometrically measured intelligence [defined for the purposes of this experiment by scores on the Scholastic Aptitude Test (SAT)] as they solved mental multiplication problems of varying difficulty (*7*). Thirty-nine male and female Caucasian undergraduate students served as subjects. The 22 subjects in the high group had combined (verbal plus quantitative) SAT scores of 1350 or more (mean 1407). The 17 subjects in the low group had combined SAT's of 950 or less (mean 877).

The two groups were also widely separated on an independent short written test of mental ability, the Wesman Personnel Classification Test, which was administered after the experimental task [$t(38) = 12.2, P < .001$]. On that test, no subject in the low group scored as high as the lowest-scoring subject in the high group. There was, however, no significant difference between the two groups in university grade point averages [$\bar{X}_{\text{high}} = 3.18$; $\bar{X}_{\text{low}} = 3.03$; $t(38) < 1$].

All phases of experimentation—from trial control and pupillometric data acquisition to data verification, reduction, and display—were performed automatically under the control of a general-purpose digital computer and laboratory interface system. Vertical pupillary diameter was measured by a television pupillometer (Whittaker 1050S), which contains a headrest and an infrared eye illuminator. The camera was aligned on the horizontal plane of the subject's left eye, and displaced 45° from the line of gaze. Momentary pupil diameter was available as analog output of the pupillometer. This output was sampled and digitized at 50-msec intervals during experimental trials.

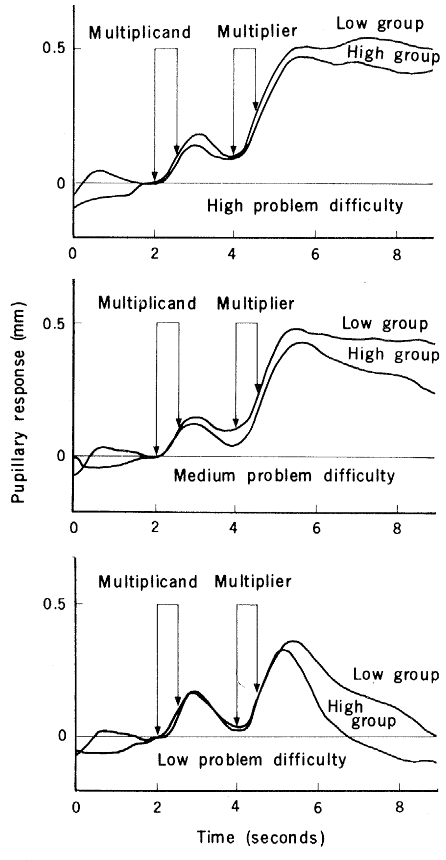

Fig. 1. Averaged task-evoked pupillary responses for correctly solved problems at three levels of difficulty for subjects in the high and low groups of psychometrically measured intelligence. At all difficulty levels, larger pupillary responses are observed for subjects in the low group.

The subject sat at a microswitch input keyboard, with his head positioned in the pupillometer. Illumination in the 6- by 9-foot room was constant at approximately 37 foot-lamberts (1 foot-lambert = 3.4263 cd/m^2). The subject viewed a closed-circuit video monitor of his own pupil, set at very low contrast, so that he could assist in keeping his pupil centered and focused. This screen was 2 m from the pupillometer headrest. To obtain a measure of noncognitive pupillary responsivity, the subjects' pupillary light and dark reflexes were measured to shifts of room illumination between 17 and 27 foot-lamberts.

During the multiplication task, auditory stimuli were generated from previously stored files of digitized natural speech and presented under computer control. The stimulus-word files, digitized at a rate of 10 kHz, were scaled to equalize root-mean-square voltage among words, producing relatively uniform stimulus intensity. The use of computer-generated speech ensured precisely timed standard stimuli.

The subject initiated each trial with a bar press, after which a multiplicand and multiplier were presented after 2-second intervals. Five seconds were allowed for solution of the problem before the answer cue was presented, after which the mentally computed product was entered on the response keyboard. Pupil diameter was recorded for the 9-second period from the bar press to the answer cue. Thirty-two problems were presented in this manner, eight each at four levels of difficulty. Problem order was randomized over subjects. As the middle two levels of problem difficulty were indistinguishable in both performance and pupillary response data, they were pooled in the results reported here.

The least difficult level was composed of problems for which the multiplicand was between 6 and 9 and the multiplier was 12, 13, or 14. The medium-difficulty problems had (i) multiplicands from 11 to 14 paired with multipliers from 11 to 14 and (ii) multiplicands of 6 to 9 paired with multipliers of 16 to 19. The most difficult problems were the numbers 11 through 14 paired with numbers 16 through 19.

After each experimental session, the pupillary records for individual trials were inspected for eye blink and other artifacts. Trials with small artifacts occurring in noncritical periods were corrected according to a linear interpolation procedure. Trials with major artifacts were discarded. From these records, averaged task-evoked pupillary responses were computed separately for each subject and for each level of problem difficulty for all trials in which the subject had correctly solved the problem.

Subject performance on the mental arithmetic task differed between groups, as expected. Individuals in the high-ability group were more accurate at every level of difficulty (Table 1). The median total score for the high group was 31 (out of 32) problems correctly solved; the low group median was 26 (Mann-Whitney $U = 58$, $P < .001$).

Figure 1 presents the averaged evoked pupillary responses for correct, artifact-free trials as a function of group and problem difficulty. All responses show a common pattern of dilation followed by a slight constriction after the multiplicand was presented. A larger dilation was evoked by the multiplier; this increase in pupillary dilation was maintained during the problem-solving period. For the easiest problems, there was a return to baseline during the period between multiplier and the answer cue.

Statistical analyses of these data confirm that both problem difficulty and ability level affect the size and form of the pupillary response in the mental arithmetic task. The extent of task-evoked activation during the period of problem solution was estimated by the mean pupillary dilation during the 4 seconds preceding onset of the answer cue (mean pupillary diameter for seconds 4.5 to 8.5 minus pupillary diameter at second 2.0). This measure provides a stable estimate of task-induced change that is independent of baseline pupillary diameter (*8*). An analysis of variance confirmed the effects that are apparent in Fig. 1. More difficult problems evoked larger pupillary dilations [$F(2, 74) = 49.75$, $P < .001$], thus reconfirming the previously demonstrated relationship between problem difficulty and the task-evoked activation (*5*). What is new in these data is that subjects of greater psychometrically defined intelligence show less task-induced activity in the performance of the mental multiplication task than do subjects of lesser intelligence [$F(1, 37) = 5.59$, $P = .03$]. Equivalent tasks appear to impose a smaller processing load in more intelligent individuals.

To test the possibility that the difference between groups in average pupillary response amplitude is wholly attributable to between-group differences in processing rate, a secondary peak analysis was performed. The single point of maximum pupillary diameter in the solution period was selected by computer for each subject and experimental condition. This procedure supplies both latency and amplitude of the peak pupillary dilation, although it is more susceptible to the effects of random variation in the pupillometric records than is the average dilation method reported above. As might be expected from visual inspection of Fig. 1, peak amplitude increases as a function of difficulty [$F(2, 74 = 28.81$, $P < .001$], as does peak latency [$F(2, 74) = 17.83$, $P < .001$]. Furthermore, the more intelligent subjects tended to display smaller peak dilations [$F(1, 37) = 3.71$, $P < .061$] at shorter latencies [$F(1, 37) = 5.39$, $P = .026$]. That less intelligent subjects tended to display larger peak dilations suggests that the larger average amplitude of the task-evoked pupillary response was not simply a function of slower information processing.

Table 1. Error rates by group and problem type.

Difficulty level	Low group	High group
Low	.12	.06
Medium	.33	.10
High	.63	.23

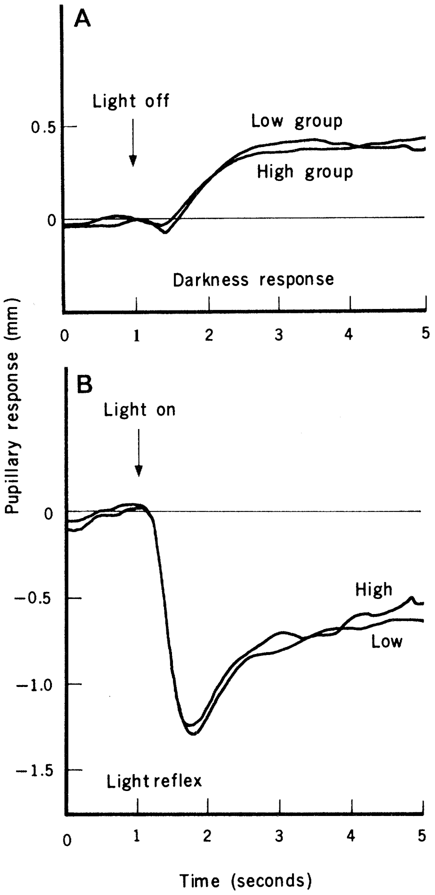

Fig. 2. Averaged pupillary responses for light offset (A) and onset (B) for subjects in the high- and low-intelligence groups. No group differences in either type of response are apparent, which suggests that the group differences observed during mental arithmetic are of central, not peripheral, origin.

These differences in task-evoked pupillary response between the groups appear to reflect differences in central, rather than peripheral, brain processes. The groups did not differ in the magnitude of light-induced pupillary constriction or dark-induced pupillary dilation (Fig. 2). In both responses, the group tracings cross each other frequently. There was no evidence of reliable group differences for either the light [$t(38) < 1$] or the dark reflex [$t(38) = 1.11$].

These results help to clarify the biological basis of psychometrically defined intelligence. They suggest that more intelligent individuals do not solve a tractable cognitive problem by bringing increased activation (*4*), "mental energy" (*1*), or "mental effort" (*2*) to bear. On the contrary, these individuals show less task-induced activation in solving a problem of given difficulty. This suggests that individuals differing in intelligence must also differ in the efficiency of those brain processes which mediate the particular cognitive task.

These results may be related to another phenomenon of autonomic nervous system response. Kintsch (*6*) examined the magnitude of the galvanic skin response as subjects learned a list of paired items. The magnitude of response was stable for each item as it was learned, but began to decrease systematically with practice after the last error. Kintsch's data suggest that the effect of further practice is to make access to the items more automatic and thereby to decrease the processing load associated with item retrieval; increasing processing efficiency decreases the autonomic response associated with that processing.

Kintsch's data open the possibility that the physiological differences in the amplitude of the pupillary response during information processing might reflect the effects of prior practice at cognitive tasks rather than genetically determined differences. For this reason, the present data do not bear upon the questions of the heritability of intelligence or the neurophysiological basis of intelligence. Furthermore, the magnitude of the between-group difference in the pupillary response is small compared with the variance within groups. We therefore see little possibility that pupillary response is appropriate for use as a physiological measure of intelligence.

Task-evoked pupillary responses thus appear to index the processing load imposed on the nervous system in the performance of mental activities (*4*). The magnitude of the physiological response systematically increased with task complexity or difficulty. Over all levels of problem difficulty for which correct performance was possible, more intelligent individuals showed smaller pupillary dilations than did their less intelligent counterparts. This result argues for more efficient and automatic information processing in individuals of higher psychometrically defined intelligence. These results provide evidence that physiological differences between individuals of differing psychometric intelligence emerge during mental activity (*9*).

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   M. P. Janisse [*Pupillometry* (Wiley, New York, 1977)] has summarized three previously unpublished experiments on pupillary response and intelligence. R. M. Daly [thesis, Loyola University, Chicago (1966)] compared groups differing in performance on a problem-solving test, with psychometrically measured intelligence held constant. The results, therefore, do not bear on the subject of this report. D. G. Crough [*Diss. Abstr.* **32**, 1870 (1971)] studied the pupillary response to items from the Raven Progressive Matrices Test and the Differential Aptitude Test Battery as a function of intelligence, which was estimated from performance on another subset of the Raven test and the SAT. His results were in accord with those presented here. Finally, S. Kuk and M. P. Janisse in two unpublished reports measured pupillary response in the digit span test for subjects differing in performance on the Digit Span Forward subscale of the Wechsler Adult Intelligence Scale. The amplitude of the task-evoked dilation for correctly solved problems was larger for the low-intelligence than the high-intelligence group, the pattern of results reported here, and contradictory to Kuk and Janisse's conclusions (figure 6-1 in Janisse).
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Developmental Fate of Skeletal Muscle Satellite Cells

Abstract. *Radioisotopically labeled satellite cells from clonal cultures were implanted into normal muscle of the original donor. Implanted cells invariably retained their myogenic potential by participating in the regeneration of damaged myofibers or in the development of existing fibers.*

Striated skeletal muscle is capable of rapid and widespread regeneration (*1*). In view of the established postmitotic nature of the nuclei in syncytial myofibers, the source of the regenerating cells in adult muscle has been considered to be the mononucleated satellite cells (*1, 2, 2a*) that lie beneath the external (basal) lamina of myofibers (*2a, 3*). Investigations in vitro have demonstrated that satellite cells recapitulate the normal embryonic development of skeletal muscle through proliferation and fusion to give rise to cross-striated, contractile myofibers (*4*). Therefore, on a functional basis, satellite cells are developmentally indistinguishable from embryonic myoblasts in that both serve as myogenic precursors.

When grown under established culture conditions (*5*), satellite cells become myoblasts by faithfully repeating the sequence of muscle cytodifferentiation as it is observed in vivo. However, if grown in less than optimal conditions, or in an environment simulating that of diseased muscle, the developmental expression of these muscle precursors is reversibly altered (*6*). As a result of this modulation, the myogenic cells assume fibroblast or adipocyte morphology and behavior as long as they are grown in the altered environment.

Do satellite cell–derived myoblasts grown in vitro under optimal or less than optimal culture conditions truly reflect the developmental behavior of satellite cells in intact tissue, or are the cultured cells merely responding to an artificial growth environment? As a first step toward answering this question, the fate of satellite cells must be studied in vivo. To identify the developmental potential of satellite cells, experiments have been carried out by others (*2a, 7*) to label intact muscle tissue with [^{3}H]thymidine and injure the labeled muscle in situ or transplant it into different hosts. Although these studies suggest that satellite cells participate in the normal regenerative response, the muscle used in these investigations is composed of a heterogeneous population of labeled cells that include satellite cells, fibro-

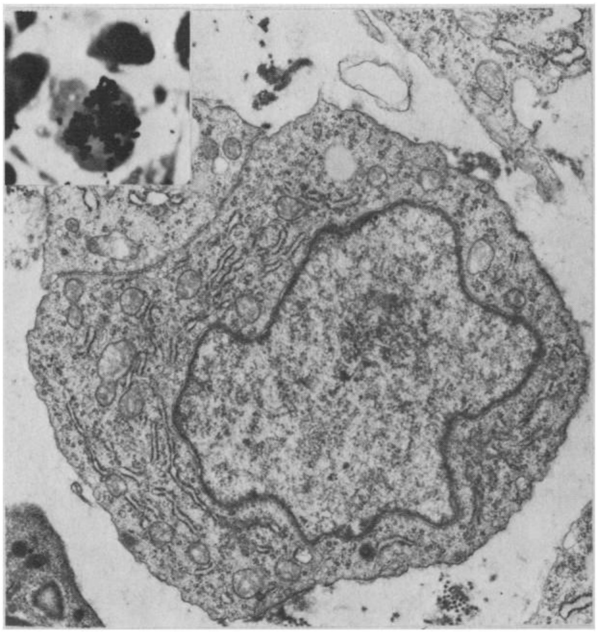

Fig. 1. Adjacent thick and thin sections of rat tibialis anterior muscle showing the same cultured myogenic cell 48 hours after implantation. The thick-section radioautograph (inset) shows silver grains over implanted cell (×1300). Electron micrograph (below inset) of the same cell illustrates typical cytology of a rat myoblast (×7400).

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