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Attention Mechanisms following Brain Bisection[1]

M. S. Gazzaniga
Department of Psychology
New York University
New York, New York

S. A. Hillyard
Department of Neurosciences
University of California, San Diego
La Jolla, California

ABSTRACT

Brain bisection that disconnects the cortical–cortical connections between the cerebral hemispheres was found to have a profound effect upon the attentional processes that are active during learned sensory–motor performance tasks. In most cases in the split-brain primate, the quantity of information that can be processed by the two hemispheres working in concert on separate tasks is substantially greater that when only one task is being solved. It is as if the split-brain operation adds an extra data-processing channel with selective attentional capabilities for the parallel processing of dual tasks. This suggests that the neuroanatomical basis of interference between concurrent tasks in normal primates is due in large part to the intact cortical–cortical connections.

At the same time, when a lateralized motor response set was induced by a particular task, substantial interhemispheric interaction was evident in the split-brain primate. Present evidence, including bilateral recordings of the cortical electroencephalogram (EEG), suggests that this disruption of one hemisphere's activities by the other occurs at the motor response end of processing rather than by disrupting the sensory or perceptual analysis of inputs.

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I. Introduction

This contribution examines the question of whether the bilateral symmetry of the telencephalic structures in the primate brain permits the operation of two independent attentional systems when the interhemispheric connections are transected. The extent to which this "split-brain" operation enables the "parallel processing" of sensory information and motor coordinations in the separated hemispheres indicates the relative roles of cortical and brainstem structures in mediating different types of selective processes.

The concept of attention has been used to describe selective processes at any of several points in a sensory–motor performance sequence. Some theorists define attention in purely perceptual terms as a process that enhances the detection of selected stimuli to the exclusion of others (Berlyne, 1970). Another view emphasizes the selective retrieval from memory of learned associations and expectations that govern behavioral sequences (Hochberg, 1970). Finally, there is the older idea of attention as the holding of a specific response in readiness (that is, response set).

Most of the studies reported here were not designed to differentiate between these and the numerous other varieties of attention. Hence, we use the term *attentional processes* in a general sense to indicate those brain mechanisms that enable either the selection of specific stimuli, the retrieval of conditioned associations, or the execution of specific conditioned responses. Thus, our measure of attention is the overall quantity of selective information transmitted through the nervous system from receptor to effector as revealed in the pattern of stimulus–response correlations, or simply stated, the overall information processing capacity.

The experiments described in Section II demonstrate that mechanisms of selective attention can operate simultaneously and independently (that is, in parallel in the two disconnected half-brains, such that the net information transmitted is greater than when either hemisphere works alone). In a few instances, the two hemispheres working simultaneously and independently can process exactly twice as much information as either working alone. In contrast, the studies described in Section III reveal departures from parallel processing in the form of a blocking of one hemisphere's performance brought about by problem solving in the other. Such evidence is interpreted as showing that bilateral coordination mechanisms in the brainstem can influence the expression of selective sensory and motor processes in the cortex, in certain tasks where one hemisphere predominates.

II. Parallel Processing in the Separated Hemispheres

The studies reported here have been carried out in either split-brain monkeys or human patients, the latter having undergone brain-bisection surgery in an effort to control the interhemispheric spread of epileptic seizures. In both instances surgical disconnection of the hemispheres included the corpus callosum and anterior commissure. In the monkeys the optic chiasm was sectioned as well. This surgery disconnects only the cortical–cortical interhemispheric exchange system and produces the well-known split-brain effects. These effects include the creation of separate and distinct cognitive systems within each hemisphere that are capable of learning, emoting, and processing at least some language, as well as certain other abilities (Gazzaniga, 1970).

Some studies in man that demonstrate parallel processing in terms of duplicate, simultaneous perceptions in the two sides are represented in Fig. 1. These tests showed that each hemisphere could register information briefly presented (100 msec) to it and could subsequently respond correctly, even after a prior and contradictory response from the other. For example, in Fig. 1d when the word "HE*ART" is flashed with the fixation point occurring between the "HE" and the "ART," thus making "ART" projected exclusively to the left hemisphere and "HE" to the right, the subject responds verbally that he saw only the word "ART." When the left hand subsequently is allowed to choose a card from a series, however, it passes over a card with "ART" or "HEART" printed on it and chooses one with "HE" (Gazzaniga, Bogen, & Sperry, 1965).

This same kind of phenomenon is seen in Fig. 1a, where the subjects say they saw a "triangle"; yet the left hand will subsequently pick up a "square." Here again the "angle" is flashed exclusively to the left hemisphere while the half-square goes to the right half-brain. In addition to the separation of percepts, the subjects tend towards figure completion and say they saw a "triangle" instead of the actual stimulus of an "angle."

In Fig. 1b an immediate spoken response "IKE" is made by the patient, even though the right hemisphere is reportedly superior in facial-recognition tasks (Milner & Teuber, 1968). Even when there is such a tendency for one hemisphere to predominate in the processing of particular kinds of information, the other nonetheless can register similar stimuli.

Each hemisphere also can process letter information separately and concurrently. In Fig. 1c each half-brain has to remember as many letters exclusively flashed to it as possible. In normal man, as good a score is obtained when 8 letters (4 in each half-field) are flashed to both hemispheres

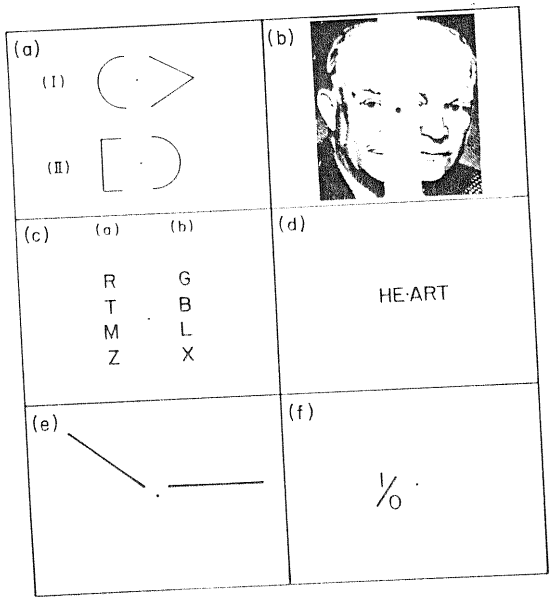

Fig. 1. (a) Figure closure: (I) patient says, "I saw a "triangle" in (II) a "circle." Yet in subsequent free choice test using left hand patient will pick a card with the figure C for (I) and I for (II). (b) Face recognition: right hemisphere dominance for this kind of task does not cause left hemisphere block. There may be specialization, but it is more one of degree. (c) ST memory: the patient remembers more information when both visual fields are presented with four letter stimuli than when either field is stimulated alone. Normal subjects do not improve, however, upon dual presentations. (d) Triple word test: splits immediately say upon presentation of the word "HEART," "ART" when fixation falls between "HE" and "ART." When the left hand is allowed to choose from a series of cards, it retrieves the card "HE" even though "ART" and "HEART" are among the choices. (e) Visual orientation: two lines are flashed simultaneously. The right-field stimulus is immediately reported accurately. If a nonverbal manual response is allowed, there is a strong tendency to make a hand movement in the form of the flashed lines. (f) Choice reaction time: each hemisphere is found to be equally fast at responding to "1" versus "0" pattern discriminations when using the contralateral hand (Gazzaniga & Hillyard, 1971); this is not a test of parallel processing, since two hemispheres acted successively rather than simultaneously.

as when only 4 are flashed to one. In split-brain subjects, the double-field presentation increases the half-brain score (Gazzaniga, 1968). Although the total score achieved by the patients fails to exceed that for normal subjects, the important point is that when one hemisphere has reached its limit of information storage; the other has an additional independent processing capacity.

As in the normal subject, spatial information in the split-brain patient is also registered appropriately. In Fig. 1e both half-brains can note the orientations of lines projected to them simultaneously and subsequently can gesture appropriately (Gazzaniga *et al.*, 1965).

Perhaps the clearest example of parallel processing in the separated hemispheres comes in our double-discrimination and reaction-time (RT) experiment (Gazzaniga & Sperry, 1966). In this study both pre- and postoperative scores were collected in two of the split-brain patients tested.

First, a single red–green discrimination task was presented in the right visual field. While the subjects fixated on a central dot, reaction times were recorded from the onset of each 100-msec stimulus to the subjects response. The correct response was to hit a translucent response button directly in front of the "correct" light, which was either red or green on a given run.

In the subsequent double-discrimination task each subject was required to respond to the brighter of two stimuli, which simultaneously appeared in the opposite, left visual field and along with the red–green discrimination. Now, with the right hand responding to the right visual-field red–green discrimination and the left hand responding to the left visual-field light–dark discrimination, the reaction time score was found to increase in normal subjects and in the patients tested before their operation (Table 1). Following callosal section, the double task of performing the red–green and the light–dark discriminations was performed at the same speed as the single task. Thus, sectioning cortical–cortical connections seems to eliminate the interhemispheric response interference exhibited by normal subjects when solving simultaneously presented two-choice tasks.

In animal studies there are several reports that give additional support to the notion of double-attentional mechanisms. These are summarized in Fig. 2. In Fig. 2a split-brain monkeys proved able to handle a great deal more visual information presented bilaterally in a brief flash than normal subjects. In the final phase of testing, each half-brain was presented exclusively with a spatial pattern of lights, which in fact were 4 two-choice light–dark discriminations presented to each hemisphere. First, 2 two-choice problems are presented; one to each hemisphere. When the animal succeeds, 2 more are added, now making 4 problems; 2 to each hemisphere. When proficiency is reached, 2 more are added, making 3 problems for each hemisphere, and so on. As a result, the task starts out being simple and becomes more complex only if the animal succeeds at each step along the way. Normal monkeys stop performing accurately when 6 lights appearing in any of 12 possible buttons are illuminated and left on for 800 msec. After the monkeys' brains are split, they can solve in a 200-msec flash which of 8 lights randomly occurring on 16 possible buttons are presented. Here, each half-brain sees only 4 lights and, when working in alternation, each

Table 1. *Reaction Times to Visual Stimuli (in msec)*[a]

Subject	Right hand (Trials 1–10)		Right hand-Left hand (Trials 11–20)				Right hand (Trials 21–30)		$p(M_2-M_1)$
	M_1	SD	M_2	SD	M_1	SD	M_1	SD	
Normal and preoperative									
GRN	438	57	695	97	694	96	391	56	< .005
TRB	465	120	770	140	800	120	496	83	< .005
HML	380	55	470	88	464	95	374	73	< .025
SRP	439	228	574	70	678	88	376	64	< .005
Case III (AA)	704	176	1272	213	1110	254	629	117	< .005
Case IV (LB)	727	158	1667	750	1227	580	682	149	< .005
Operated									
Case I (WJ)	1150	138	869	92	−98	104	848	110	n.s.
Case II (NG)	766	156	777	153	369	224	706	280	n.s.
Case III (AA)	705	175	724	170	−41	199	582	237	n.s.
Case IV (LB)	700	152	594	92	566	114	600	161	n.s.

[a]Right hand responds to red–green discrimination in right half visual field.
Left hand responds to bright–dark discrimination in left half visual field.
Probability calculated from paired observations by one-tailed *t* test. n.s. > .05

hand starts at the bottom of the panel and proceeds upward, hitting the correct buttons along the way (Gazzaniga & Young, 1967).

In Fig. 2b a naive half-brain, one which has not been trained on a visual discrimination observes the errorless performance of a knowledgeable half-brain. After 40 "observation" trials, the naive half-brain is tested separately, and it is discovered it too has learned the problem. Here with one half-brain clearly taking the lead and initially directing responses, the other

(a) (b)

Fig. 2. The split-brain monkey is activating a start switch which initiates a spatial discrimination. Here, four lights pseudo-randomly appearing on any of eight possible response panels are projected to one hemisphere while four others are simultaneously projected to the other. The lights are left on for only 200 msec following split-brain surgery, and each level of lights, starting at the bottom, must be responded to before advancement is allowed to the next row. (b) The trained hemisphere works while the naive half-brain watches.

half nonetheless is capable of attending to the relevent cues. Here again it would seem clear the responses of the "one" brain do not necessarily interfere with the attentional process of the other (Johnson & Gazzaniga, 1970).

Discussion

These studies indicate that independent, parallel processing channels exist in the two separated hemispheres. The human patients are capable of perceiving and interpreting verbal, pattern, and spatial stimuli correctly and simultaneously in each half-brain. The clearest evidence of dual information-processing channels comes from the multiple-choice light experiment in the monkey; each hemisphere can process 4 bits of information (4 two-choice problems) when disconnected from the other, while only an average of 3 bits per hemisphere are transmitted in the normal animal. In other words, the severing of the cortical–cortical connections actually increases the net channel capacity of the nervous system.

The simultaneous double-discrimination RT experiment also provides strong evidence of dual-attentional mechanisms, which are freed to operate in parallel following callosal section. This suggests that the corpus callosum normally mediates an integration of the selective processes of the two hemispheres, which has the effect of restricting the total number of stimulus–response transactions permissable in the normal condition. From this, it would seem fair to propose that cortical–cortical interactions in general precipitate interference in multiple sensory–motor tasks (see Treisman and Davies's contribution to this volume).

Since two separate stimulus–response sequences may be executed concurrently in the commisurotomized primate, for the kinds of tasks described we can reject the notion of a stimulus–response selection mechanism residing in the brain stem that can only "energize" one behavioral sequence at a time. Indeed, the double-discrimination RT experiment suggests that the corpus callosum integrates the sensory fields such that attention only can be linked to one portion of it at a time.

III. Interhemispheric Interaction and Lateralization Response Systems

In the previous section, the selective attentional processes functioned bilaterally to an extent that permitted simultaneous and comparable performance from the two hemispheres. In the types of tasks now considered,

the active response systems are strongly lateralized, and there is a concomitant disruption of learning and performance in the contralateral half-brain.

It has been reported, for example, that if a chiasm–callosum-sectioned monkey is restricted to the use of only one hand when learning a visual pattern discrimination, it is generally found upon subsequent testing that only the contralateral eye–brain has learned the problem, despite equivalent exposure to the visual stimulus–respond–reward contingency (Trevarthen, 1962). The mechanism by which such a strongly lateralized "response set" interferes with processing of the disconnected hemisphere is unresolved. In most cases it is difficult to ascertain whether the "supressed" hemisphere is subjected to an inhibition of its sensory–perceptual apparatus, a disruption of its selective, learned stimulus–response chains, or simply a decoupling of its processing from motor output.

Trevarthen (1970) has reported one of the few cases where perceptual suppression *per se* seems to have occurred in a split-brain patient. A "unilateral neglect" of one visual half-field occurred when a visually guided pointing task to a spatial target was lateralized to either the right or the left hand. For example, when the left hand (largely under control of the right cerebrum) aimed at a visual form, the portions of the target in the right visual field (projecting to the contralateral hemisphere) at times were blocked out of perception, according to the subject's verbal report. The implication is that the normal pathways from the geniculostriate system to the speech apparatus in the left hemisphere are somehow inhibited via brainstem connections, while the right hemisphere is actively directing the motor outflow. A similar process of interhemispheric suppression of visual perception as a function of lateralized response set (in this case, speech set in normal subjects) was proposed by Kinsbourne (1970) to explain the relative increase in detection thresholds in the left visual field during verbalization. Similarly, a blocking of somesthetic sensations from one-half of the body has been reported as a function of attentional and response sets in the split-brain patients (Gazzaniga, Bogen, & Sperry, 1963).

Not all types of lateralized response sets, however, result in a profound suppression of perceptual sensitivity in the ipsilateral sensory fields of the split-brain patient. During a strong right-hemisphere response set created by demanding a prompt thumb press from the left hand in a choice reaction-time (RT) task (see Fig. 1), visual pattern cues flashed to either hemisphere were discriminated and responded to with equal speed (Gazzaniga & Hillyard, 1971).[2] Moreover, a strong left-hemisphere verbal response set to name a small flashed numeral as fast as possible did not prevent the accurate

[2] This patient could control the left hand from either hemisphere with equal facility, etc.

discrimination and storage of an unpredictable series of numbers by the right hemisphere (Gazzaniga & Hillyard, 1971). While some degree of perceptual suppression may have existed in the right hemisphere in the latter study, it was not sufficient to prohibit discrimination of the 1° stimulus patterns flashed for 100 msec. The quality of the response set that determines the degree of contralateral perceptual suppression is not clear, but the available data suggests that the sensory-guided motor acts in which feedback or reafference must be monitored and utilized maximize suppression, whereas balistic, triggered movements tend not to interfere with contralateral perception.

The initiation of motor activity by one hand also can block the execution of well-learned responses controlled from the opposite hemisphere of split-brain primates. A demonstration of this is given in experiments by Trevarthen (1970), where the two hemisphere–hand combinations of a split-brain baboon had learned separate, complementary motor components of a manipulative latch-box problem; often when one hand spontaneously began to perform its own manipulations, there was total inhibition and neglect of the other, which assumed a reflex grasping posture. Less severe apraxia of the limb of the nonperforming hemisphere has been observed in other contexts as well, indicating that a lateralized response set can restrict the contralateral motor outflow via brainstem connections. The experiment described below in commissurotimized man illustrates that preparation to respond lateralized to the minor hemisphere at times may retard normal sensory–motor performance by the dominant left-hemisphere–right-hand ensemble.

Lateralization of Warning Stimulus and Response in a Foreperiod RT Task

This experiment was designed to create expectancy of an impending tone and motor response in only one of the surgically separated hemispheres of a human patient, in order to study the extent to which the contingent negative variation (CNV) or expectancy wave (Walter, Cooper, Aldridge, McCallum, & Winter, 1964; Besrest and Requin's contribution to this volume) might be lateralized to the "expectant" half-brain (Hillyard, 1971). Besides yielding evidence of the mechanism of this electrophysiological sign of expectancy and preparatory set, some unexpected behavioral interactions were observed between the two hemispheres when one of them was warned and alerted and the other governed the motor response.

In this task, a button was pressed with one hand to a loud tone burst, which followed a visual warning signal presented exclusively to one or the other hemisphere on a given trial. The warning was a 1° numerical pattern

flashed for 100 msec to either the right or left of a fixation point. When this flash was the number "1," it signified that, after a 1.3-sec foreperiod, a tone that demanded a prompt press would occur. On the other half of the trials, the warning flash was the number "0," followed by no tone and hence no response. Each subject was given 4 blocks of 25 RT trials each, the right hand responding on blocks 1 and 4 and the left hand on blocks 2 and 3. Within each block the warning signal was randomized from trial to trial among the 4 possibilities of "1" and "0" flashed to the right and left sides. Intertrial intervals were randomized between 10 and 30 sec.

In Table 2 the mean RTs of button presses following tone onset are compared for the different hand–hemisphere combinations in the three subjects. The RTs for the dominant right hand following the alerting of the minor (right) hemisphere were prolonged significantly in relation to those of the other combinations, which did not differ significantly from each other. Subject NW was not able to bring the left hand under sufficient voluntary control to perform the button press; this was an extreme case of the left-sided apraxia sometimes observed in adult commissurotomy patients (Gazzaniga, 1970). While neurological patients often have great variability in their RTs from one run to the next due to effects of practice, motivation, and the like, we believe the significant effect shown in Table 2 to be reliable since comparisons were made within a hand-use condition (right versus left

Table 2. *Reaction Times (in msec, ± standard error) for Button Press to Tone following Selective Warning of Right and Left Hemispheres, Respectively*

	Warning signal flashed to	
Response made by	Right hemisphere	Left hemisphere
Subject NG		
Right hand	1050 ± 82 ($p < .01$)[a]	390 ± 43
Left hand	430 ± 57	370 ± 48
Subject LB		
Right hand	345 ± 42 ($p < .025$)[a]	257 ± 12
Left hand	260 ± 12	255 ± 12
Subject NW		
Right hand	447 ± 30 ($p < .025$)[a]	360 ± 17

[a]The p values are two-tailed significance levels of the comparison of mean RT in right-hand-right-hemisphere condition against the other means, using analysis of variance.

visual field), and the sequence of hand-use conditions was balanced for order effects.

Our initial hypothesis for these delayed RTs—that the motor-response set induced in the left hemisphere during right-hand usage had suppressed the attentional and perceptual capacity of the right hemisphere to detect the warning cue—was inconsistent with other results. First, in subject NG the RTs for this condition (averaging 1050 msec) scarcely overlapped with the other RTs and were much longer than even the simple, unwarned RT, which ranged between 300 and 500 msec for NG.[3] Thus, there appeared to be an active inhibition of the normal control of the right hand by the left hemisphere, brought about by the selective warning of the right hemisphere. One possible mechanism for this might be that the alerted right hemisphere attempted to take control of the right hand via ipsilateral pathways, resulting in competitive interference between the response on the two sides in attempting to control the same hand. The absence of such interference for the left-hemisphere–left-hand combination is probably a consequence of the capacity of both hemispheres for controlling the left hand in simple acts, whereas the right hand is controlled predominantly from the left hemisphere (Gazzaniga & Hillyard, 1971).

A second reason to doubt the occurrences of perceptual suppression in the right hemisphere when the right hand was in use is the CNV evidence from all subjects, indicating that the warning flashes were being discriminated accurately. Figure 3, for example, shows CNVs recorded simultaneously over the right and left hemisphere, with scalp electrodes placed 5 cm lateral to the midline-referred-to linked electrodes behind the ears. Each tracing is the CNV computer averaged over 12 trials under the indicated stimulus and hand-usage conditions. The CNVs following the "1" are larger that those after the "0" since this wave constitutes an index of a preparatory process variously characterized as expectancy, preparatory set, or motor priming (Cohen, 1969). This difference in CNVs during right-hand usage (Fig. 3, left column, compare top and bottom tracings) indicates that the right hemisphere in fact did discriminate the "prepare to act" signal ("1") from the "no-go" cue ("0"). This suggests that the CNV can serve as a measure of perception of the light-tone contingency in a hemisphere that has its motor output suppressed, presumably on account of the response set lateralized in the other hemisphere. Use of the CNV as an indicator of perception and comprehension of "sign-significate" relationships may prove to be a useful

[3] Simple RTs in subject LB were also faster (range 260–405 msec; mean 312) than in the right-hand–left-hemisphere combination but the difference is not as striking. Simple RTs were not measured for subject NW.

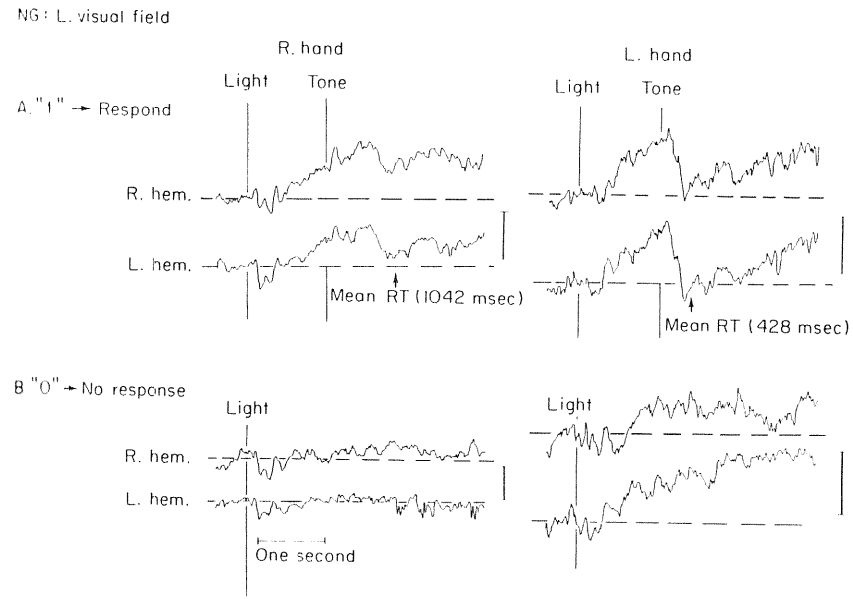

Fig. 3. Computer-averaged CNV, (N = 12) recorded simultaneously from the scalp over the right and left hemispheres under conditions of right- and left-hand usage with the right hemisphere warned. Nonpolarizing electrodes were placed 5 cm to the right and left of the vertex, along the interaural line. Records are shown only for those trials (one-half of total) when the warning flash was given to the left visual field. Trials containing eye-movement artifacts were excluded from these averages; DC amplification was used. Calibrations: 20μV.

clinical tool as a test of mental functioning in pathological states of motor paralysis.

The CNV was bilaterally symmetrical in two of the patients (NG, LB) under all visual-field–hand combinations (Figs. 3 and 4; Table 3). The small right–left discrepancies in CNV amplitude can be attributed to spontaneous EEG variations, measurement error, and scalp-placement asymmetries. More importantly, the right–left differences in these patients did not correlate with either hand usage or which hemisphere was warned. In subject NW, however, a larger asymmetry was found in both CNV amplitude and waveform, with larger CNVs localized above the warned hemisphere during the S_1–S_2 interval. In addition, it appears (Fig. 5) that the CNV is incremented *after* the tone onset above the hemisphere that controls the response.

Caution must be exercised when inferring a bilaterality of brain processes from these findings of CNV symmetry in two patients and a small departure from this in a third (average asymmetry in NW was 6 out of 27μV). First, the possibility must be considered that electric fields generated in one

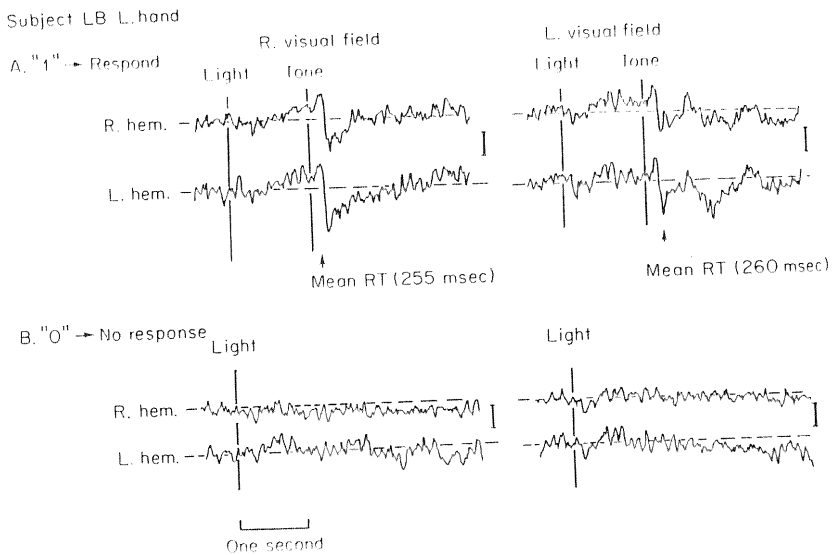

Fig. 4. Computer-averaged CNVs ($N = 12$) from subject LB in the same experiment as in Fig. 4, but here only records taken with the left hand in use are presented. The four pairs of CNVs (from right and left scalp) were from trials when the warning cue was a "1" and a "0," presented to right and left visual fields, respectively. Calibration: 20 μV.

hemisphere may spread to the other side by volume conduction. Available evidence, however, indicates that field spread would not contribute more than a small fraction of the observed contralateral negativity. The CNVs are greatly attenuated over even small, localized cortical lesions (McCallum, Walter, Winter, Scotton, & Cummings, 1970), and those EEG and evoked-potential fields that are slow and diffuse like the CNV spread to the lateral portions of contralateral scalp by less than 20% after hemispherectomy (Hazemann, Olivier, & Fischgold, 1969) and unilateral amytal injections (Barlow, Rovit, & Gloor, 1964). Second, it is possible that on some trials the "unwarned" hemisphere received stimulus information by extracranial crosscueing (Gazzaniga, 1970), since control tests showing that the cue was lateralized were done only on a few trials within an experiment. Third, a bilaterally symmetrical component conceivably might have arisen from an artifactual source such as the skin or tongue [but not from eye movements that were controlled (Hillyard, 1973)].

Despite these reservations, our results do suggest that a substantial portion (somewhere between 50 and 100%) of the CNV in the foreperiod RT task is bilaterally symmetrical and therefore is governed from bilaterally activated structures in the brainstem or thalamus. Whether there is an

Table 3. *Bilateral Symmetry of CNVs from Right and Left Hemispheres, Quantified as the Mean Amplitude (in μV) over the .30 Sec Prior to Tone Onset*

	Warning signal ("1") flashed to	
Response made by	Right hemisphere	Left hemisphere
Subject NG		
Right hand		
Right Hemisphere	13.4	15.7
Left Hemisphere	10.7	15.1
Left hand		
Right Hemisphere	19.2	17.0
Left Hemisphere	18.5	16.3
Subject LB		
Right hand		
Right Hemisphere	7.1	3.5
Left Hemisphere	4.2	6.1
Left hand		
Right Hemisphere	7.2	11.2
Left Hemisphere	4.3	8.7
Subject NW		
Right hand		
Right Hemisphere	30.4	28.2
Left Hemisphere	20.2	30.5

asymmetrical CNV component in addition, as NW's data suggest, is more speculative. It has not been established whether the CNV in this RT task can be decomposed into two or more distinctive portions, each with a different behavioral correlate and physiological generator, or whether the CNV is a unitary phenomenon. While anatomically different types of CNV have been distinguished in purely sensory versus purely motor tasks (Järvilehto & Fruhstorfer, 1970; Hillyard, 1973), there is no evidence that the CNV during foreperiod RT tasks is a composite of these components. In fact, if the asymmetrical, purely motor "readiness potential" (Kornhuber & Deecke, 1965) were such a component, the foreperiod RT CNVs should also be asymmetrical in normal subjects, which has yet to be demonstrated (Cohen, 1969; Otto, 1972). Therefore, while it is attractive to propose a lateralized, task-specific CNV additive with a bilateral "generalized" CNV [as McAdam and Whitaker's (1971) experiments suggest], the present evidence is inconclusive.

Serious questions may be raised concerning the psychological correlates

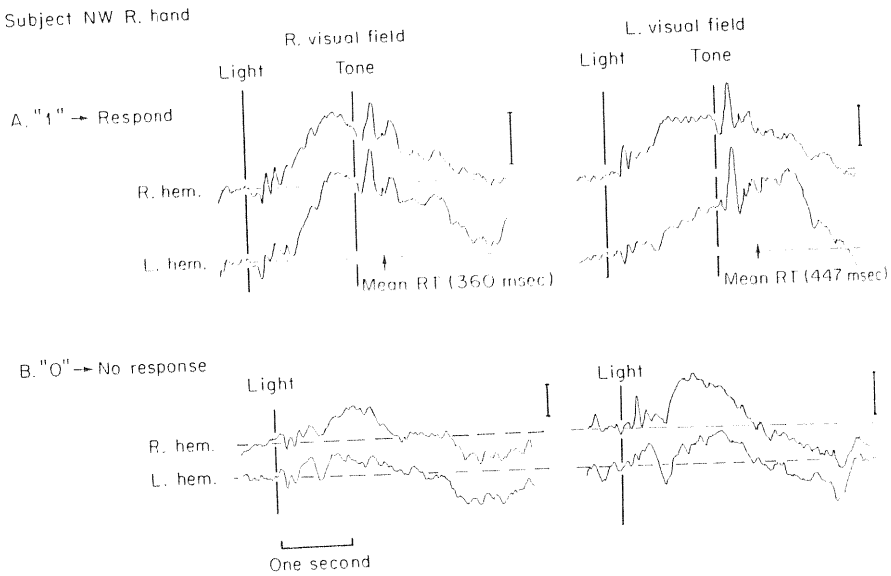

Fig. 5. Computer-averaged CNV ($N = 12$–15) from subject NW, who was able to respond only with the right hand (same notation as in Figs. 4 and 5). Calibration: 20 μV.

of "the CNV." Our evidence, though clearly preliminary, weighs against the entire CNV being a direct physiological index of the patterned neuronal activity underlying expectancy or motor preparation, since these processes were activated only in the warned hemisphere. While the bilateral portion of the CNV may yet prove to be generated in conjunction with specific psychological states such as attention, motivation, or response set, and may in fact be necessary for high levels of performance, its functional seems to be relatively nonspecific, since it is present in the nonperforming hemisphere.

IV. General Discussion

It emerges from these experiments that there is frequently more "channel capacity" in a split-brain primate than in a callosum-intact normal primate. Exceptions to this principle were found only in certain tasks eliciting a response set that was strongly lateralized to one hemisphere. In such cases a disruption of contralateral processing was observed. At present, however, the evidence is insufficient to decide whether the lateralized response set interferes with the contralateral performance sequence at the perceptual, retrieval from memory, or motor output stages. Only Trevarthen's (1970) report suggests that perceptual interference may occur. In all other demonstrations of interhemispheric interactions, interference between the response outputs of the two sides can explain the results.

Assuming that such interference occurs at the output end, it may be proposed that the responsible brainstem mechanisms function normally to coordinate response outputs from the two sides when they operate in compatible or cooperative tasks. It seems, however, that at times the output of one hemisphere can preempt this brainstem coordinator and deny output to the other. A fundamental question then is to specify the property of a given task that determines whether subcortically mediated interhemispheric interference will occur. We can speculate that such interaction occurs when one hemisphere is generating those sorts of responses that require preparation. Perhaps putting a response in readiness and holding it requires extensive physiological management, which produces a general inhibition of competing response systems.

In addition to the above, the role of the forebrain commissures in integrating the attentional processes of the two cerebral hemispheres is revealed by the increases of total processing capacity upon the removal of the corpus callosum. It is as if in the normally interconnected brain the callosum is involved in inhibiting the transmission of information undergoing processing extraneous to the dominant cognitive activity under consideration. The brain cannot consider all things at all times, and perhaps order only is brought about by what amounts to a cognitive counterpart of a reciprocal inhibition kind of mechanism.

In summary, the foregoing studies are consistent with the proposal that commissural mechanisms act more to integrate the sensory sphere of activity, while the brainstem is involved in coordination and selection of response outputs.

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The Control of Attention by Interaction between the Cerebral Hemispheres

Marcel Kinsbourne

Division of Pediatric Neurology
Duke University Medical Center
Durham, North Carolina

ABSTRACT

Each cerebral hemisphere guides attention towards contralateral space, and the two hemispheres are in mutually inhibitory balance. In right-handed subjects, the left hemisphere chiefly subserves linguistic processes, and the right hemisphere subserves spatial processes. It is proposed that cognitive activity lateralized to one hemisphere overflows so as to cause contralateral orientational shifts. This model, which can account for laterality effects in perception, is experimentally validated by showing that:

1. Gaze and head turning occur contralateral to the preponderantly active hemisphere when subjects engage in verbal or spatial thought.
2. Concurrent subvocalization (that is, left-hemisphere activity) introduces right-sided advantage into right-handed subjects' ability to detect a gap in a briefly exposed square.
3. Concurrent subvocalization induces right half-field superiority for recognition of briefly presented nonsense shapes by right-handed subjects.

In left-handed subjects, both verbal and spatial processes appear to be programmed from one hemisphere at a given time.

I. Introduction

Throughout the evolutionary ascent from worm to man, behavior is controlled by a basically mirror symmetrical central nervous system. Each of its two laterally adjacent but separate divisions can control the full range